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Ecological niche modeling of the Macedonian mouse, *Mus macedonicus* (Mammalia, Rodentia), under climate change conditions

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Abstract

Mus macedonicus Petrov & Ružic, 1983, also known as the Macedonian mouse or Balkan short-tailed mouse, lives in the southern Balkans and the Middle East. While this species is common in Mediterranean ecosystems and is listed as "least concern" by the IUCN, little is known about how its distribution may shift with climate change. This study explores the 'species' potential distribution in three different periods: during the Last Glacial Maximum (LGM) and under current and future climate scenarios, using Maximum Entropy modelling. Modelling was based on 137 georeferenced occurrence records from Macedonia, Bulgaria, Greece, Turkey, Syria, Lebanon, Israel, Iran, Georgia, and Russia and ten bioclimatic variables from the WorldClim database. We show that a combination of precipitation and temperature variables appear to shape the geographical range of the Macedonian mouse and that its predicted distribution during the LGM is consistent with its survival in multiple refugia, as suggested by previous genetic studies. Modelled future distributions are subtly but significantly different from the current, with population losses and gains in different regions. Our results provide a sound framework for future studies on this model species' range dynamics, suggesting that the overall geographical range of *M. macedonicus* is relatively stable in the long term.

Keywords: Bioclimatic variables, Ecological niche modeling, Jackknife test, MaxEnt, Mediterranean climate zone

Introduction

Mus macedonicus Petrov & Ružic, 1983 (the Macedonian mouse or Balkan short-tailed mouse) is found in the southern Balkans, Anatolia, Transcaucasia, northwest Iran, and the Levant (Macholán et al. 2007; Macholán 1999). This species is common in Mediterranean climate zones and is rated as "least concern" in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Kryštufek & Vohralík 2016). The Macedonian mouse is a mesic species living in habitats containing areas with medium and relatively constant humidity (Haim et al. 1999). As a common species, the Macedonian mouse is also relatively eurytopic, inhabiting various habitats, including long grass, bushes, cultivated lands, woodland borders, and stream banks (Auffray et al. 1990).

Molecular studies (Orth et al. 2002; Kryštufek & Vohralík 2016) have revealed that *M. macedonicus* appears to have persisted in several separate refugia (western Georgia or eastern Azerbaijan, southern Turkey, or around the Euphrates and Tigris and the Levant) during the Last Glacial Maximum (LGM) and the species would appear to be an excellent model organism for studies of refugia and colonization patterns after the LGM in the region. However, to date, no attempt has been made to model the species' potential distribution based on climatic data in the LGM, an approach that could be most illuminating. Indeed, studies on bioclimatically suitable areas and the ecological requirements of *M. macedonicus* are extremely limited, and no attempt has been made to assess how this model species may respond to ongoing anthropogenic climate change.

The Köppen–Geiger climate classification system is a widely used ecological niche modeling (ENM) study. This system is divided into five major groups: Tropical (A), dry (B), temperate (C), continental (D), and polar (E) (Köppen 1884) in which second and third letters further sub-divide the climate group based on seasonal precipitation type and the level of temperature patterns, respectively. Mediterranean climate zone is warm temperate with moderate and relatively constant levels of humidity, and warm summer; represented as C and D in the Köppen-Geiger classification (Peel et al. 2007; Beck et al. 2018), making it suitable for Macedonian mouse. According to the IUCN distribution map, the known distribution range of *Mus macedonicus* have a total of six sub-climate zones in which Csa (hot-summer Mediterranean), Csb (warm-summer Mediterranean), Cfb (warm-summer humid Mediterranean), Dsa (Mediterranean-influenced hot-summer continental), Dsb (Mediterranean-influenced warm-summer continental), Dfb (Mediterranean-influenced warm-summer humid continental).

ENM has been widely used to predict the distribution of taxa across given geographical regions, using climatic variables (Peterson et al. 1999; Soberón & Peterson 2005; Soberón 2010; Peterson et al. 2011). This method is based on the fact that if the species or population's geographic location is known, the potential distribution area at unsampled locations in the past, current, or future can be estimated using environmental variables. Maximum Entropy modeling (MaxEnt) (Phillips et al. 2006; 2017) is one of the most widely used approaches in ENM, producing a spatial habitat suitability map and evaluating the significance of individual bioclimatic variables in shaping a 'species' range. Although several studies have examined morphological, karyological, and genetic variation in *M. macedonicus*, as well as its phylogenetic position within the genus (Ivantcheva & Cassaing 1999; Gündüz et al. 2000; Orth et al. 2002; Çolak et al. 2006; Macholán et al. 2007; 2008; Rajabi & Azizi 2013; Abi-Said & Karam 2017), very little information, is available about the factors shaping the 'species' range (Auffray et al. 1990; Abi-Said & Karam 2017). This study uses a large, mainly genetically-based occurrence dataset for the Macedonian mouse to explore the importance of bioclimatic variables in determining the 'species' range. We explore the past, current, and future potential geographical distribution of the species, addressing the following questions: 1. What are the key bioclimatic variables affecting the distribution of species today? 2. What was the potential distribution of *M. macedonicus* in Europe and Asia during the Last Glacial Maximum? 3. Is the modelled potential distribution during the LGM compatible with multiple refugia, suggested by molecular studies? 4. How will *M. macedonicus* respond to future changes under different climate scenarios?

Materials and Methods

Species Data Source

Occurrence records of *M. macedonicus* were obtained from literature sources (Gündüz et al. 2000; Orth et al. 2002; van der Wal et al. 2003; Macholán et al. 2007; 2008; Gündürü 2008; Rajabi & Azizi 2013; Abi-Said & Karam 2017; unpublished data from Demirtaş et al. 2022) as well as TRAMEM (http://www.tramem.org), and our field observations which together added a significant number of new Turkish records for the species (supplementary material, Table SI). All literature records used in this study were based on genetic identifications and cranial measurements since *M. macedonicus* can be confused with *Mus musculus domesticus* Rutty, 1772 on external morphological characters alone. TRAMEM records with habitat information and field observations were based on external morphology and habitat type but are considered reliable because we avoided using occurrence records in the human settlements and cultivated areas where they coexist with other wild mammals such as *Microtus* sp., *Apodemus* sp., and *Crocidura* sp. Macholán (1999) revealed the Macedonian mouse prefers mainly open places with tall and dense vegetation such as grasses, reeds, and bushes, whereas it does not prefer forests and human settlements. To correct for sampling bias and ensure high geographical heterogeneity (Pearson et al. 2006; Fourcade et al. 2014), multiple presence records within 20 km of each other were spatially filtered and removed. Our complete filtered dataset contained 137 georeferenced occurrences (Figure 1). Geographic Distance Matrix Generator version 1.2.3 (http://biodiversityinformatics.amnh.org) and Google Maps (http://maps.google.com) were used to calculate and verify the occurrence records and the spatial geographic distances between localities.

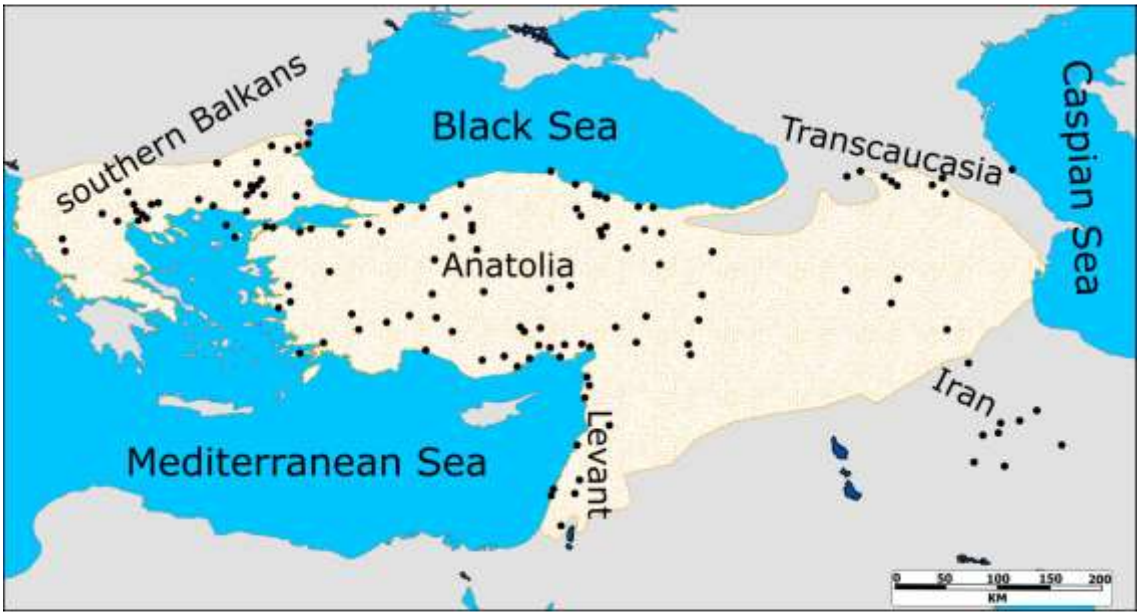

Figure 1. Known distribution of *Mus macedonicus.* Black dots represent occurrence records from our dataset, the yellow dotted area indicating the 'species' distribution according to IUCN. Note that some records fall outside this distribution, particularly in Iran.

Environmental Variables

We used bioclimatic variables from WorldClim archive version 1.4 (www.worldclim.org), including a set of free climate data with a high resolution (~1 km^2), to reconstruct past (LGM, approximately 22 kya), current (1960-1990) and future (average 2070) distribution scenarios for *M. macedonicus*. The Community Climate System Model (CCSM version 4) was used to predict potential distributions for past and future periods. Future climate scenarios used for ENM were representative concentration pathways RCP 4.5 (medium greenhouse gas emission scenario) and RCP 8.5 (maximum greenhouse gas emission scenario), as presented in the Fifth Assessment Report (IPCC5) of the Intergovernmental Panel on Climate Change (IPCC, 2014).

GeoTIFF raster files were downloaded and converted to ".ascii" format using SDM toolbox version 2.4 (http://www.sdmtoolbox.org, Brown 2014; Brown et al. 2017) in ArcGIS version 10.2 (https://www.esri.com). Data processing, mapping, and other file conversions were conducted using ArcGIS and DIVA-GIS version 7.5 software (https://www.diva-gis.org). The ".ascii" files were clipped to include only 19° to 52° east and 30° to 47° north. Highly correlated independent variables were removed from these files to eliminate multicollinearity (which can lead to overfitting problems) (Elith et al. 2011;

Dormann et al. 2013; Tanner et al. 2017; Feng et al. 2019) using Pearson correlation coefficients (r > 0.90) in the SDM toolbox. A resulting dataset of ten bioclimatic variables was employed for niche modelling (see Table I).

Modelling Methods and Statistical Analyses

MaxEnt version 3.4.1 (Phillips et al. 2004; 2017) was used to calculate the percentage contribution and permuted importance of the ten selected bioclimatic variables. MaxEnt analyses were conducted with cloglog output format, ten random replicate analyses with the cross-validation method, maximum training presence threshold, random seed, and fade by clamping subsets; all other options were set as defaults. The performance of ENM was tested by receiver operating characteristic analyses (ROC) (Swets 1979) using AUC (area under the curve) for ten replicate runs to determine the discriminating capacity of the model. The closer the AUC test value is to 1, the better the distinction - i.e., the model is sensitive and descriptive; models with AUC test values between 0.75-1.00 are also considered applicable as they have high predictive power (Swets 1979; 1988). If the AUC value is less than 0.5, the model is not sensitive enough and is considered unsuitable (Phillips & Dudík 2008). Moreover, we calculated the percentage of suitable and unsuitable habitats based on the maximum test sensitivity plus specificity threshold (MSS). In addition, the Jack-knife test (Shcheglovitova & Anderson 2013) option in MaxEnt was used to evaluate the relative importance of each environmental variable in the model, again with ten replicate runs.

Results

Model Perfomance and Key Bioclimatic Variables

AUC scores for all models were above 0.85 (see Table I), indicating good accuracy. We found that under the current climate scenario, 70.3% of the habitat was unsuitable and 29.7% suitable. In contrast, all the remaining scenarios had less suitable habitats than the current one, ranging from 22.8% to 28.0% (Table I).

Table I. AUC values with standard deviation, MSS values, and the percentage of suitable and unsuitable habitats for LGM, present, and two future climate scenarios.

Distribution scenario	**AUC±Sd**	**MSS**	**Suitable Habitat (%)**	**Unsuitable Habitat (%)**
LGM	0.865±0.036	0.4277	22.9	77.1

Current	0.859±0.018	0.2908	29.7	70.3
RCP 4.5	0.874±0.042	0.3007	28.0	72.0
RCP 8.5	0.873±0.023	0.3886	22.8	77.2

Table II shows the ten bioclimatic variables predicting the current potential distribution of *M. macedonicus* across Europe and Asia. Of the bioclimatic variables with a high percentage contribution, BIO12 annual precipitation (41.1%), BIO11 mean temperature of coldest quarter (18.4%), and BIO9 mean temperature of the driest quarter (18.3%) appeared to play significant roles in determining the distribution of *M. macedonicus*. Moreover, bioclimatic variables with the highest permutation importance were BIO11 (35.3%), BIO12 (13.7%), and BIO9 (11.9 %).

Table II

Percentage contribution (*PC*) and permutation importance (*PI*) values for selected bioclimatic variables.

Abbreviation and variables	***PC***	***PI***
BIO1 = Annual mean temperature (°C)	1.8	3.4
BIO2 = Mean diurnal range (mean of monthly (max temp - min temp)) (°C)	0.9	1.5
BIO8 = Mean temperature of the wettest quarter (°C)	8.6	7.5
BIO9 = Mean temperature of the driest quarter (°C)	18.3	11.9
BIO11 = Mean temperature of the coldest quarter (°C)	18.4	35.3
BIO12 = Annual precipitation (mm)	41.1	13.7
BIO13 = Precipitation of the wettest month (mm)	0.8	10.4
BIO14 = Precipitation of the driest month (mm)	4.7	7
BIO15 = Precipitation seasonality (coefficient of variation) (mm)	1.2	3.8
BIO19 = Precipitation of the coldest quarter (mm)	4.3	5.6

According to the Jackknife test (Figure 2), the bioclimatic variable with the highest gain when isolated was BIO19 precipitation of the coldest quarter, and this variable alone provided the most useful information. Moreover, BIO11 mean temperature of the coldest quarter, was the bioclimatic variable whose exclusion produced the largest decrease in gain; this variable contained the most information not incorporated by other variables. These variables suggest that *M. macedonicus* is highly affected by rainfall and temperature during the year's coldest quarter.

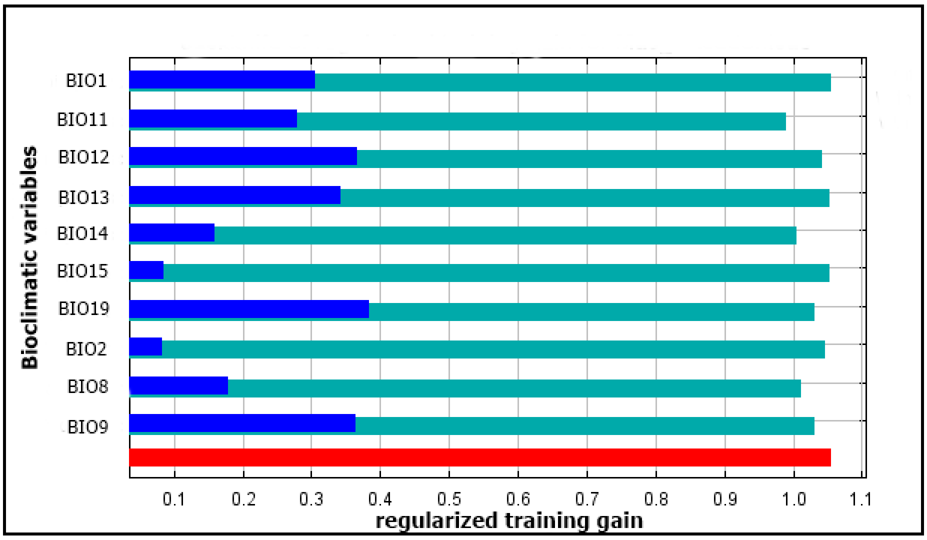

Figure 2. Jackknife test for variable importance in the Macedonian mouse. Blue bars = each predictor variable alone, teal blue bars: how much the total gain is diminished without the given predictor variable, and red bar: all bioclimatic variables.

Current Potential Geographical Distribution of M. macedonicus

The results of ENM revealed that *M. macedonicus* prefers to be present in areas where the annual mean temperature (BIO1) is between 4.63-22.09°C (mean 13.57°C), and annual precipitation (BIO12) between 281-1197 mm (mean 593 mm). Additionally, the Macedonian mouse is found in geographical regions where BIO9 is up to 29.16 °C, BIO11 is up to 14.18 °C, and BIO19 is up to 679 mm °C. According to occurrence records, *M. macedonicus* was recorded at altitudes ranging from -195 m to 1965 m (mean 567 m) above sea level. ENM analyses also revealed that *M. macedonicus* has a potential distributional area between latitudes 30.5° to 44.1°N and longitudes 19.3° to 51.4°E under current climatic conditions (Figure 3). The distribution map provided by the IUCN has *M. macedonicus* distributed between latitudes 31.3° to 43.0˚N and longitudes 19.3° to 49.3°E (Figure 1).

The potential distribution preference of species was inferred by comparing potential ecological niches to the Köppen-Geiger climate classification. Therefore, the geographical range of species can be generalised as mainly Csa (hot-summer), Csb (warm-summer), and partially Dsb (warm-summer humid continental) under the Köppen-Geiger classification, temperate in the coast and inner regions and continental on high plateaus.

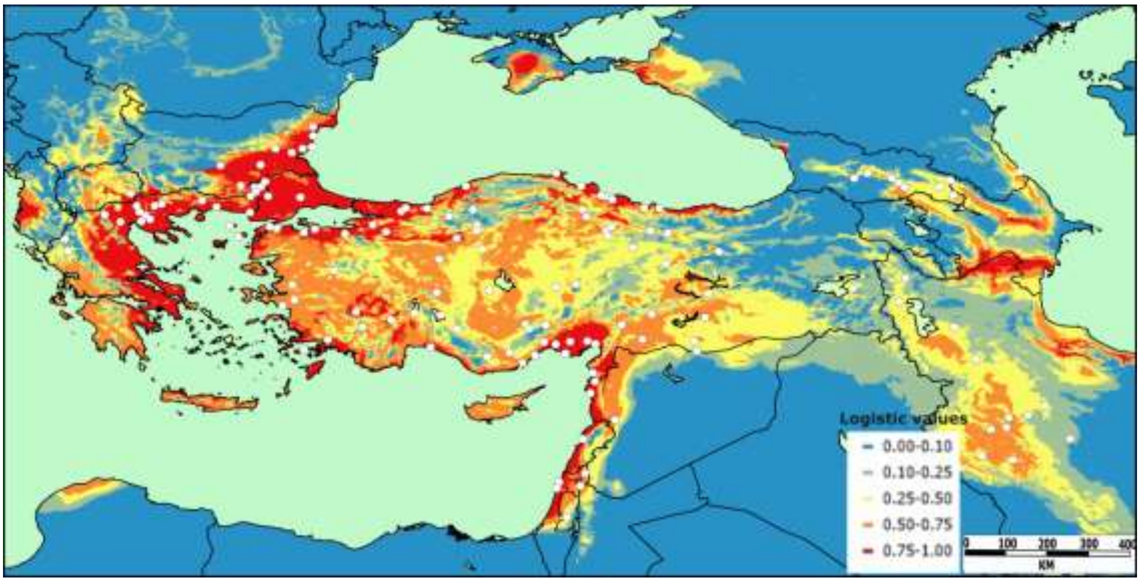

Figure 3. Ecological niche model showing the potential geographical distribution of the Macedonian mouse under current bioclimatic conditions**.** Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability). Open circles indicate occurrence records.

Past Potential Geographical Distribution of M. macedonicus

The predicted potential geographical distribution during the LGM was subtly but significantly different from the current distribution (Figure 4). In the LGM model, 77.1% of the habitat was unsuitable, and 22.9% was suitable, suggesting a smaller area of suitable habitat for the species than today. The predicted distribution in the LGM of the species can be generalised as mainly Csa and Csb climate types. Unlike today, ENM inferred that the Macedonian mouse did not prefer the Dsb climate type. Namely, it preferred lower altitude and temperate areas instead of high plateau and cool areas throughout the LGM. Moreover, Csa and Csb sub-climate zones contained more suitable habitats than today. ENM pointed out two evident corridors that allowed the spread of the species. These were a northern corridor reaching the Caucasus along the Black Sea coast in the north and a southern corridor running through northern Iraq to northwestern Iran. While the south corridor is vague, the north is indistinct in the current period. ENM also showed the niche suitability is more favorable, and the predicted distribution is wider than it is in the current period in the Levant region.

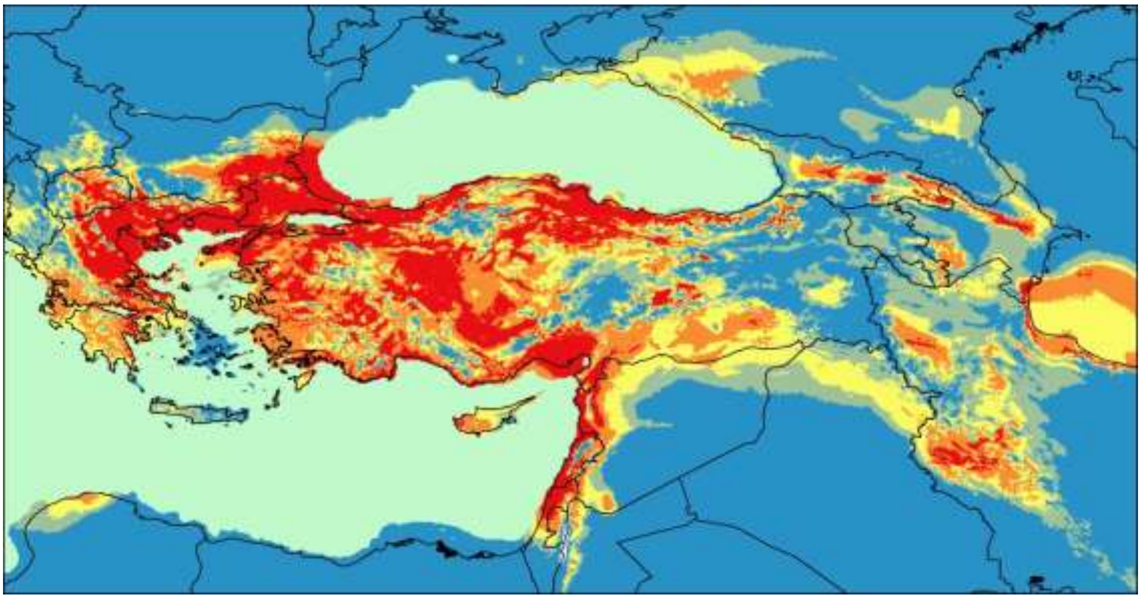

Figure 4. Ecological niche model showing the potential geographical distribution of the Macedonian mouse under LGM bioclimatic conditions. Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability).

Future Potential Geographical Distribution of M. macedonicus

The predicted potential geographical distributions under RCP 4.5 and RCP 8.5 climate change scenarios for 2070 are shown in Figures 5 and 6. Both scenarios closely resemble each other. However, in the future model with RCP 4.5, 72.0% of the habitat was unsuitable and 28.0% suitable, broadly similar to today. In the future model with RCP 8.5, 77.2% of the habitat was unsuitable and 22.8% suitable, significantly lower than today. The results of both models showed that the predicted distributions partially overlapped with the current model compared to LGM model. Nevertheless, the niche suitability was different inner Anatolian Peninsula and along the Aegean Sea and Black Sea coasts. Moreover, the niche suitability had increased in northwest Iran and shifted to more eastern areas including in eastern Georgia and central Azerbaijan. The two corridors detected in the past model have entirely disappeared.

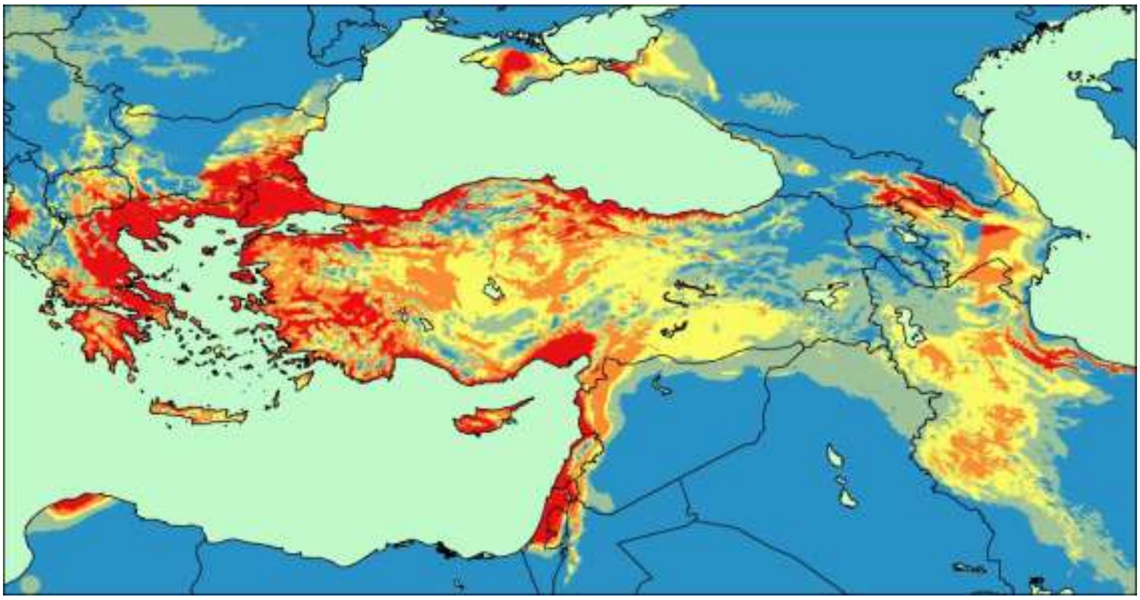

Figure 5: Ecological niche model showing the potential geographical distribution of the Macedonian mouse under future bioclimatic conditions (RCP 4.5). Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability).

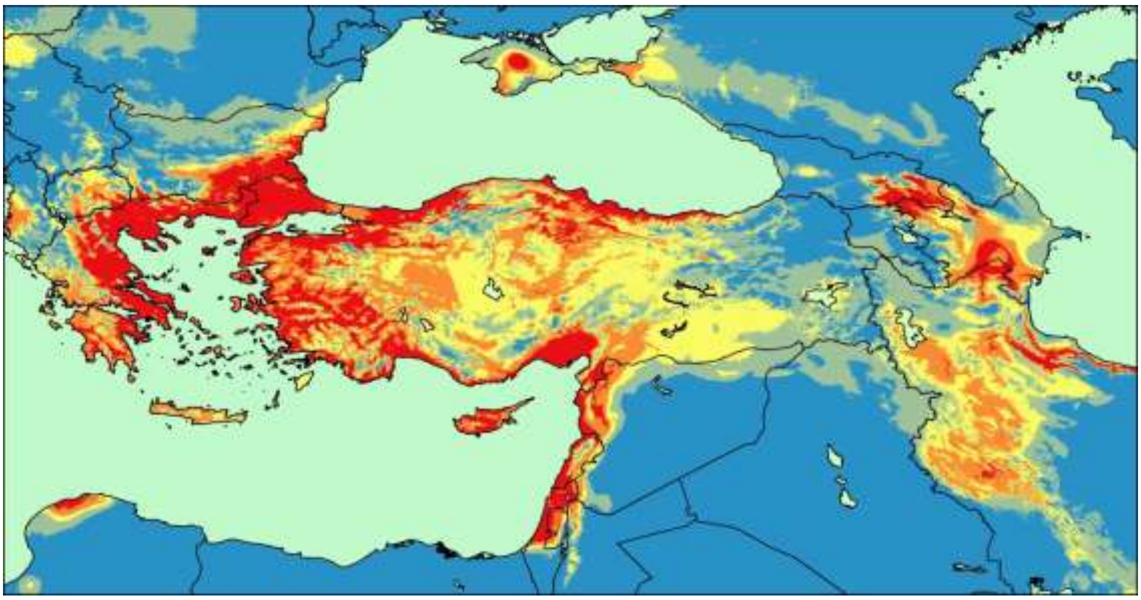

Figure 6: Ecological niche model showing the potential geographical distribution of the Macedonian mouse under future bioclimatic conditions (RCP 8.5). Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability).

Discussion

ENM provides information about the potential geographical distribution of species using several bioclimatic variables, representing a 'species' ecological niche within a set of environmental dimensions (Rotenberry et al. 2006). A species realised niche, or geographical range is often smaller than its potential ones due to historical factors, competition, predation, and the realized environment (i.e., current conditions) across localities (Pulliam 2000; Anderson & Martínez-Meyer 2004). Better knowledge of the nature of organismal niches is critical for both present and future management and conservation, but such studies are lacking for most taxa. This is the first study to employ ENM to explore the requirements and distribution of the Macedonian mouse, making several important contributions to our understanding of this species's ecology and population history.

Our MaxEnt results strongly suggest that precipitation is an important variable shaping the range of this species and that the Macedonian mouse is adapted to biomes with a particular annual precipitation regime characterised by warm, hot, dry summers and cool, wet winters. The mean temperature of the driest and coldest quarters of the year also appeared crucial and are likely related to the physiological requirements of *M. macedonicus*, including its capacity for natural hypothermia (Schubert et al. 2010). Studies conducted on the house mouse (*M. musculus domesticus*), a close relative of the Macedonian mouse, indicate that *M. m. domesticus* exhibits hypothermic responses to overnight fasting (Hudson & Scott 1979) and low ambient temperatures (Tomlinson et al. 2007). Moreover, physiological studies on the house mouse have shown that daily torpor is not restricted to starvation conditions and depends on the environment (Schubert et al. 2010). Our Jackknife test results support the ENM analyses, suggesting that physiological activity may shape the distribution of the species.

The results of ENM based on current bioclimatic variables demonstrate that the Macedonian mouse is a species adapted to relatively mesic habitats in the Mediterranean climate zone, with moderate and fairly constant humidity and warm-hot temperature levels. Studies of nonshivering thermogenesis capacity in the Macedonian house also conclude that it is a mesic species (Haim et al. 1999; Shabtay et al. 2000). *M. macedonicus* often occupy the same habitat as other mesic species, such as *Apodemus flavicollis* (Melchior, 1834*)*, *Apodemus uralensis* (Pallas, 1811), and *Apodemus mystacinus* (Danford & Alston, 1877*)*. Moreover, the Macedonian mouse is also a relatively eurytopic species, coexisting with similar taxa such as *Apodemus sylvaticus* (Linnaeus, 1758) and *Apodemus witherbyi* (Thomas, 1902) (Kryštufek & Vohralik 2009).

Some of our confirmed occurrence data are outside the range boundaries suggested by the IUCN, particularly in northwest Iran, northeast Bulgaria, and the Dagestan region of Russia. On the other hand, there are no occurrence records of *M. macedonicus* in many apparently climatic suitable regions (see Figure 3), including in the west (Albania), north (Crimean peninsula and Russia's Black Sea coast), and south (Cyrenaica region of northern Libya, Peloponnesos peninsula, Crete and Cyprus) of the 'species' distributional area. A combination of demographic history, ecological and dispersal barriers, and competition may explain the absence of the species in these areas. In much of the Balkans and Crimea, *Mus spicilegus* Petényi, 1882 may outcompete *M. macedonicus*, the two species rarely being sympatric in contact zones (Orth et al. 2002). The absence of *M. macedonicus* from Cyrenaica may be due to a failure of the species to disperse to this relatively isolated pocket of suitable habitat. Still, it may also be down to the area occupied by *Mus spretus* Lataste, 1883, another potential competitor. On Cyprus and Crete *Mus cypriacus* (Cucchi et al. 2006) and *Acomys minous* (Bate, 1906) are found, respectively. Again the absence of *M. macedonicus* may result from the 'species' failure to reach these islands and/or the presence of ecologically similar species. It is worth noting that the Macedonian mouse is known from some islands in the Aegean, showing that it is able to cross some marine barriers and establish populations in the absence of close competitors. The remaining two regions (Crimea and Russian Black Sea Coast and Peloponnesos) may have been affected by topographic barriers such as high mountains and water masses or historical factors such as floods, forest fires, and glaciation, all of which would have prevented the spread of *M. macedonicus*.

Our LGM range prediction is compatible with previous studies on molecular and morphological variation in *M. macedonicus* (Hewitt 1996; 1999; Orth et al. 2002; Çolak et al. 2006; Macholán et al. 2007), which suggest that separate glacial refugia were located in the south of the Caucasus and the Black Sea, southern Turkey and the Levant. Populations from the Levant have been considered to belong to a separate subspecies (*Mus macedonicus spretoides*) (Orth et al. 2002), which diverged from *M. macedonicus macedonicus* ca. 300,000 BP (Macholán et al. 2007). Time to a most recent common ancestor for *M. macedonicus macedonicus* populations in Europe, and Asia has been suggested to be in the order of 160,000 years, meaning that population subdivision over multiple glacial cycles has been essential in generating the genetic diversity seen in this mouse today (Macholán et al. 2007). Our bioclimatic model for the LGM provides an important tool for further exploration of the genetic structure of Macedonian mouse populations, suggesting, as it does, other areas where the species is likely to have persisted during glacial episodes. Our ENM results showed that the LGM model significantly differed from the present and future models. Because the sub-climate type in LGM was different from today. Although we showed that the Levant population had a broader distribution in the LGM period, it did not provide enough knowledge to indicate a separate subspecies. However, this foresight may become prominent with more regional analyzes. The two corridors indicated by the LGM map show that the Caucasian and Iranian populations separated from the main population after LGM. Moreover, this separation will be evident in the near future. However, other climate methods and molecular data need to support this prediction. Future climate change scenarios showed significant geographical range differences between the current and future periods, especially in the central Anatolian Peninsula, the Aegean Sea and Black Sea coasts, and northwest Iran. These regions are expected to be drier and experience less precipitation under continued global climate change. However, these analyses also identified several potentially suitable future areas including in eastern Georgia and central Azerbaijan. Such regions were located at lower altitudes than those in western Georgia and northern Azerbaijan, which become unsuitable for *M. macedonicus* under the future IPCC scenarios. Under both scenarios, the range of the Macedonian mouse is likely to retreat in more arid regions such as central Anatolia, the Turkey-Syria border region, and northwest Iran, but it seems likely to expand its distribution range into central Iran and Azerbaijan. Such an observation for this mesic species is consistent with the suggestion that coniferous forests are likely to undergo a contraction in the eastern Mediterranean over the same period (Zeydanlı et al. 2011), and predicted reductions in the potential distributional areas of a variety of taxa in the region in the future (Perktaş et al. 2015; Gür et al. 2017; Malekian & Sadeghi 2019; Örücü 2019; Walas et al. 2019).

In summary, our study has evaluated habitat suitability and the potential geographical distribution of *M. macedonicus* throughout its range in the Balkans, Anatolia, the Levant, Russia, Transcaucasia, and Iran using Maximum Entropy Modelling based on bioclimatic variables and known occurrence records. Models for past (LGM), current, and future climatic scenarios were robust and pointed to the importance of a suite of precipitation and temperature variables in determining the 'species' range. Modelled distribution during the LGM is consistent with the view that the species survived cold periods in multiple glacial refugia and suggests the existence of additional refugial areas to those proposed to date based on genetic studies. Shifts in the 'species' range are predicted under both modelled future climate change scenarios, with population losses and gains suggested across its distribution. Our findings provide a sound framework to explore Macedonian mouse range dynamics in more detail and highlight the relatively limited shifts in the distribution of this species during changing climates – something which is in sharp contrast to the situation with similar taxa further north in Eurasia.

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Declarations

Conflict of interest

The authors declare that they have no conflict of interest

Ethical approval

This article does not contain any studies with human and animal subjects performed by any of the authors

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Figure Legends

Figure 1. Known distribution of *Mus macedonicus.* Black dots represent occurrence records from our dataset, the yellow dotted area indicating the 'species' distribution according to IUCN. Note that some records fall outside this distribution, particularly in Iran.

Figure 2. Jackknife test for variable importance in the Macedonian mouse. Blue bars - each predictor variable alone, teal blue bars - how much the total gain is diminished without the given predictor variable, and red bar - all bioclimatic variables.

Figure 3. Ecological niche model showing the potential geographical distribution of the Macedonian mouse under current bioclimatic conditions**.** Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability). Open circles indicate occurrence records.

Figure 4. Ecological niche model showing the potential geographical distribution of the Macedonian mouse under LGM bioclimatic conditions**.** Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability).

Figure 5: Ecological niche model showing the potential geographical distribution of the Macedonian mouse under future bioclimatic conditions (RCP 4.5). Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability).

Figure 6: Ecological niche model showing the potential geographical distribution of the Macedonian mouse under future bioclimatic conditions (RCP 8.5). Color gradient indicates the logistic probability of species occurrence, increasing from blue (low probability) to red (high probability).

Supplementary Material

Table S1. Occurrence records of Macedonian mouse