Identifying the Past, Present, and Future Distribution Patterns of the Balkan Wall Lizard (Sauria: Lacertidae: *Podarcis tauricus*) by Ecological Niche Modelling

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Abstract: Pleistocene glacial and interglacial periods have been greatly affected the distribution pattern of the species. The impact of the global climate change upon species distributions such as range shifts in latitude or elevation has been widely studied. In this study, it was aimed to have a better understanding on the effects of the Late-Pleistocene climatic oscillation and the global climate changes on a widely distributed reptile species, the Balkan wall lizard (*Podarcis tauricus*). To find out the dynamics of the species' range shifts, ecological niche modelling approach was applied. Bioclimatic variables and regenerated species occurrence records were used to construct models. The chosen model was projected to the present, reconstructed past and predicted future bio-climatic conditions. Moreover, distribution change and landscape connectivity analyzes were executed. Under present conditions, model prediction for the Balkan wall lizard was largely caught its known distribution area. The LGM distribution prediction was limited to a few spots (57,596.19 km²) in the southern Balkans, mainly due to the negative effect of the mean winter temperature. From the LGM to the present, distribution area of the species remarkably extended, particularly noticeable during Mid-Holocene (1,254.59%). The model predicted the distribution area of the species would extend due to high mean summer and high mean winter temperatures in the future and move basically towards northern latitudes and at higher elevations. A connectivity pattern in between the southwestern and northeastern populations of the Balkan wall lizard was found with high connectivity predicted predominantly over the southern Balkans.

Keywords: Late-Quaternary climatic oscillations, glacial refugia, global climate change, maxent, wallace.

Ekolojik Niş Modellemesi ile Balkan Duvar Kertenkelesinin (Sauria: Lacertidae: *Podarcis tauricus*) Geçmiş, Günümüz ve Gelecek Yayılış Örüntüsünün Tanımlanması

Öz Pleyistosen buzul ve buzullar arası dönemler, türlerin dağılım desenini büyük ölçüde etkilemiştir. Bu çalışmada, geç Pleyistosen iklim dalgalanmalarının ve küresel iklim değişikliklerinin, yaygın olarak yayılış gösteren bir sürüngen türü olan Balkan duvar kertenkelesi (*Podarcis tauricus*) üzerindeki etkilerinin daha iyi anlaşılması amaçlanmıştır. Türün dağılım değişimine yönelik dinamikleri bulmak için ekolojik niş modellemesi yaklaşımı uygulanmıştır. Biyoiklimsel değişkenler ve yeniden oluşturulmuş tür gözlem kayıtları kullanılarak, ekolojik niş modelleri hazırlanmıştır. Seçilen model, yeniden oluşturulmuş geçmiş ve tahminlenen gelecek bio-iklimsel koşullara projekte edilmiştir. Ayrıca, dağılım değişikliği ve peyzaj bağlantısallığı analizleri gerçekleştirilmiştir. Mevcut koşullar altında, Balkan duvar kertenkelesi için model tahmini, büyük ölçüde bilinen dağılım alanını yakalamıştır. SBM dağılım tahmini, esas olarak ortalama kış sıcaklığının olumsuz etkisinden dolayı güney Balkanlar'da birkaç noktayla (57,596.19 km²) sınırlanmıştır. SBM'den günümüze, türün dağılış alanı, özellikle Orta Holosen'de belirgin şekilde (1,254.59%) genişlemiştir. Model, türün gelecekte yüksek ortalama yaz ve yüksek ortalama kış sıcaklıkları nedeniyle yayılış alanını genişleteceğini ve temel olarak kuzey enlemlere ve daha yüksek rakımlara doğru hareket edeceğini öngörmüştür. Balkan duvar kertenkelesinin güneybatı ve kuzeydoğu populasyonları arasında bir bağlantısallık bulunmuş olup, ağırlıklı olarak güney Balkanlar'da yüksek bağlantısallık tahminlenmiştir.

Anahtar kelimeler: Geç Kuvaterner iklim dalgalanmaları, buzul sığınağı, küresel iklim değişikliği, maxent, wallace.

1. Introduction

The wall lizards of the genus *Podarcis* (Wagler, 1830) is a member of the family Lacertidae (Reptilia: Squamata: Sauria). They are abundant and diverse taxon with 26 currently recognized species mainly due to several vicariance events (Yang et al., 2021). The origin of the taxon is from Western Europe (Oliverio et al., 2000; Psonis et al., 2018) but also distributed in North Africa and introduced into North America due to animal trade (Kolbe et al., 2013).

Among the wall lizards, the Balkan wall lizard (*Podarcis tauricus*, Pallas, 1814) is one of a few species of the wall lizard genus having large distribution range from the Crimean Peninsula, and southwestern Ukraine to the

southeastern part of Czech Republic (Fischer et al., 2019; Rehák et al., 2022) in the north and Greece (Gasc et al., 1997; Sindaco & Jeremčenko, 2008; Uetz & Hallermann, 2022) and northwestern part of Türkiye (Başoğlu & Baran, 1977; Baran et al., 1992; Tok & Çiçek, 2014; Bülbül et al., 2015; Gül & Tosunoğlu, 2017) in the south. The Balkan wall lizard is a diurnal, heliothermic, medium-size, actively foraging ground-dwelling lizard having a total body length up to 22 cm (Başoğlu & Baran, 1977; Ljubisavljević et al., 2010). The coloration varies geographically and seasonally and matches its surrounding environment. The Balkan wall lizards as a dominant group of Mediterranean lacertids (Böhme & Corti, 1993) are known to be ecologically generalists, occupying wide variety of

habitats (Arnold, 1987) and a common species in suitable habitats such as stony scrublands, meadows, field and forest edges, open parts of steppes and grasslands, sandy dunes with sparsely halophyte vegetation, cultivated lands, sides of highways, and rural gardens (Covaciu-Marcov et al., 2006; Kati et al., 2007). It was found that the presence of the Balkan wall lizards is being affected positively by tussock height which distributes generally in open, sandy patches with low vegetation cover (Mizsei et al., 2020). The altitudinal distribution of the species ranges from 0 to 2350 m (Böhme et al., 2009). According to the IUCN Red List categories, conservation status of the Balkan Wall Lizard is evaluated as Least Concern (LC, IUCN 3.2, accessed in June, 2022) and listed in Appendix II of the Bern Convention (1979) and in Annex IV of the European Union Habitats Directive (1992) as a strictly protected species due to local threats in parts of its range such as habitat loss and pollution.

The spatiotemporal responses of the species (e.g. range contractions and expansion) during Quaternary climatic oscillations have been studied for some decades (Hewitt, 1996; Taberlet et al., 1998; Stewart et al., 2010; Gür et al., 2013). Pleistocene glacial periods were characterized by cold and dry climate. Most of the temperate species could not survive in their current range but usually at lower latitudes glacial refugia. During the interglacial periods, species expanded their ranges mostly towards higher latitudes from their refugia (Hewitt, 1996, 1999,

2000, 2004). The Balkan Peninsula, as one of the lower latitude glacier refugia, has played a key role for postglacial re-colonization of central and northern Europe (Taberlet et al., 1998; Hewitt, 1999, 2000; Feliner, 2011). Several studies have highlighted the impact of global climate change upon species distributions and climate-driven range shifts in latitude or elevation (Parmesan et al., 1999; Thomas, 2010; Chen et al., 2011; Vicenzi et al., 2017; Bezeng et al., 2018). As it is mentioned in Le Galliard et al. (2012), substantial range shifts with northward or upward movements have been predicted for most of the reptiles in Europe in the future according to niche modelling studies.

Ecological niche models (ENMs) have been widely used to understand further response of species to global climate changes through the past and future time periods (Guisan & Zimmermann, 2000; Peterson et al., 2002; Hijmans & Graham, 2006; Waltari et al., 2007; Nogués-Bravo, 2009). ENM makes a relation between georeferenced occurrence data where species has been observed and environmental data to construct models of species' potential geographical distribution (Guisan & Thuiller, 2005). Under the assumptions of species-climate equilibrium and stability of ecological niches through time, ENMs are able to be extrapolated to other scenarios, either in time (past or future projections; Peterson et al., 2002; Nogués-Bravo, 2009) or in space (projections to other study areas: Peterson et al., 2007).

Figure 1. Species occurrence data and its distribution in the range of the Balkan Wall Lizard.

Dispersal capacity of reptile species is basically limited as they are highly dependent on their environment (Huey, 1982; Joger et al., 2007) which makes it possible to expect relationship between distribution areas and climate of their habitats. Distribution pattern of the evolution history of reptile species has been studied either only with ecological niche modelling approach (Kaliontzopoulou et al., 2008; Sillero & Carretero, 2013; Gül et al., 2015; Yousefkhani et al., 2016; Ćorović et al., 2018; Mothes et al., 2019; Kurnaz & Yousefkhani, 2019; Kurnaz & Yousefkhani, 2021) or together with molecular phylogeography (Melville et al., 2016; Psonis et al., 2018; Promnun et al.,

2021). In a detailed phylogeographical study on *Podarcis* taxon (Psonis et al., 2018), existence of extensive genetic structure within *P. tauricus* and the distribution of two main clades corresponding with the eastern and western sides of the Pindus Mountains (See Fig. 1) was confirmed (see also Çördük et al., 2018). The potential distribution of *P. tauricus* for the recent and past time periods (the LIG and the LGM) has been shown as a supportive analysis to the molecular studies. On the basis of this study, the Taxonomic Committee of the European Herpetological Society accepted the split of the species into two species: eastern species retained the name *P. tauricus*, including

nominate subspecies *P. tauricus tauricus* and *P. t. thasopulae (Kattinger, 1942),* and western species took the name *P. ionicus* (*Lehrs*, 1902). Therefore, *P. tauricus tauricus* and *P. tauricus thasopulae* have been included in this study.

In the face of the global climate change, suitable habitats reduce and as an outcome, the distance between convenient habitat patches and the cost of dispersal increase (Le Galliard et al., 2012). Therefore, landscape connectivity is an enabling tool to measure connections among populations and to draw connecting corridors among populations of the species (Hodgson et al., 2009; Brown, 2014). Landscape connectivity tool together with species distribution models (SDMs) and/or population genetics data has been applied formerly in a spatially explicit framework (e.g. Chen et al. 2011; Yu et al., 2015; Zhang et al., 2019). To estimate the least costly routes in which a population can move through (cost accepted as the inverse of habitat suitability), the least-cost corridors (LCCs) and least-cost paths (LCPs) methods are used (Rudnick et al., 2012).

The main goal of this study is to assess the distribution pattern of the Balkan wall lizard as a temperate and widely distributed reptile species in present, under the past and the future global climate models and scenarios. To predict the potential geographical distribution of the species, ecological niche modelling, with the presence records (recorded by the author and reconstructed from published articles) and bioclimatic data (from the WorldClim v. 1.4 database for the present, the past, and the future, Hijmans et al., 2005) was used. Distribution change of the Balkan wall lizard among different time periods and potential glacial refugium were assessed to understand the response of the species to the global climate changes throughout the Quaternary glacial–interglacial cycles and to the predicted future climate changes. Furthermore, the bioclimatic variables were evaluated in terms of contribution to the model prediction and effects of climate on shaping the distribution pattern of the species. The LCCs and the LCPs analyses were executed and bioclimatic connectivity in the distribution area of the species populations was analyzed.

2. Material and Methods

2.1. Occurrence data

The species occurrence records were obtained from the former published articles and the previous field research of the authors. In most of the articles, the geographical coordinates of the occurrence data are not given, instead the locations of the species specimens are explained. Therefore, the information in the papers was transformed into decimal coordinate data on Google Earth pro v.7.3.2 (http://www.google.com/earth) where possible. Totally, 370 occurrence records were gathered from Crimea, Czech Republic, Hungary, Ukraine, Moldova, Romania, Serbia, Kosovo, North Macedonia, Albania, Bulgaria, Greece, and Türkiye (Fig. 1) between the years 1977 and 2019 (mostly after 1990) and 10% of the occurrence records have coordinates. The species occurrence records that were used to construct the articles were as follows: Altunışık et al., 2016; Başoğlu & Baran, 1977; Bülbül et al., 2015; Cogălniceanu et al., 2013; Çördük et al., 2018; Eroğlu et al., 2017; Fischer et al., 2019; Iftime & Iftime, 2016; Koç et al., 2018; Kukushkin & Doronin, 2013; Mollov & Valkanova,

2009; Petrov et al., 2006; Poulakakis et al., 2005a, 2005b; Psonis et al., 2017; Sokolov, 2019; Stănescu et al., 2013; Tomovic et al., 2018; Tok & Çiçek, 2014; Urošević et al., 2015. The location information of the collection of COMU Zoology Research Laboratory ZDEU-COMU and new specimens collected for the current study under COMU-Ethical Committee permission (No: 2018/04-01) were used for modelling. They are ZDEU-49/2009-1/1♂ Demirköy/Kırklareli, Leg. C. V. Tok, B. Y. Yakın; ZDEU-58/2010/1♂ Dupnisa/Kırklareli, Leg. C. V. Tok, B. Y. Yakın; ZDEU-17/2011-1/1♂ Saray/Tekirdağ, Leg. C. V. Tok, B. Y. Yakın; ZDEU-127/2009/1♀ Dereköy/Kırklareli, Leg. C. V. Tok, B. Y. Yakın; ZDEU-28/2018/1♂ Karasu/Sakarya, Leg. C. V. Tok, Ç. Göcek; ZDEU-27/2019/1♀ Çardak/Çanakkale, Leg. C. V. Tok, Ç. Göcek.

The Maxent algorithm assumes that all occurrence records on the study area are equally likely to be sampled (Merow et al., 2013). To reduce the clustering of occurrence points, caused by the survey bias, they were filtered (Boria et al., 2014; Kadmon et al., 2004) by 10 km, 15 km, and 20 km distance thresholds via using 'spatial thinning' application on the Wallace platform v. 1.0.6 (Kass et al., 2018) and; as a result, 20 Km spatial thinning with 153 occurrence points was used to construct the model due to 10 Km (243 occurrence points) and 15 Km (193 occurrence points) spatial thinning were not able to remove clustering (Fig. 2).
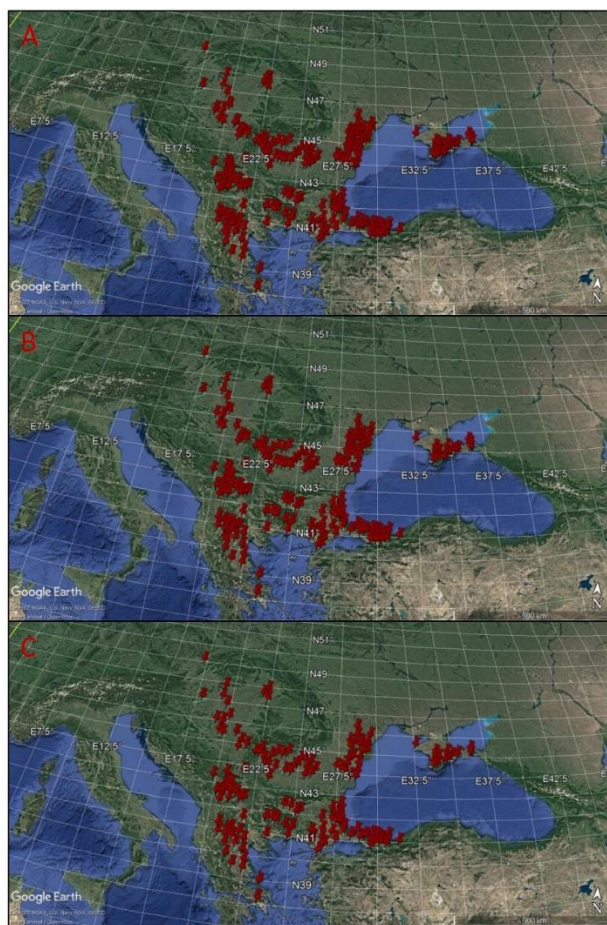

Figure 2. A, B, and C maps are 10 Km, 15 Km, and 20 Km spatially rarified species occurrence points, respectively.

The background extent of the study region has been defined as a rectangular bounding box around the boundary of the occurrence points with 2^0 (~200 km) buffer

zone (i.e. the study area, 15.25° to 38.33° E and 36.08° to 50.92° N; Supplemental Fig. 1) considering species dispersal limits (Soberón & Peterson, 2005).

2.2. Bioclimatic data

The bioclimatic data were downloaded from the WorldClim database version 1.4 database (Hijmans et al., 2005) at a spatial resolution of 5 arc-minutes to be in accordance with the certainty of the occurrence data (~ 8.3 km at the equator; Araújo et al., 2019; Feng et al., 2019; Sofaer et al., 2019). The bioclimatic data includes the present (between years 1960–1990); two past time periods: the Last Glacial Maximum (LGM, ~22 kya) and Mid-Holocene (~7 kya); and two future time periods (2050, the average of 2041-2060 and 2070, the average of 2061-2080).

Under Coupled Model Intercomparison Project Phase 5 (CMIP5), three global climate models (CCSM4 - The Community Climate System Model Version 4, Gent et al., 2011; MPI-ESM - Max Planck Institute Earth System Model, Giorgetta et al., 2013; and MIROC-ESM - Model for Interdisciplinary Research on Climate, Watanabe et al., 2011) for the past and the future time periods were used for modelling. These global climate models were taken from four Representative Concentration Pathways (RCPs) scenarios (from the low to the medium to the high forcing levels: RCP2.6 (low), RCP4.5 (medium), RCP6.0 (medium), and RCP8.5 (high). Via using different models and scenarios, the uncertainty in the ecological niche modelling due to a broad range of the global climate change in the past and the future time periods were taken into account (Varela et al., 2015). The data include 19 bioclimatic variables derived from monthly temperature and precipitation values (for detailed descriptions, see http://www.worldclim.org and Supplemental Table 1). The bioclimatic variables, having known spatial artefacts (i.e. artificial discontinuities in climate gradients; Mean Temperature of Wettest Quarter (BIO8), Mean Temperature of Driest Quarter (BIO9), Precipitation of Warmest Quarter (BIO18), Precipitation of Coldest Quarter (BIO19), variables with extreme values and variables that are not in accordance with the study aims, Max Temperature of Warmest Month (BIO5), Min Temperature of Coldest Month (BIO6), Temperature Annual Range (BIO7), Precipitation of Wettest Month (BIO13), and Precipitation of Driest Month (BIO14) were excluded. The exclusion of these bioclimatic variables reduced uncertainty of the predictions (Varela et al., 2015) and; as a result, 10 bioclimatic variables, Annual Mean Temperature (BIO1), Mean Diurnal Range (BIO2), Isothermality (BIO3), Temperature Seasonality (BIO4), Mean Temperature of Warmest Quarter (BIO10), Mean Temperature of Coldest Quarter (BIO11), Annual Precipitation (BIO12), Precipitation Seasonality (BIO15), Precipitation of Wettest Quarter (BIO16), and Precipitation of Driest Quarter (BIO17) were used for constructing the model. The correlation between the bioclimatic variables were checked using 0.8 threshold value in SDM ToolBox v. 2.4 (Brown et al., 2017). Four different bioclimatic data sets emerged, with the largest number of variables in each and without including the climatic variables having a correlation of 0.8 ≥ among each other in the same data set (Supplemental Table 2, Supplemental Table 3).

Table 1. Model evaluation statistics of candidate models for each group ordered based on decreasing Average AUCTEST value.

Candidate models: Used variables	FC	RM	Average AUC$_{TEST}$	Variance AUC$_{TEST}$	Average AUC$_{DIFF}$	Variance AUC$_{DIFF}$	Average Test OR$_{MIN}$	Variance Test OR$_{MIN}$	Average Test OR$_{10}$	Variance Test OR$_{10}$	AICc	Delta AICc	PM
M:1 BIO 1,2,4,12,15	L	5.0	0.788	0.016	0.061	0.006	0.033	0.001	0.221	0.04	3,025.769	57.172	5
M:2 BIO 1,2,4,15,16	L	5.0	0.788	0.017	0.058	0.007	0.033	0.002	0.221	0.04	3,027.198	67.859	5
M:3 BIO 2,10,11,12,15,17	LQ	5.0	0.8	0.013	0.059	0.005	0.038	0.006	0.247	0.031	2,984.674	26.649	9
M:4 BIO 2,10,11,15,16,17	LQ	5.0	0.794	0.015	0.06	0.05	0.038	0.06	0.215	0.022	2,991.321	30.373	9

For detailed descriptions of variables, see Supplemental Table 1. FC, feature classes (L = Linear, Q = Quadratic, H = Hinge, P = Product). RM, regularization multiplier. AUCTEST, value of the area under the curve of the receiver operating characteristic (ROC) plot calculated based on testing bins. AUCDIFF, the difference between training and testing AUC. ORMIN, minimum training presence omission rate. OR10, 10% training omission rate. AICc, the Akaike information criterion corrected for small sample sizes. Delta AICc, the difference between the lowest AICc and each AICc. PM, number of parameters in candidate model. Bold values refer to the chosen model details.

2.3. Ecological niche modelling

Maximum entropy modeling algorithm Maxent v. 3.4.1 (Phillips et al., 2017) was used for modelling the ecological niche and concluding bioclimatic suitability throughout the study area under the present, past, and future climatic conditions for the Balkan wall lizard since it is one of the most effective ecological niche modelling algorithms (Phillips et al., 2004; 2006; Elith et al., 2006) requiring presence-only data for creating a model (Peterson et al., 2011). WALLACE v. 1.0.6 software which is an open-source platform, having R-scripted user-friendly workflow (Kass et al., 2018; Available from Url: https://wallaceecomod.github.io/; for methodological descriptions, see Muscarella et al., 2014, and for a Turkish tutorial, see Gür, 2019) was used for selecting optimal set of variables and model settings (Elith et al., 2011; Merow et al., 2013). The model settings were as follows on WALLACE interface: 20 km thinned occurrence dataset was used to eliminate clustering. Final model were projected onto the present, past, and future climatic conditions for 3⁰ (~300 km) buffer zone encompassing occurrence records (i.e. 14.25° to 39.33°E and 35.08° to 51.92°N).

All pixels within the buffer zone were sampled as the background data (n=36,619 pixels) and; thus, full representation of environments available for the Balkan wall lizard was provided (Guevara et al., 2018). To adjust the model complexity, following combinations were used: 1) Four sets of non-collinear variables (Supplemental Table 3), 2) 5 combinations of feature classes (**L**inear -L, **L**inear-

Quadratic -LQ, **H**inge -H, **L**inear-**Q**uadratic-**H**inge -LQH, **L**inear-**Q**uadratic-**H**inge-**P**roduct -LQHP), and 3), and 5 different regularization multiplier values (1 to 5 in increments of 1). As a result, 100 candidate models were tested to select the most favorable set of variables. To evaluate model significance and the performance, the partial ROC analysis was executed (Peterson et al., 2008) in NicheToolBox v.0.6.0.1 software (Osorio-Olvera et al., 2020) with the following settings: Proportion of omission = 0.001, Random points % = 50, Number of iterations for the bootstrap = 1000.

To calculate model evaluation statistics, the spatial k-fold cross-validation method was used (Supplementary Fig. 1). This method is suitable for transferring to other geographical extents and time periods (for methodology see Muscarella et al., 2014; Kass et al., 2018). In this method, the full dataset (presence and background data) was partitioned into 4 (k=4) spatially distinct, non-overlapping bins with equal numbers of observation points by the latitude and longitude lines. Then, for each candidate model, five models were tested. Four out of five models were built iteratively via using 3 bins for training the model and one bin is left out for model testing and; then, threshold-independent evaluation statistics (the area under ROC -A receiver operating characteristic- curve AUC_{TEST}, AUC_{DIFF}) and threshold-dependent evaluation statistics (10% training omission rate, OR_{10} and 'Minimum Training Presence' omission rate, OR_{MIN}) as averaged over the iteration were calculated. One out of five models was built using non-partitioned, full dataset to calculate the Akaike information criterion corrected for small sample sizes (AICc). The highest average AUC_{TEST} value was chosen as the best performing model for discrimination ability (Table 1; Phillips et al., 2004) and; thus, the most favorable set of variables and model settings were used (Elith et al., 2011; Merow et al., 2013).

After choosing the final ecological niche model, the final model with partitioned dataset (153 presence records and 36,619 background points) was projected onto the present, past, and future climatic conditions with both extrapolation and fade by clamping options to regulate the probable model reaction to the environmental values that were more extreme than those of the training dataset (Elith et al., 2010). The multivariate environmental similarity surface analysis (MESS) (Elith et al., 2010) were executed on Maxent both for analyzing prediction capability of the model in novel bioclimatic conditions and finding out possible similar and/or non-similar conditions between training and projection datasets. The limiting bioclimatic variables driving the MESS value in each grid cell for the future and the past time projections were also provided in the analysis (Elith et al., 2010). The response curves of the model (bioclimatic suitability vs. response variable) were analyzed to discover how the bioclimatic conditions affect the model predictions (Anderson, 2013). The relative contributions of the variables to the final model were checked via Jackknife test and percent contribution of each variable were assessed. For bioclimatic suitability maps, the cloglog output format, having values indicating suitability from 0 to 1 was used (Phillips et al., 2017). To identify the main drivers for the bioclimatic suitability, Maxent Explain tool (Elith et al., 2010) was checked at any pixel chosen from the study area.

Each bioclimatic suitability map was divided into five classes to interpret easily: very low suitability (< 0.2), low suitability (0.2-0.4), moderate suitability (0.4-0.6), high suitability (0.6-0.8), and very high suitability (> 0.8). Areas of moderate, high, and very high suitability were also defined as suitable bioclimatic areas based on the '10 percentile training presence' threshold (=0.415). To simplify the explanation of the past and future bioclimatic suitability maps, for each time period (for the past, LGM and Mid-Holocene; for the future, 2050, average of 2041-2060 and 2070, average of 2061-2080), and for each scenario, only one consensus bioclimatic suitability map was presented as an average of three global climate models (1 average of: LGM, Mid-Holocene, 2050/RCP2.6, 2050/RCP4.5, 2050/RCP7.0, and 2050/RCP8.5, 2070/RCP2.6, 2070/RCP4.5, 2070/RCP6.0, and 2070/RCP8.5) via using 'raster calculator' in SDM Toolbox 2.4. Since there is no MPI-ESM-LR model for RCP6.0 2050 and RCP6.0 2070, averages of only two global climate models were taken for this scenario. To execute distributional change analyses initially, consensus bioclimatic suitability maps were transformed into presence/absence binary maps using the threshold value (0.415). The outcomes were represented as follows: range expansion, no occupancy (absence in both), no change (presence in both), and range contraction under reconstructed past and projected future. For the workflow of ecological niche modelling, Gür (2022) was followed as a methodological curriculum.

2.4. Dispersal corridors and paths

Landscape connectivity analysis for the present potential distribution area was executed to find out population connectivity. The least Cost Corridors and Least Cost Paths (LCCs and LCPs) maps were generated with 70 Km spatially thinned occurrence dataset and; as a result, 50 occurrence points were used to deduce connectivity in a spatially explicit framework among the Balkan wall lizard populations (Chen et al., 2011; Brown, 2014; Yu et al., 2015). For calculations, prediction under the present bioclimatic conditions were inverted to use as friction layers (i.e. areas of high suitability were converted to areas of low dispersal cost) and used together with spatially rarified occurrence records. All the analyses, unless stated otherwise, were executed in SDM ToolBox v. 2.4. All GIS operations were conducted using ArcGIS v.10.5 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources).

3. Results

Out of 100 tested candidate models based on four different non-correlated bioclimatic variable datasets and different model settings, the final model was provided by the 3rd bioclimatic data set with six input bioclimatic variables (BIO2, BIO10, BIO11, BIO12, BIO15, BIO17); the feature classes of linear and quadratic (LQ); and a regularization multiplier of 5. The highest $Avg.AUC_{TEST}$ (0.80) among all models was in M3 (Model 3, Table 1) and this model performed better than a random prediction (statistics for AUC ratio, mean ± SD = 1.69 ± 0.03, range=1.60–1.77, P<0.001).

The univariate response curves gave more insights into the precise effect of each variable on the distribution of the species in the study area. The response curves of

bioclimatic variables BIO11 and BIO17 were bell-shaped which means for these bioclimatic variables, background extent contains the full range of conditions that are inhabitable for the species. The rest four bioclimatic variables were truncated when habitat suitability was decreasing (Supplemental Fig. 2). Marginal response curves indicated that the Balkan wall lizard primarily prefers areas having not mild winter, not too hot and dry summer, and annually stable precipitation regime with moderate amount of summer rain (Supplemental Fig. 3). Nevertheless, the mean temperature of the coldest quarter (BIO11, 56.2%) and the precipitation seasonality (BIO15, 40.9%) gave the most contribution to the model (together, 97.1%) almost equally and mostly shaped the geographic distribution of the species (having the most useful information that is not present in the other variables and having the most useful information by itself) (Supplemental Fig. 4, Table 2). The bioclimatic suitability decreased with increasing winter (especially>5°C) and summer temperatures (especially28>°C) and precipitation seasonality (highest around 10%) characterized by hot and dry summers and wet winters at lower latitudes and cooler summer temperatures and spring and summer precipitation at higher latitudes of the study area (see Fig. 3, Supplemental Fig. 3).

Table 2. Contributions of the bioclimatic variables to the model.

Variables	Percent contribution	Permutation importance
BIO11	56.2	62.3
BIO15	40.9	28.1
BIO12	1.6	4.8
BIO10	0.8	2.2
BIO17	0.6	2.4
BIO2	0	0.2

The predicted suitable bioclimatic areas for the species for the present time conditions (sum of moderate, high, and very high suitability, 778,605.39 km², 28.7% of the study area) were mainly including the Crimean Peninsula, high latitudes of the east, and the central Europe until southeastern edge of the Czech Republic (forming the northernmost distribution border) and covering mostly the Balkan Peninsula at low latitudes (excluding high mountain ranges). The potential distribution area of the Balkan wall lizard was found mostly to be similar to its known distribution area (Fig. 3). In addition, high mountain ranges (Rhodope, Balkan, Carpathian, and Crimean Mountains) were predicted correctly low bioclimatic suitability due to low winter temperatures (BIO11; Supplemental Fig. 6). Besides, areas where the species is not known to occur also have been over predicted such as southwestern part of Russia that is adjacent to the Crimean Peninsula, southeastern coastline of the Black Sea, and inner parallel lines (where the elevation is low), adjacent scattered areas in central Anatolia, the Italian Peninsula, and the northern coastline of the Adriatic Sea. (Fig. 3, for the IUCN Red List present distribution, see Böhme et al., 2009).

3.1. Past Projection

For the reconstructed past climatic conditions, final summary predictions were generated for the LGM and Mid Holocene (averaged over global climate models).

According to the average LGM prediction, distribution area was withdrawn to some specific locations (northern coastline of the Aegean Sea, the Italian Peninsula and Sicily, totally 57,596.19 km²) mainly due to the negative effect of mean winter temperature (BIO11; see Fig. 4; Supplemental Fig. 7). From LGM to the present, distribution area of the species remarkably extended (1,251.83%, Table 3; Fig. 4; Fig. 6).

Mid-Holocene predictions were considerably different than the LGM and had much closer distribution pattern and distribution extent to the present geographical distribution of the species (Distributional change from Mid-Holocene to present is -0.2% and from the LGM to Mid-Holocene is 1,254.59%). Mid-Holocene distribution projection expanded to more northern latitudes and inner side of the Balkan and the Crimean Peninsulas, the Europe, and also vicinity of the Black Sea due to total contribution of bioclimatic variables with changing amounts from pixel to pixel within the study area (totally 780,190.61 km²; Table 3; Fig. 5; Fig. 6; Supplemental Fig. 8).

Table 3. Bioclimatic suitability (km²) under present and past conditions (i.e. for each time period, LGM and Mid-Holocene) for the Balkan wall lizard (*Podarcis tauricus*).

	Present	LGM	Mid-Holocene
Expansion	--	28,181.62	79,260.81
Suitable areas in both	--	29,414.57	700,929.79
Total suitable areas	778,605.39	57,596.19	780,190.61
Contraction	--	749,190.82	7,7675.60
Unsuitable areas in both	--	1,903,580.54	1,852,501.34
Total unsuitable areas	1,931,762.16	2,652,771.36	1,930,176.94

3.2. Future Projections

The effect of the global climate change on the bioclimatic suitability was quite clear for each scenario for each time period in the future. Consistent with each other in all scenarios, potential suitable bioclimatic areas have expanded mostly to the north-northwestern direction and at higher elevations in the south including interior of the Europe, north of Ukraine, but also inner Anatolia (Fig. 7). These results are broadly agreed upon by all global climate models. The differences of potential suitable bioclimatic areas among scenarios were more marked for 2070 than for 2050. In the most drastic scenario (RCP 8.5 scenarios for 2070), the distribution pattern of the species expanded heavily towards northernmost of the distribution range. Under the future bioclimatic conditions, suitable bioclimatic areas were projected to increase by 77.42 – 124.41% (RCP2.6 on the low and RCP8.5 on the high end) and 75.96 – 174.95% (RCP2.6 on the low and RCP8.5 on the high end) in 2050 and 2070, respectively (Table 4; Fig. 7; Fig. 8) mainly due to the increase in summer and winter temperature in northern latitudes of the study area (BIO10 and BIO11; Supplemental Fig. 9).

The analog and the non-analog conditions and extrapolation risks in model transfers were identified by MESS analysis (Elith et al., 2010). The extrapolation in high-predicted areas of distribution was not a critical issue except for LGM projections showing extrapolation in limited areas at the northern coastline of the Aegean Sea for CCSM4 and MIROC-ESM models (Supplemental Fig. 10) due to mean diurnal range (BIO2). For the future

climatic models, novel conditions were located mainly in the southeastern part of the study area where bioclimatic suitability is very low and in a few pixels (around Thessaloniki) due to the mean summer temperature

(BIO10) where high bioclimatic suitability was projected (Supplemental Fig. 11). To sum, the model was required to extrapolate into some limited novel bioclimatic conditions.

Table 4. Bioclimatic suitability (km²) under present and future conditions (i.e. for each scenario, RCP2.6, RCP4.5, RCP7.0, and RCP8.5, for each time period, 2050 and 2070) for the Balkan wall lizard (*Podarcis tauricus*).

	Present	2050				2070			
		RCP2.6	RCP4.5	RCP6.0	RCP8.5	RCP2.6	RCP4.5	RCP6.0	RCP8.5
Expansion	--	629,418.93	686,927.05	823,872.12	1,009,254.36	614,975.84	1,144,614.21	1,050,205.78	1,437,967.29
Suitable areas in both	--	752,008.98	753,770.34	755,883.96	738,006.24	755,091.35	733,602.86	724,355.77	702,779.21
Total suitable areas	778,605.39	1,381,427.91	1,440,697.39	1,579,756.08	1,747,260.60	1,370,067.19	1,878,217.08	1,774,561.55	2,140,746.50

Table 4. (Continued)

	Present	2050				2070			
		RCP2.6	RCP4.5	RCP6.0	RCP8.5	RCP2.6	RCP4.5	RCP6.0	RCP8.5
Contraction	--	26,596.41	24,835.05	22,721.43	40,599.15	23,514.04	45,002.53	54,249.62	75,826.18
Unsuitable areas in both	--	1,302,343.23	1,244,835.11	1,107,890.04	922,507.80	1,316,786.31	787,147.94	881,556.38	493,794.87
Total unsuitable areas	1,931,762.16	1,328,939.64	1,269,670.16	1,130,611.47	963,106.95	1,340,300.36	832,150.47	935,806.00	569,621.05

3.3. Dispersal Corridors and Paths

Putative dispersal corridor and paths as a sign of population connectivity under present conditions were visualized (Fig. 9). High population connectivity generally followed the way beneath Carpathian Mountains and in between Balkan and Rhodope Mountains in the north and Pindus Mountains in the south. This route partially overlaid with the valleys in between these mountains.

4. Discussion

This study presents a first attempt to assess the detailed past (the LGM and Mid-Holocene) and the future (2050 and 2070) potential distribution patterns of the Balkan wall lizard as a common lizard species having large range of distribution area. Accordingly, ENM (Franklin, 2010; Peterson et al., 2011) approach was used to predict the probable suitable bioclimatic areas.
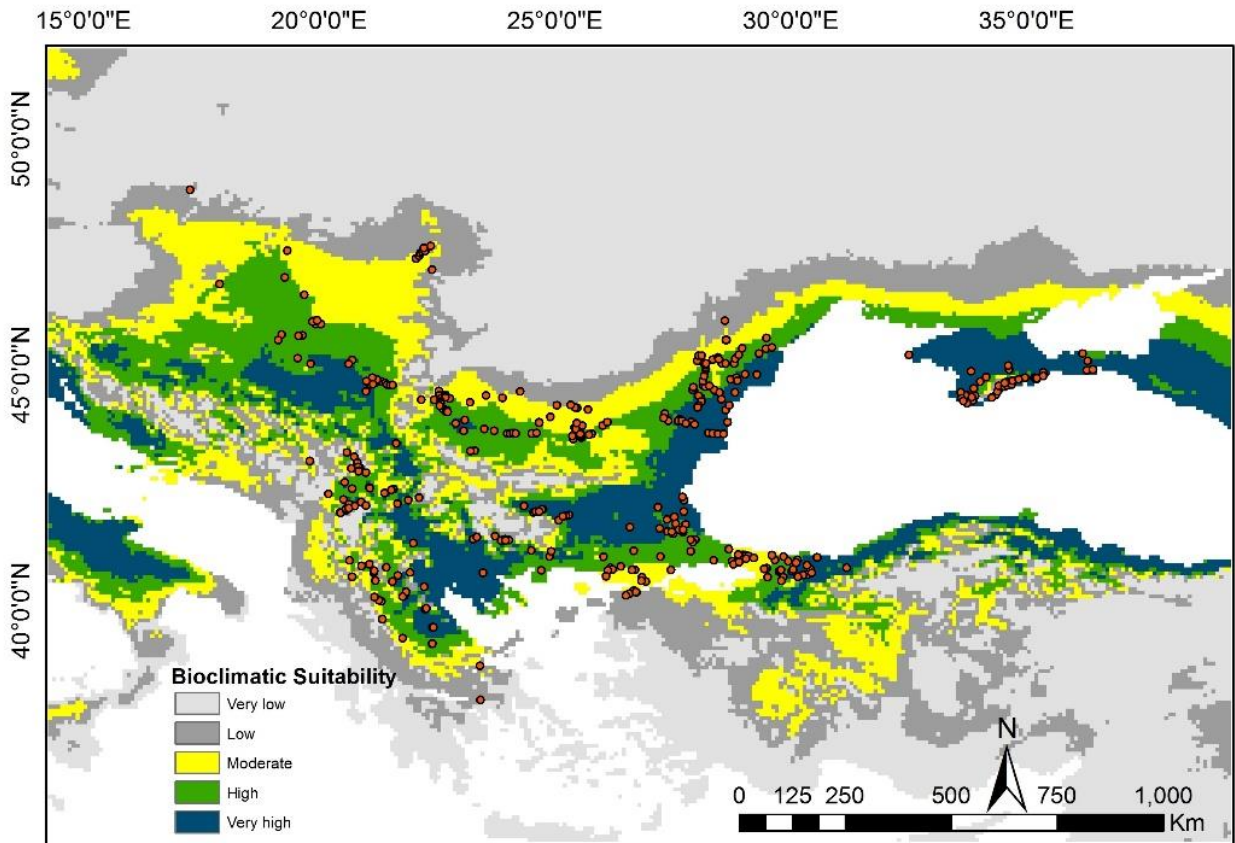
Figure 3. Bioclimatic suitability under present (1960-1990) conditions for the Balkan wall lizard (*Podarcis tauricus*). Red circles indicate 153 presence records. The visible area in maps is 14.25° to 39.33°E and 35.08° to 51.92°N.
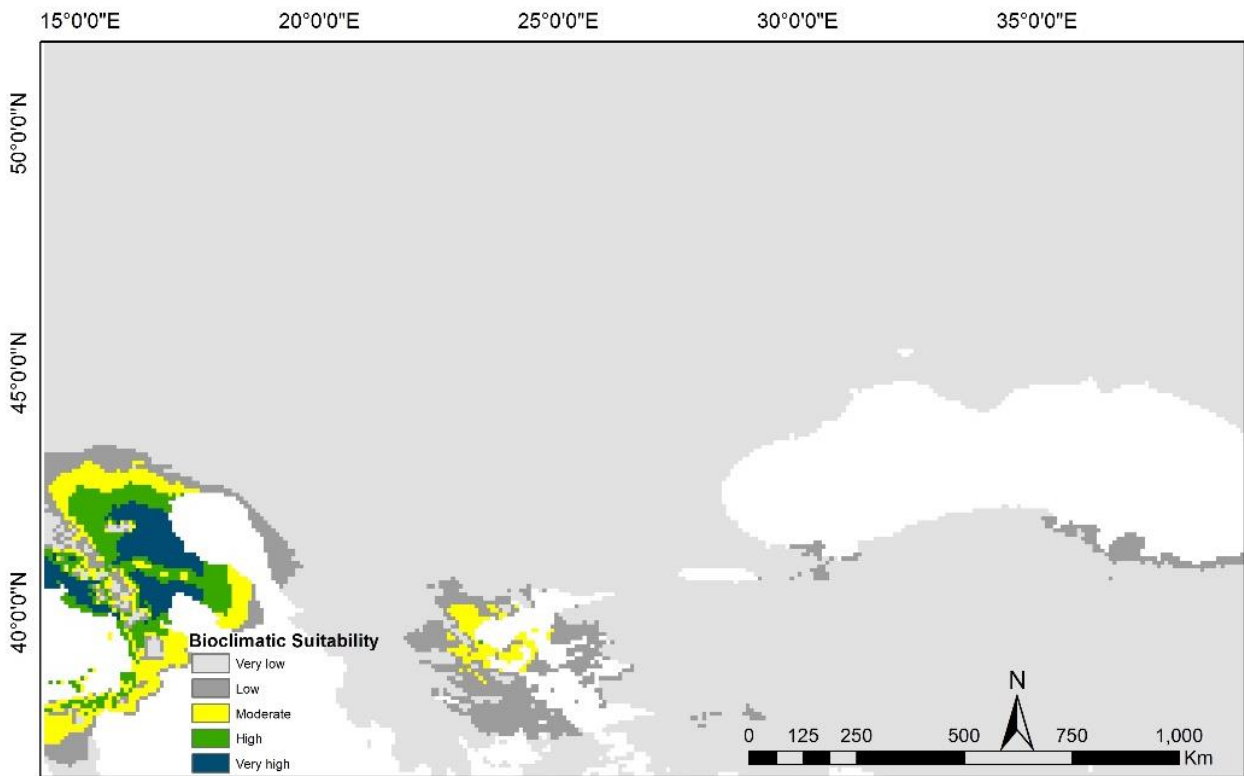
Figure 4. Habitat suitability and glacial refugia under reconstructed LGM conditions as averaged over global climate models (CCSM4, MIROC-ESM, MPI-ESM-LR) for each scenario for each time period for the Balkan wall lizard (*Podarcis tauricus*). The visible area in maps is 14.25° to 39.33°E and 35.08° to 51.92°N.
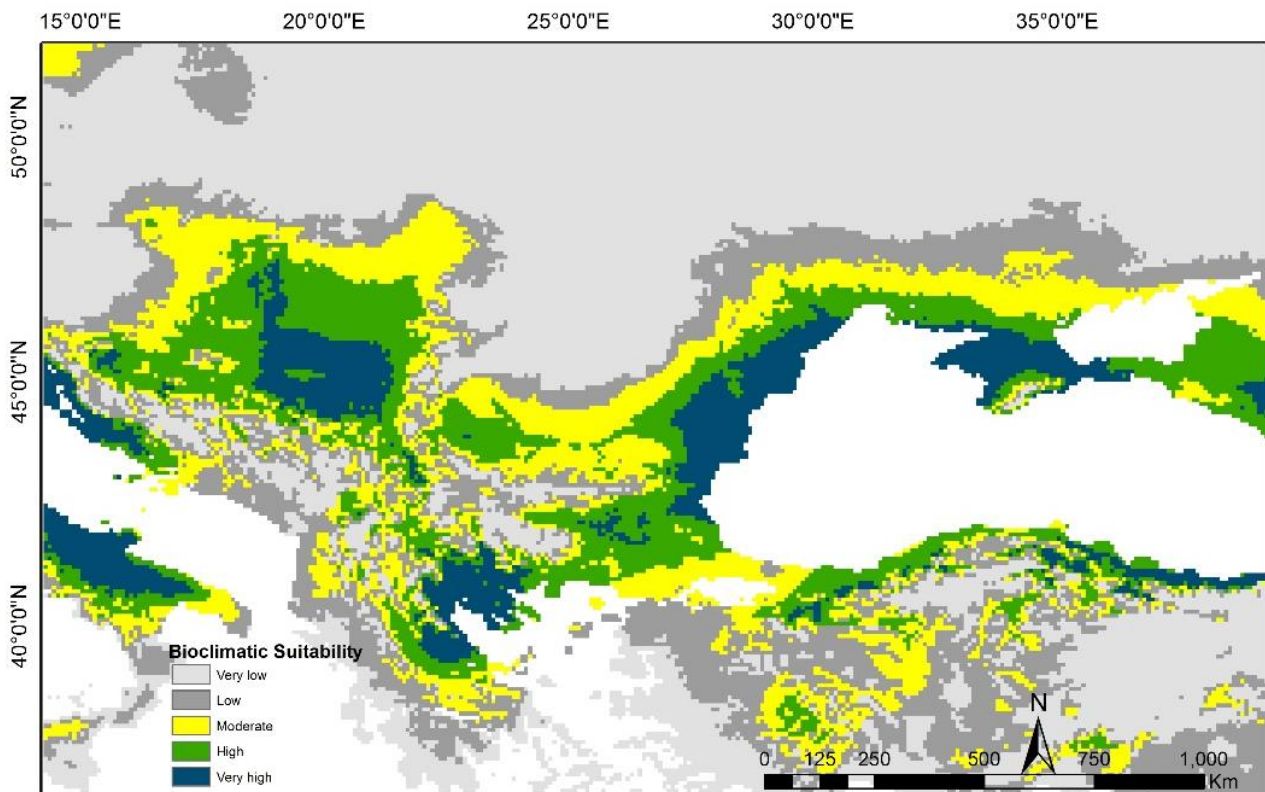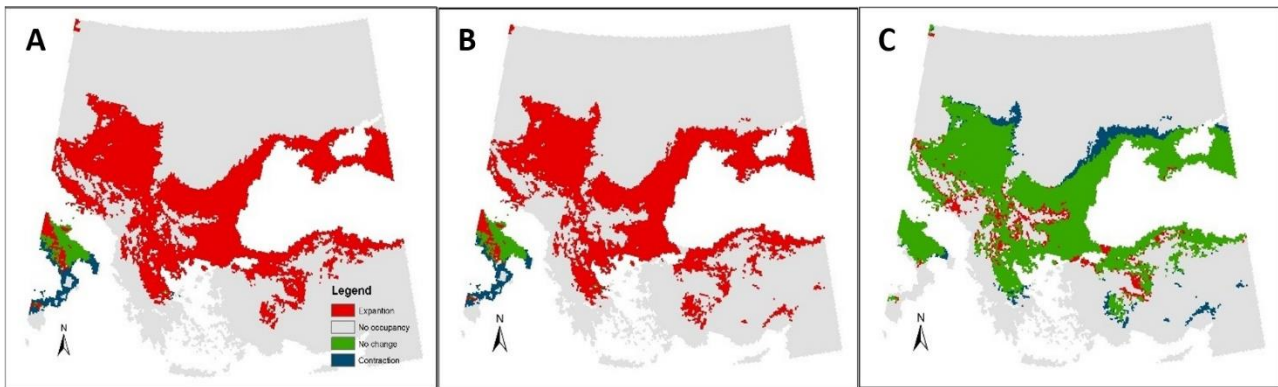

Figure 5. Habitat suitability under reconstructed Mid-Holocene conditions averaged over global climate models (CCSM4, MIROC-ESM, MPI-ESM-LR) for each scenario for each time period for the Balkan wall lizard (*Podarcis tauricus*). The visible area in maps is 14.25° to 39.33°E and 35.08° to 51.9°N.

Figure 6. Areas of expansion, no change, contraction, and no occupancy in suitable bioclimatic areas under past conditions (for each time period, LGM and Mid-Holocene as averaged over global climate models) for the Balkan wall lizard (*Podarcis tauricus*). A: From LGM to present, B: From LGM to Mid-Holocene, C: From Mid-Holocene to present, respectively.
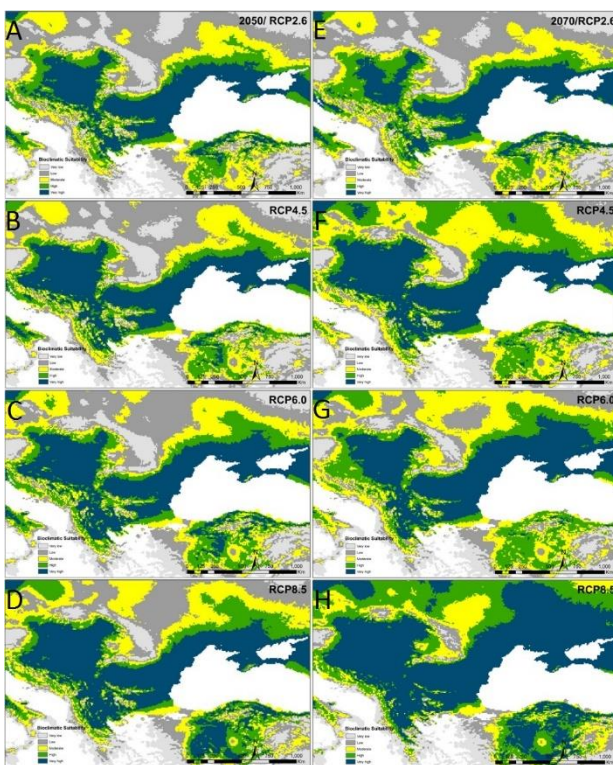

Figure 7. Habitat suitability under future bioclimatic conditions averaged over global climate models (CCSM4, MIROC-ESM, MPI-ESM-LR) for each scenario for each time period (A, B, C, D for 2050 and E, F, G, H for 2070) for the Balkan wall lizard (*Podarcis tauricus*). The visible area in maps is 14.25° to 39.33°E and 35.08° to 51.92°N.

4.1. The Present, the Past and the Future Distribution Pattern of the Balkan Wall Lizard

The results of the study indicate that the Balkan wall lizards have responded to global climate changes through the Late Quaternary in a fashion that in the LGM (22,000 years ago), the potential distribution range considerably contracted and during the interglacial period (Mid-Holocene and the present) it was expanded. To sum, the classical paradigm of glacial range contraction and interglacial range expansion for temperate species (Hewitt, 1996, 1999, 2000, 2004) has been met for the Balkan wall lizard.

Under the present bioclimatic conditions, areas having high bioclimatic suitability were predicted across most of the known distribution area of the species. The model correctly predicted as very low suitability for the Balkan wall lizard at the western part of the Pindus Mountains, which is the distribution area of *P. ionicus*. This shows that the predictive ability of the model was very high for this area. In Psonis et al. (2018), it was found in niche similarity analysis that there was low niche overlap between *P. tauricus* and *P. ionicus*. These findings are also in accordance with the study result. However, the model over-predicted the distributions in some areas at southwestern and northeastern parts of the study area including south of Dinaric Alp Mountains, the Italian Peninsula, Sicily, east of the Black Sea Basin, and inner Anatolia (Fig. 3). This could be due to several reasons: 1) Known distribution area of the species is expanded with new studies (Tok & Çiçek, 2014; Bülbül et al., 2015; Gül & Tosunoğlu, 2017; Fischer et al., 2019) and the results of the study might support it, 2) Italy and the south part of Dinaric Alp Mountains are not inside the distribution area of the species historically, even though it had been, the barrier status of the Alps could have blocked northwards directed range expansions from the Italian Peninsula (Sudhaus et al., 1997). Likewise Italy, Sicily was also over-predicted and these findings could be the result of modelling weakness. The temporal accordance between the occurrence data and the bioclimatic data is a limitation of this study (Roubicek et al., 2010). Bioclimatic data were from the period 1960-1990 and the occurrence data were from the period 1977-2019 (mostly after 1990).

Podarcis taxon came from the western parts of Europe and they colonized the Balkan Peninsula (Oliverio et al., 2000). The phylogeographic scenario suggests in Psonis et al. 2017 and 2018 that the diversification within *Podarcis* started in the Upper Miocene (~9.60 Mya) due to orogenic activity and went on with differentiation of the Balkan species group (started at 8.63 Mya in Mid-Aegean Trench). This was followed by the differentiation of *P. tauricus* species subgroup during the Messinian Salinity Crisis in Late Miocene (MSC=5.96-5.33 Mya) due to the geomorphological alterations and climatic oscillations. Finally, genetically different lineages have been revealed which could be due to geographic fragmentation in the glacial and inter-glacial periods as a result of the Pleistocene climatic oscillation.

The Balkan Peninsula was a source for postglacial colonization of central and northern Europe by species

populations (Hewitt, 1999, 2000). The southern Balkans is considered by other phylogeographic studies as a local climatic refugium (Taberlet et al., 1998; Joger et al., 2007; Sagonas et al., 2014; Marzahn et al., 2016). In this study, it was found that during the LGM, the distribution range restricted to a few spots in the southern Balkans. The LGM projections could catch southern Balkan refuge since the coastline of the Aegean Sea was predicted as suitable bioclimatic area (Fig. 4). During Mid-Holocene, the Balkan wall lizard substantially expanded its range from the restricted area of the LGM glacial refugium to its present range. Therefore, recent findings support former suggestion in that the species is a post-glacial colonizer (Psonis et al., 2018; Fig. 5). Mid-Holocene potential distribution area and the present distribution area of the Balkan wall lizard were almost the same in size which may indicate that the climatic conditions during Mid-Holocene

was the main driver for expansion of the distribution area of the species after significant LGM contraction due to the positive effects of bioclimatic variables with changing contributions from one pixel to the other (Supplemental Fig. 8). These findings are mostly in accordance with Psonis et al. (2018) in that being Southern Balkan as a LGM refuge and present range expansion of the species. Yet, the difference between the studies could be due to several factors such as using different bioclimatic variables, occurrence records, and Maxent calibration values to contract a model. These findings are compatible with the results of demographic and ENM analyzes in Psonis et al. (2018) in that the LGM possibly caused a bottleneck for the species and a recent spatial expansion of the species population occurred from the south to the north after the end of the LGM.
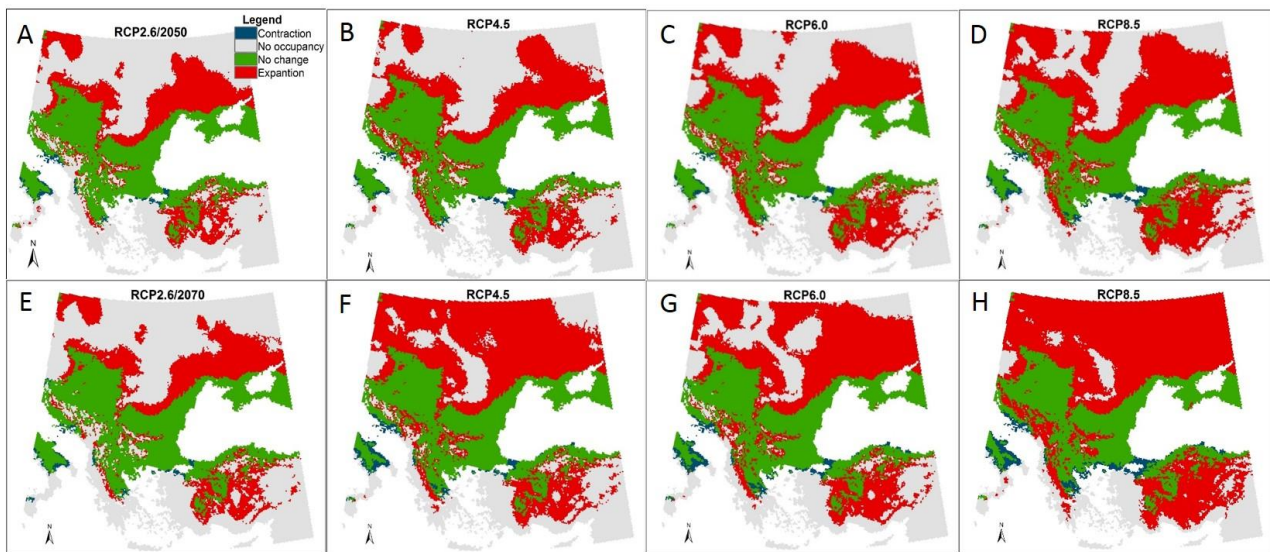

Figure 8. Areas of expansion, no change, contraction and no occupancy in suitable bioclimatic areas under future conditions (for each time period (A, B, C, D for 2050 and E, F, G, H for 2070) and for each scenario (RCP2.6, RCP4.5, RCP6.0 and RCP8.5) as averaged over global climate models for the Balkan wall lizard (*Podarcis tauricus*).
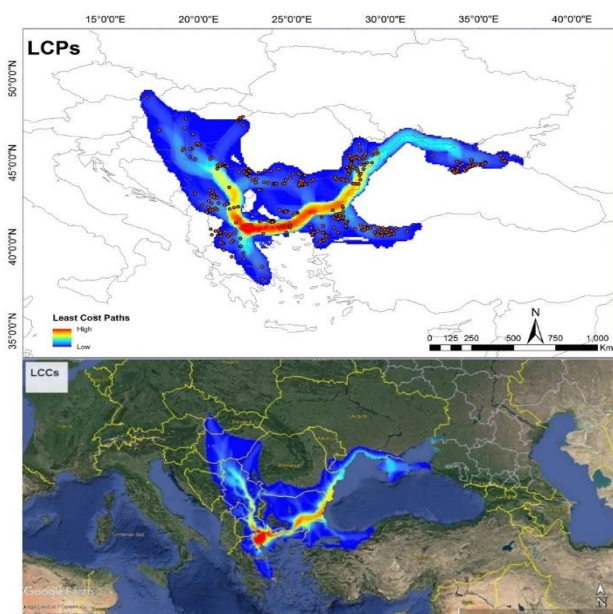

Figure 9. Construction of dispersal corridors (LCCs) and paths (LCPs) for the Balkan wall lizard (*Podarcis tauricus*). Warmer colors depict higher population connectivity.

Furthermore, together with the global climate change, the predicted distribution area of the species will expand towards northern latitudes, higher elevations of the mountain ranges, and inlands of the European and the Asian continents (Fig. 7). Many studies suggest that global warming is driving species ranges northwards and toward higher elevations at temperate latitudes (Parmesan, 2006; Wilson et al., 2007; Chen et al., 2011). The bioclimatic suitability for the species was predicted to increase in northern latitudes due to mainly high mean summer and winter temperatures (BIO10 and BIO11; Supplemental Fig. 9). According to IPCC 5th Assessment Report (IPCC, 2014), global average temperature would increase between 0.3 and 4.8 °C by the end of 21st century to be in agreement within all RCPs. Mediterranean region was projected to be much drier and hotter in the warm seasons (Giorgi & Lionello, 2008) and the central/north Europe to be much warmer and wetter in the cold seasons (Kjellstrom & Ruosteenoja, 2007) compared to recent climatic conditions. These projections are in accordance with the predictions of the northernmost distribution expansion of the Balkan wall lizards under the future bioclimatic conditions. All these results were evaluated under the assumption that the ecological requirements of the species have remained the

same through time periods (Nogués-Bravo, 2009). However, given low dispersal capacity, it is unlikely that the species could reach all of the potential distribution area (Huey, 1982).

4.2. Dispersal Corridors and Paths

Connectivity among populations was assessed via LCCs and LCPs analyses. By virtue of the approach integrated with ENMs, possible dispersal corridors among populations of the Balkan wall lizard in present bioclimatic conditions have been identified. Even though distribution area of the species included several high mountain ranges, no noticeable barriers have been observed between south-western and north-eastern populations of the Balkan wall lizard. Moreover, there is a high connectivity via valleys among Dinaric Alp, Balkan, Rhodope, Pindus Mountains and until the coastline of the Black Sea. Predicted high connectivity followed the way beneath Carpathian Mountains and above Dinaric Alp Mountains and went on between Balkan and Rhodope Mountains on the north and Pindus Mountains on the south (Fig. 9).

Although validity of the lineages was not clear due to low representation, three lineages were found within *P. tauricus* (Psonis et al., 2018). The current LCCs analyses could catch high connectivity in one of that lineage (including populations from Albania, Bulgaria, FYROM, Greece, Hungary, Romania, Serbia, and Türkiye) and also low connectivity among those three lineages.

4.3. Effects of the Bioclimatic Variables

Our results offer insights into the ecological factors related to the distribution of the Balkan wall lizard in the study area. The most significant bioclimatic variables in predicting the present potential distribution (which characterized environmental space) of *P. tauricus* is BIO11 and BIO15 (Supplemental Fig. 3). The bioclimatic suitability decreased with increasing BIO15 and increasing BIO10 and BIO11. Moreover, for BIO11 and BIO17, the background extent contained the full range of conditions that are inhabitable for the species. These findings emphasize the preference of the species for annually stable precipitation regime with summer rains and avoiding too warm and too cold winter conditions. These preferences also express itself in the distribution area of the Balkan wall lizards that mainly includes Balkans and more northern latitudes. Moreover, western part of Pindus Mountains was predicted as bioclimatically very low suitable for the species due to BIO12 and BIO15 (Supplemental Fig. 12). These findings are mostly in accordance with former studies. Kaliontzopoulou et al. (2008) mentioned the preference of *Podarcis* in the northern Africa for humid conditions but not extremely high temperatures without giving details about the species specific preferences. Psonis et al. (2018) discussed the most important climatic parameter was the annual range of the temperature.

The species spatial distributions depend on three general, interacting types of factors: the abiotic environment (e.g. temperature, humidity), the biotic environment (e.g. competition), and accessibility of areas across landscapes (migration) (Pulliam, 2000; Soberón & Peterson, 2005; Soberón, 2007). It is known that ecological competition among Balkan Podarcis species has been one

of the main driver of their evolutionary history (Oliverio et al., 2000; Poulakakis et al., 2005a, 2005b). Moreover, changing climatic conditions may reform the community and new competitors may arise (Le Galliard et al., 2012). Besides, herptiles are known to be poor dispersers but dispersal ability may vary substantially within taxa (Smith & Green, 2005). In this study, biotic factors and dispersal ability of the species in shaping the distribution pattern remained unknown and bioclimatic variables as abiotic factors were taken into account exclusively. Moreover, in the face of the global climate change, land-use practices are also changing and habitat loss appears as an important driver shaping the species distributions (Huey, 1982; Zakkak et al., 2015) and the Balkan wall lizards have been facing this threat in some of their distribution range (Böhme et al., 2009). Therefore, using bioclimatic data and land-use data together in the future ecological niche modelling studies would give deeper insight for distributional pattern of the Balkan wall lizard.

Ethics committee approval: This study was conducted in accordance with the ethical standards of animal experiments. Ethics committee permission for the study was obtained from Çanakkale Onsekiz Mart University Experimental Animals Ethics Committee (No: 2018/1800053914).

Conflict of interest: The authors declared that there is no conflict of interest.

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Supplemental Tables

Supplemental Table 1. Bioclimatic variables. Highlighted variables were used to create four sets of non-correlated variables.

Short name	Description	Unit
BIO1	Annual Mean Temperature	^{0}C
BIO2	Mean Diurnal Range (Mean of monthly max temp - min temp)	^{0}C
BIO3	Isothermality (BIO2/BIO7) (×100)	%
BIO4	Temperature Seasonality (standard deviation ×100)	^{0}C
BIO 5	Max Temperature of Warmest Month	^{0}C
BIO6	Min Temperature of Coldest Month	^{0}C
BIO7	Temperature Annual Range	^{0}C
BIO8	Mean Temperature of Wettest Quarter	^{0}C
BIO9	Mean Temperature of Driest Quarter	^{0}C
BIO10	Mean Temperature of Warmest Quarter	^{0}C
BIO11	Mean Temperature of Coldest Quarter	^{0}C
BIO12	Annual Precipitation	mm
BIO13	Precipitation of Wettest Month	mm
BIO14	Precipitation of Driest Month	mm
BIO15	Precipitation Seasonality (Coefficient of Variation)	%
BIO16	Precipitation of Wettest Quarter	mm
BIO17	Precipitation of Driest Quarter	mm
BIO18	Precipitation of Warmest Quarter	mm
BIO19	Precipitation of Coldest Quarter	mm

Supplemental Table 2. Correlation Matrix of Bioclimatic variables

	BIO1	BIO2	BIO3	BIO4	BIO10	BIO11	BIO12	BIO15	BIO16	BIO17
BIO1	1	0.15831	0.46289	0.49141	**0.90417**	**0.95238**	0.00596	0.47657	0.22899	0.45993
BIO2		1	0.76516	0.16014	0.08889	0.15429	0.17890	0.33977	0.05153	0.45400
BIO3			1	0.74147	0.16099	0.60212	0.18693	0.52871	0.33357	0.38805
BIO4				1	0.07716	0.72711	0.46817	0.42953	0.53480	0.10247
BIO10					1	0.73979	0.21423	0.32895	0.00378	0.47045
BIO11						1	0.17171	0.51910	0.36864	0.39375
BIO12							1	0.09192	**0.85977**	0.55185
BIO15								1	0.55066	0.72152
BIO16									1	0.11176
BIO17										1

Supplemental Table 3. Four sets of non-correlated (r ≤|0.80|) bioclimatic variables.

| Bioclimatic Sets		1	2	3	4
	Bioclimatic variables	BIO1	BIO1	BIO2	BIO2
		BIO2	BIO2	BIO3	BIO3
		BIO3	BIO3	BIO4	BIO4
		BIO4	BIO4	BIO10	BIO10
		BIO12	BIO15	BIO11	BIO11
		BIO15	BIO16	BIO12	BIO15
		BIO17	BIO17	BIO15	BIO16
				BIO17	BIO17

Supplemental Figures
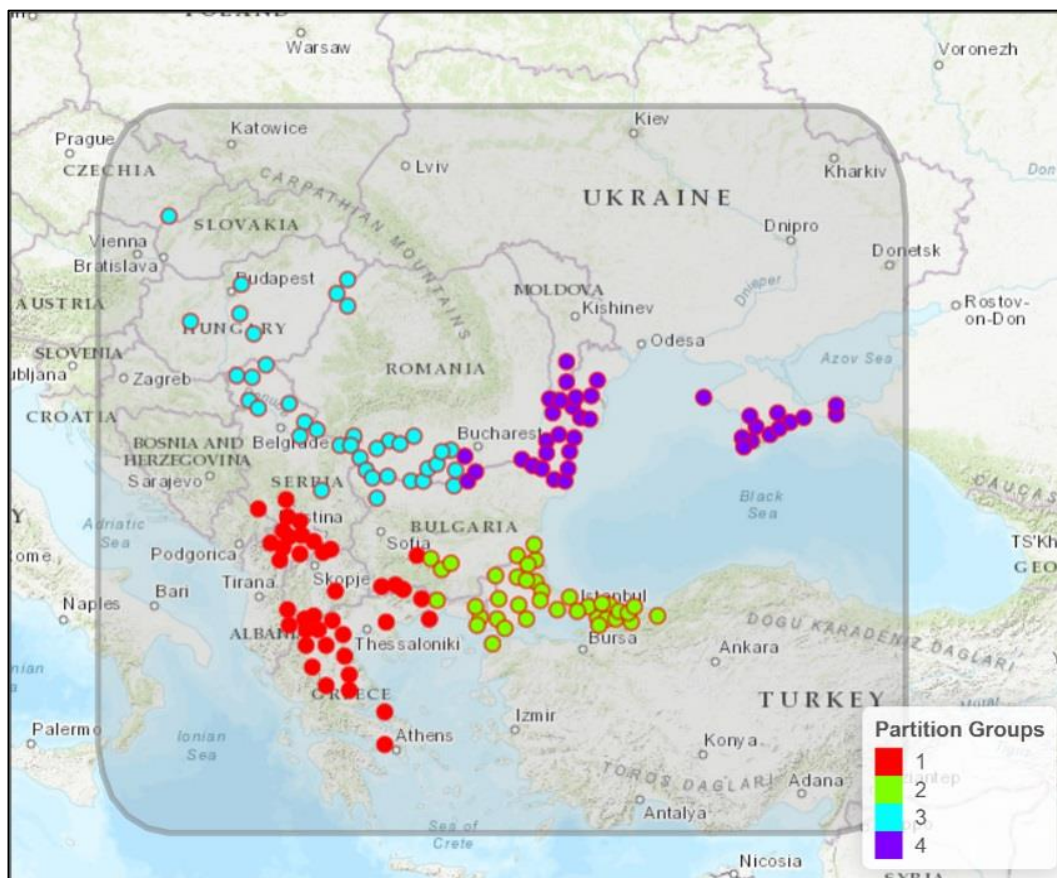
Supplemental Figure 1. The bounding box polygon from the presence records (circles) to which a 2-degree buffer (corresponds to 15.25° to 38.33° E and 36.08° to 50.92° N) was applied and the presence data partitioned into four bins of equal numbers.
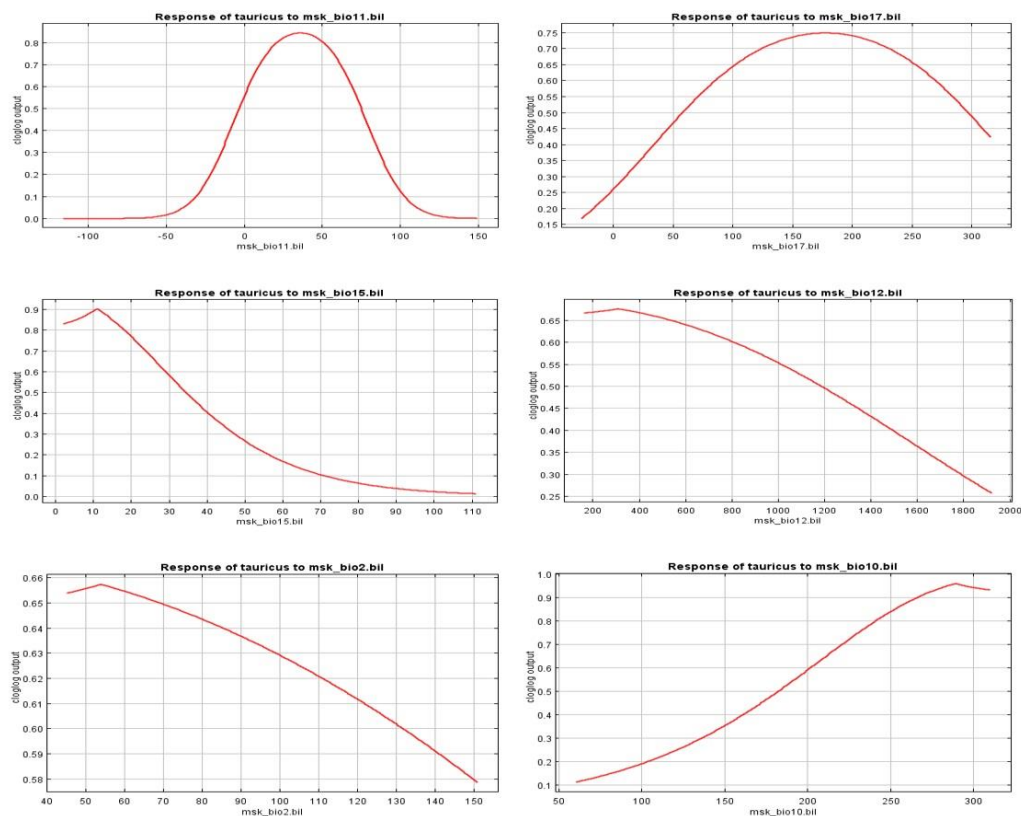
Supplemental Figure 2. The univariate response curves.
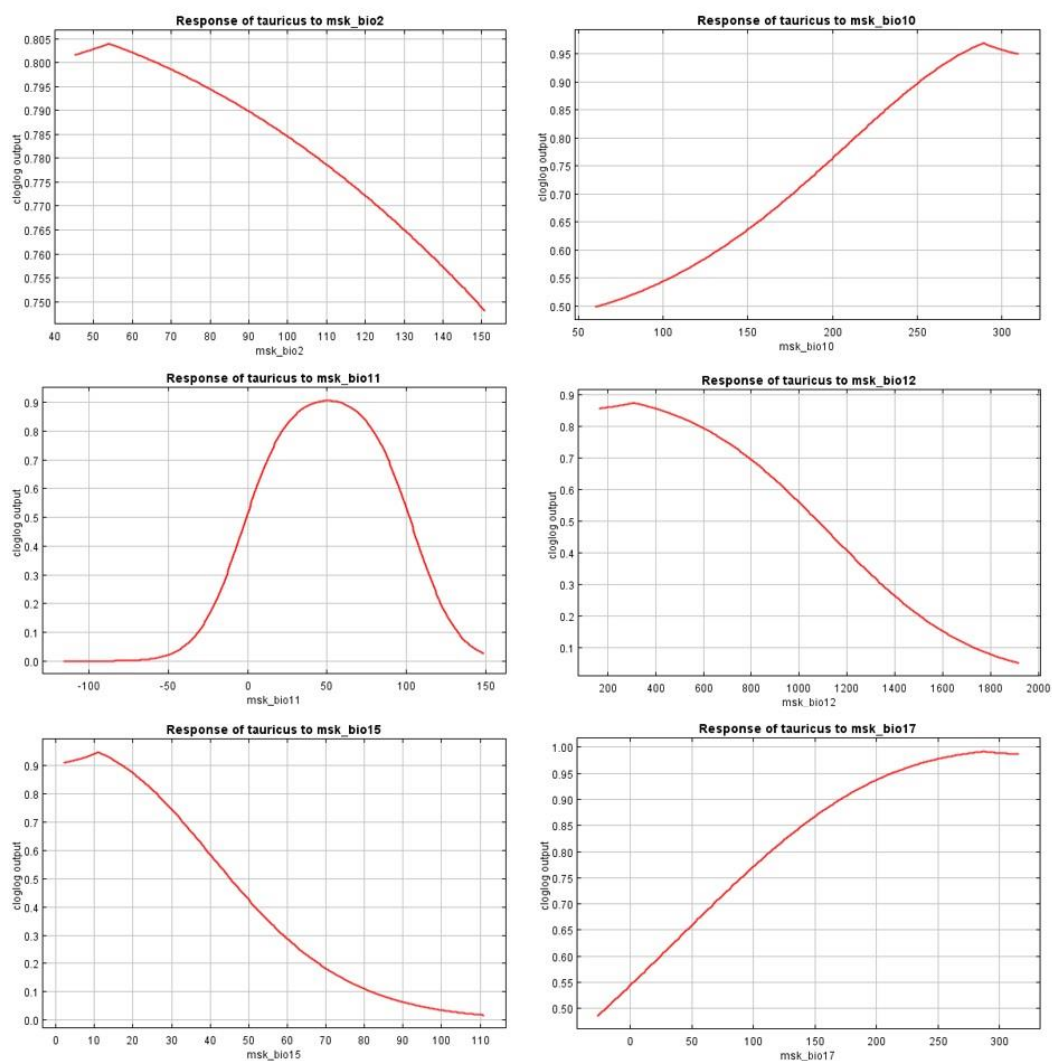
Supplemental Figure 3. The marginal response curves.
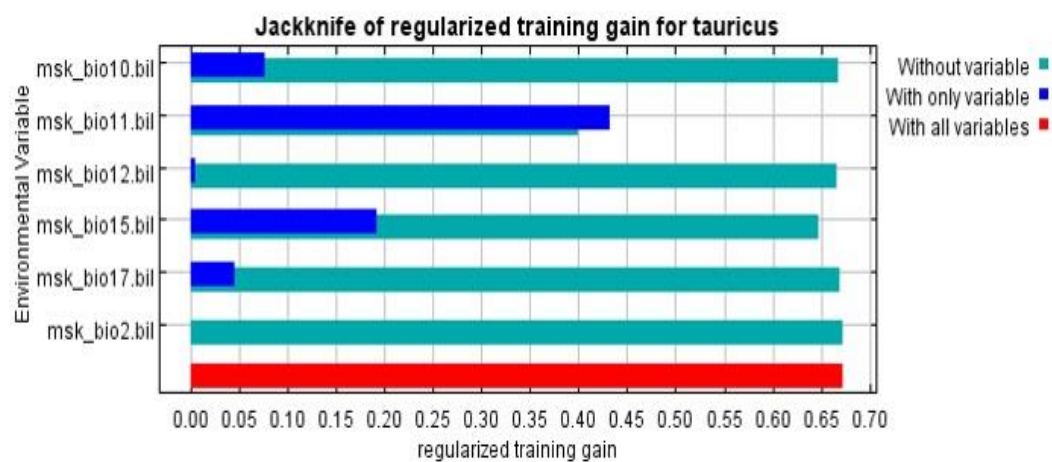
Supplemental Figure 4. The results of the jackknife test of variable importance.

Maxent Lambdas File

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[2] "bio11.bil, 10.39136031319209, -94.0, 127.0"
[3] "bio12.bil, 0.0, 309.0, 1773.0"
[4] "bio15.bil, -3.185050864237784, 11.0, 102.0"
[5] "bio17.bil, 1.7986466238465624, 2.0, 287.0"
[6] "bio2.bil, 0.0, 54.0, 142.0"
[7] "bio3.bil, 0.0, 19.0, 43.0"
[8] "bio4.bil, 0.0, 4730.0, 10226.0"
[9] "bio10.bil^2, 1.2888186807473745, 6561.0, 83521.0"
[10] "bio11.bil^2, -7.4885622396314755, 0.0, 16129.0"
[11] "bio12.bil^2, -3.1424326881260245, 95481.0, 3143529.0"
[12] "bio15.bil^2, -1.289763940255604, 121.0, 10404.0"
[13] "bio2.bil^2, -0.1389729264813303, 2916.0, 20164.0"
[14] "linearPredictorNormalizer, 6.637145946138369"
[15] "densityNormalizer, 4615.114023936132"
[16] "numBackgroundPoints, 36619"
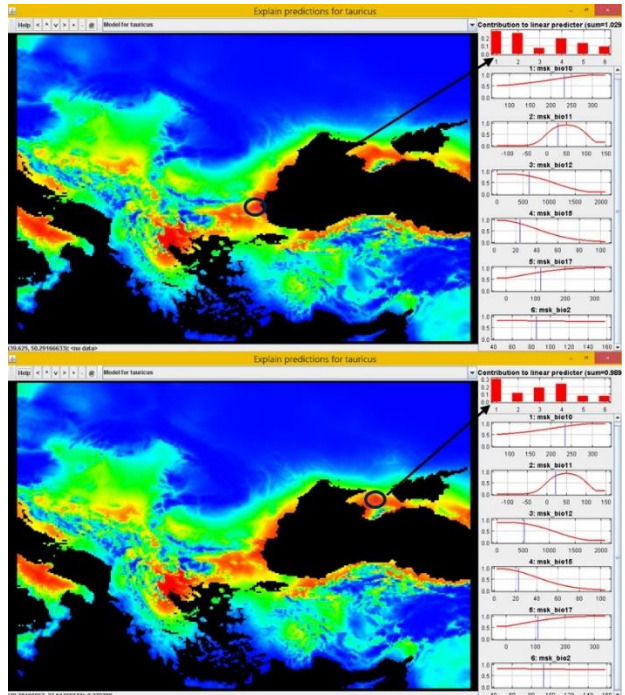[17] "entropy, 9.835222031250549"

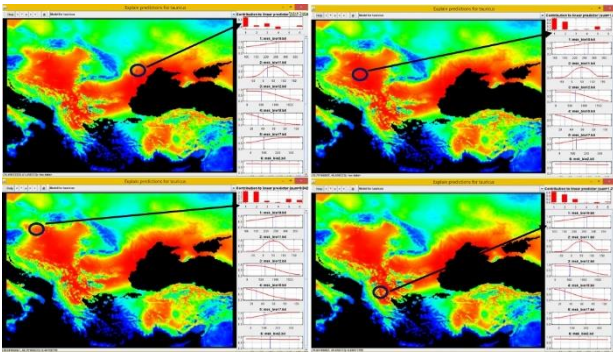Supplemental Figure 5. The coefficients of the final model.
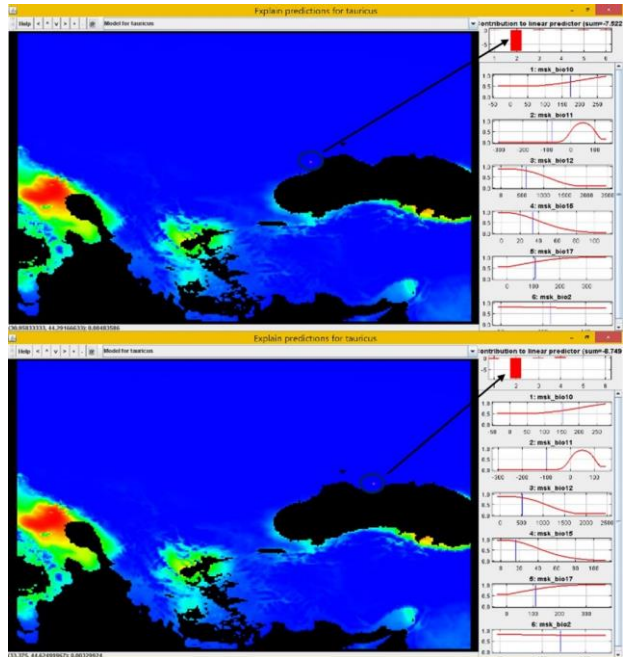
Supplemental Figure 7. Explain tool from Maxent. Warm map colors represent high and cold colors represent low habitat suitability for the Balkan wall lizard (*Podarcis tauricus*) under LGM conditions (CCSM4 model). The effect of variables is explored at northern locations. Very low suitabilities in these regions were driven mainly by BIO11.
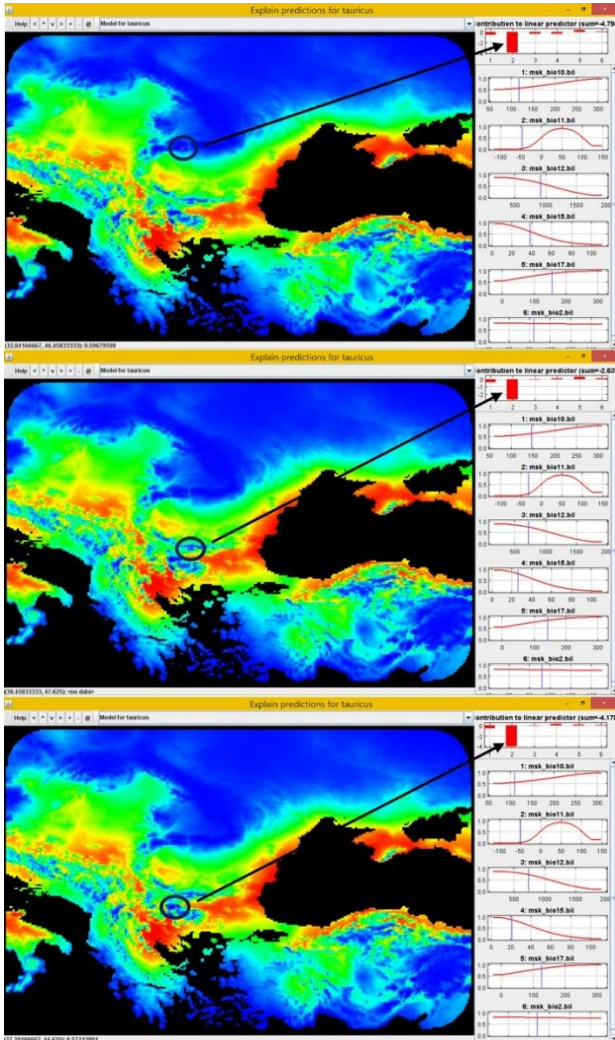

Supplemental Figure 6. Explain tool from Maxent. Warm map colors represent high and cold colors represent low habitat suitability for the Balkan wall lizard (*Podarcis tauricus*) under present conditions. The effect of variables is explored at point locations in Eastern Europe. Very low suitabilities in these regions were driven by BIO11.
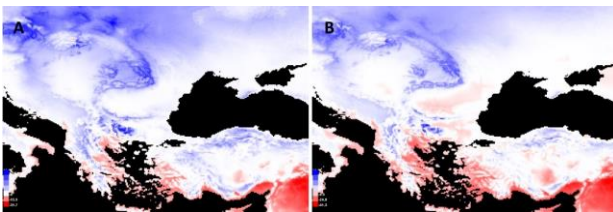
Supplemental Figure 8. Explain tool from Maxent. Warm map colors represent high and cold colors represent low habitat suitability for the Balkan wall lizard (*Podarcis tauricus*) under Mid-Holocene conditions (CCSM4 model). The bioclimatic suitability has shown more northern latitudes due to the positive effects of the bioclimatic variables with changing contribution from one pixel to the other.
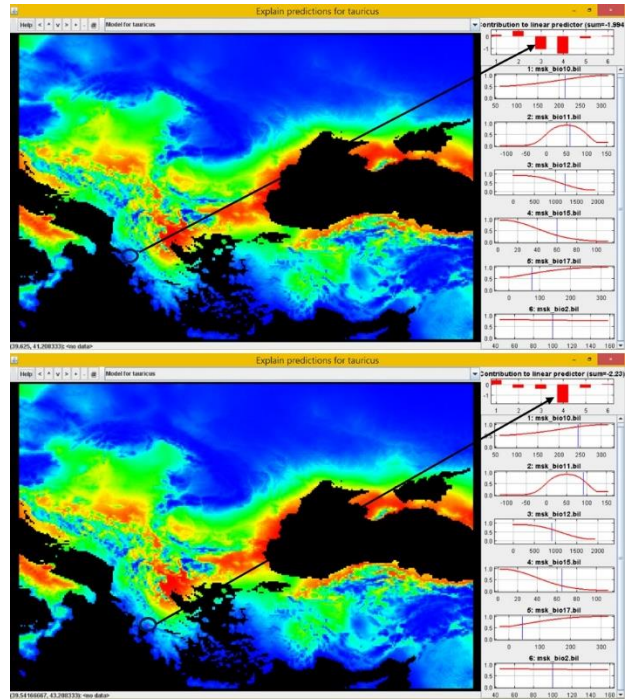
4

Supplemental Figure 9. Explain tool from Maxent. Warm map colors represent high and cold colors represent low habitat suitability for the Balkan wall lizard (*Podarcis tauricus*) under future conditions (MIROC-ESM, RCP8.5, 2070). The effect of variables is explored at northern locations. Very high suitabilities were driven mainly by BIO10 and BIO11.
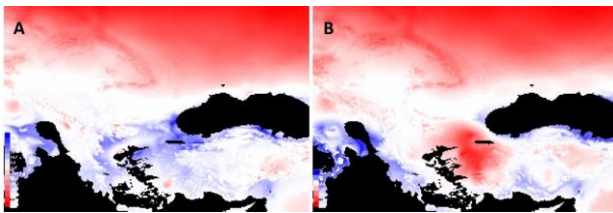
Supplemental Figure 10. Multivariate environmental similarity surface (MESS) analysis for LGM for the Balkan wall lizard (*Podarcis tauricus*), A: for CCSM4 and B: for MIROC-ESM models. Cells shown in red indicate areas for at least one environmental variable value occurs outside the range of values in the training region. In both, some pixels in pink around Thessaloniki were highly predicted.

Supplemental Figure 11. Multivariate environmental similarity surface (MESS) analysis for 2070 for the Balkan wall lizard (*Podarcis tauricus*), A: for RCP4.5 MIROC-ESM and B: for RCP8.5 MIROC-ESM models. Cells shown in red indicate areas for at least one environmental variable value occurs outside the range of values in the training region. In both, some pixels in pink around Thessaloniki were highly predicted.

Supplemental Figure 12. Explain tool from Maxent. Warm map colors represent high and cold colors represent low habitat suitability for the Balkan wall lizard (*Podarcis tauricus*) under present conditions. Very low suitability on the western part of Pindus Mountains were driven mainly by BIO12 and BIO15.