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

3

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17

18 **Abstract**

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

30 current, with population losses and gains in different regions. Our results provide a sound framework for
31 future studies on this model species' range dynamics, suggesting that the overall geographical range of *M.*
32 *macedonicus* is relatively stable in the long term.

33

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

36

37 **Introduction**

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

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

55 The Köppen–Geiger climate classification system is a widely used ecological niche modeling (ENM)
56 study. This system is divided into five major groups: Tropical (A), dry (B), temperate (C), continental
57 (D), and polar (E) (Köppen 1884) in which second and third letters further sub-divide the climate group
58 based on seasonal precipitation type and the level of temperature patterns, respectively. Mediterranean

59 climate zone is warm temperate with moderate and relatively constant levels of humidity, and warm
60 summer; represented as C and D in the Köppen-Geiger classification (Peel et al. 2007; Beck et al. 2018),
61 making it suitable for Macedonian mouse. According to the IUCN distribution map, the known
62 distribution range of *Mus macedonicus* have a total of six sub-climate zones in which Csa (hot-summer
63 Mediterranean), Csb (warm-summer Mediterranean), Cfb (warm-summer humid Mediterranean), Dsa
64 (Mediterranean-influenced hot-summer continental), Dsb (Mediterranean-influenced warm-summer
65 continental), Dfb (Mediterranean-influenced warm-summer humid continental).

66 ENM has been widely used to predict the distribution of taxa across given geographical regions, using
67 climatic variables (Peterson et al. 1999; Soberón & Peterson 2005; Soberón 2010; Peterson et al. 2011).
68 This method is based on the fact that if the species or population's geographic location is known, the
69 potential distribution area at unsampled locations in the past, current, or future can be estimated using
70 environmental variables. Maximum Entropy modeling (MaxEnt) (Phillips et al. 2006; 2017) is one of the
71 most widely used approaches in ENM, producing a spatial habitat suitability map and evaluating the
72 significance of individual bioclimatic variables in shaping a 'species' range. Although several studies have
73 examined morphological, karyological, and genetic variation in *M. macedonicus*, as well as its
74 phylogenetic position within the genus (Ivantecheva & Cassaing 1999; Gündüz et al. 2000; Orth et al.
75 2002; Çolak et al. 2006; Macholán et al. 2007; 2008; Rajabi & Azizi 2013; Abi-Said & Karam 2017),
76 very little information, is available about the factors shaping the 'species' range (Auffray et al. 1990; Abi-
77 Said & Karam 2017). This study uses a large, mainly genetically-based occurrence dataset for the
78 Macedonian mouse to explore the importance of bioclimatic variables in determining the 'species' range.
79 We explore the past, current, and future potential geographical distribution of the species, addressing the
80 following questions: 1. What are the key bioclimatic variables affecting the distribution of species today?
81 2. What was the potential distribution of *M. macedonicus* in Europe and Asia during the Last Glacial
82 Maximum? 3. Is the modelled potential distribution during the LGM compatible with multiple refugia,
83 suggested by molecular studies? 4. How will *M. macedonicus* respond to future changes under different
84 climate scenarios?

85 **Materials and Methods**

86 *Species Data Source*

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



105

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

109 ***Environmental Variables***

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

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

124 Dormann et al. 2013; Tanner et al. 2017; Feng et al. 2019) using Pearson correlation coefficients ($r >$
 125 0.90) in the SDM toolbox. A resulting dataset of ten bioclimatic variables was employed for niche
 126 modelling (see Table I).

127 ***Modelling Methods and Statistical Analyses***

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

141 **Results**

142 ***Model Performance and Key Bioclimatic Variables***

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

147

148 Table I. AUC values with standard deviation, MSS values, and the percentage of suitable and unsuitable
 149 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

150

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

157

158 Table II

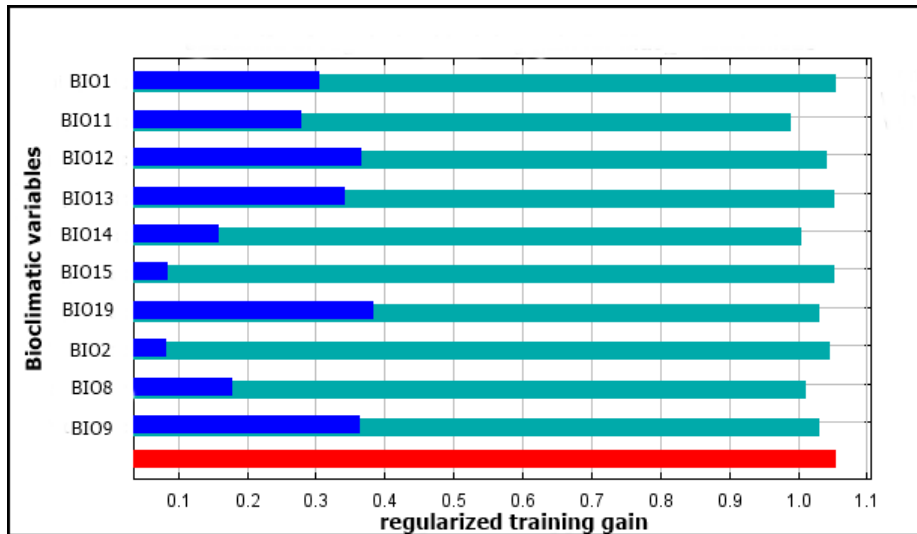
159 Percentage contribution (*PC*) and permutation importance (*PI*) values for selected bioclimatic variables.

Abbreviation and variables	<i>PC</i>	<i>PI</i>
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

160

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

167



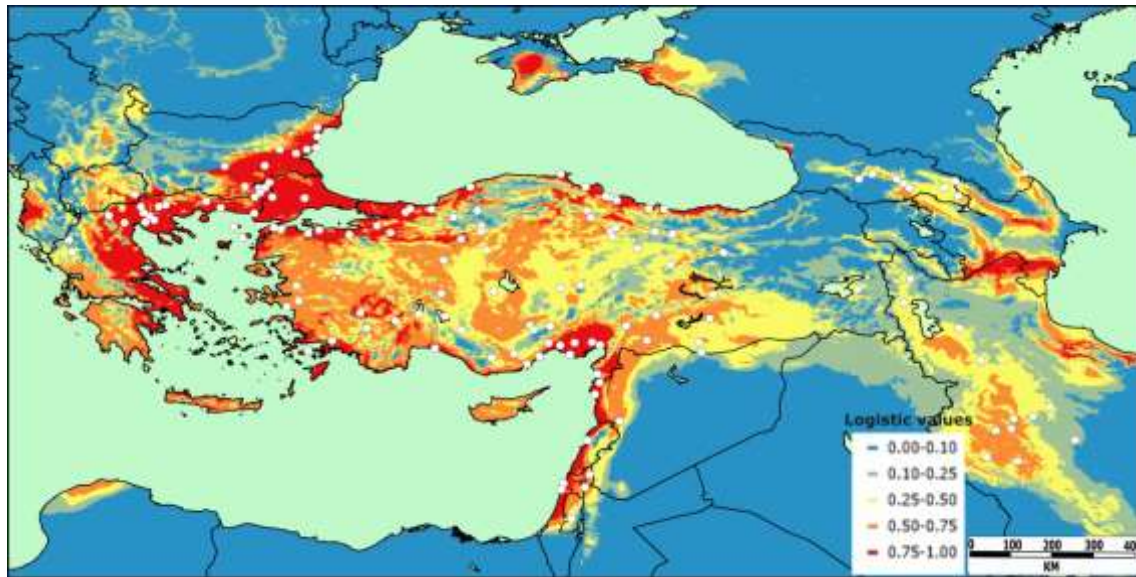
168

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

172 ***Current Potential Geographical Distribution of M. macedonicus***

173 The results of ENM revealed that *M. macedonicus* prefers to be present in areas where the annual mean
 174 temperature (BIO1) is between 4.63-22.09°C (mean 13.57°C), and annual precipitation (BIO12) between
 175 281-1197 mm (mean 593 mm). Additionally, the Macedonian mouse is found in geographical regions
 176 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
 177 occurrence records, *M. macedonicus* was recorded at altitudes ranging from -195 m to 1965 m (mean 567
 178 m) above sea level. ENM analyses also revealed that *M. macedonicus* has a potential distributional area
 179 between latitudes 30.5° to 44.1°N and longitudes 19.3° to 51.4°E under current climatic conditions
 180 (Figure 3). The distribution map provided by the IUCN has *M. macedonicus* distributed between latitudes
 181 31.3° to 43.0°N and longitudes 19.3° to 49.3°E (Figure 1).

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



187

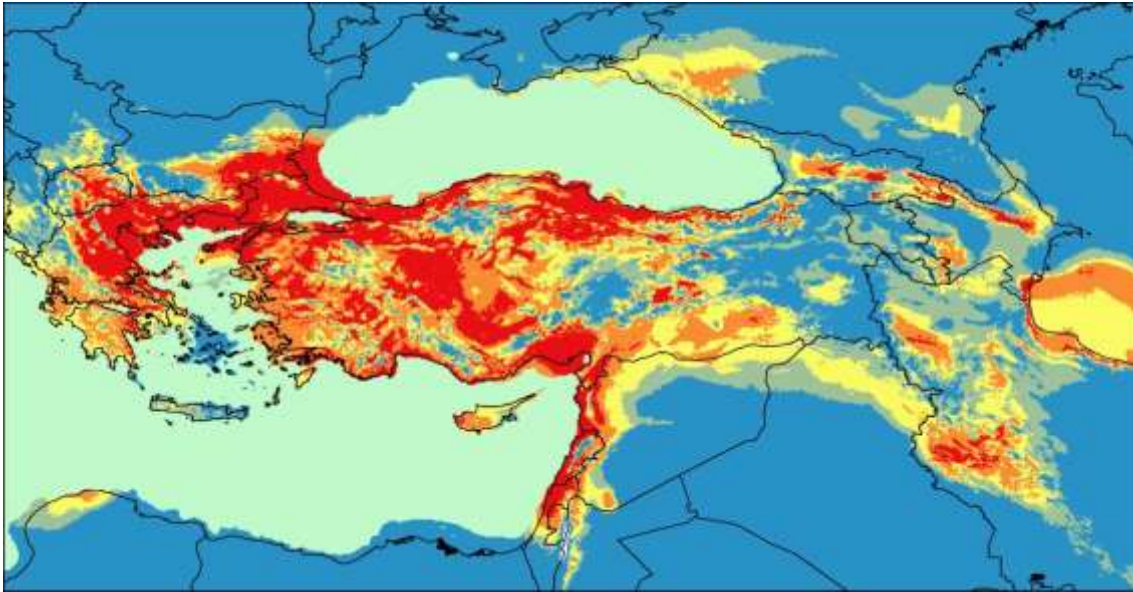
188 Figure 3. Ecological niche model showing the potential geographical distribution of the Macedonian
 189 mouse under current bioclimatic conditions. Color gradient indicates the logistic probability of species
 190 occurrence, increasing from blue (low probability) to red (high probability). Open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

192

193 ***Past Potential Geographical Distribution of *M. macedonicus****

194 The predicted potential geographical distribution during the LGM was subtly but significantly different
 195 from the current distribution (Figure 4). In the LGM model, 77.1% of the habitat was unsuitable, and
 196 22.9% was suitable, suggesting a smaller area of suitable habitat for the species than today. The predicted
 197 distribution in the LGM of the species can be generalised as mainly Csa and Csb climate types. Unlike
 198 today, ENM inferred that the Macedonian mouse did not prefer the Dsb climate type. Namely, it preferred
 199 lower altitude and temperate areas instead of high plateau and cool areas throughout the LGM. Moreover,
 200 Csa and Csb sub-climate zones contained more suitable habitats than today. ENM pointed out two evident
 201 corridors that allowed the spread of the species. These were a northern corridor reaching the Caucasus
 202 along the Black Sea coast in the north and a southern corridor running through northern Iraq to
 203 northwestern Iran. While the south corridor is vague, the north is indistinct in the current period. ENM
 204 also showed the niche suitability is more favorable, and the predicted distribution is wider than it is in the

205 current period in the Levant region.

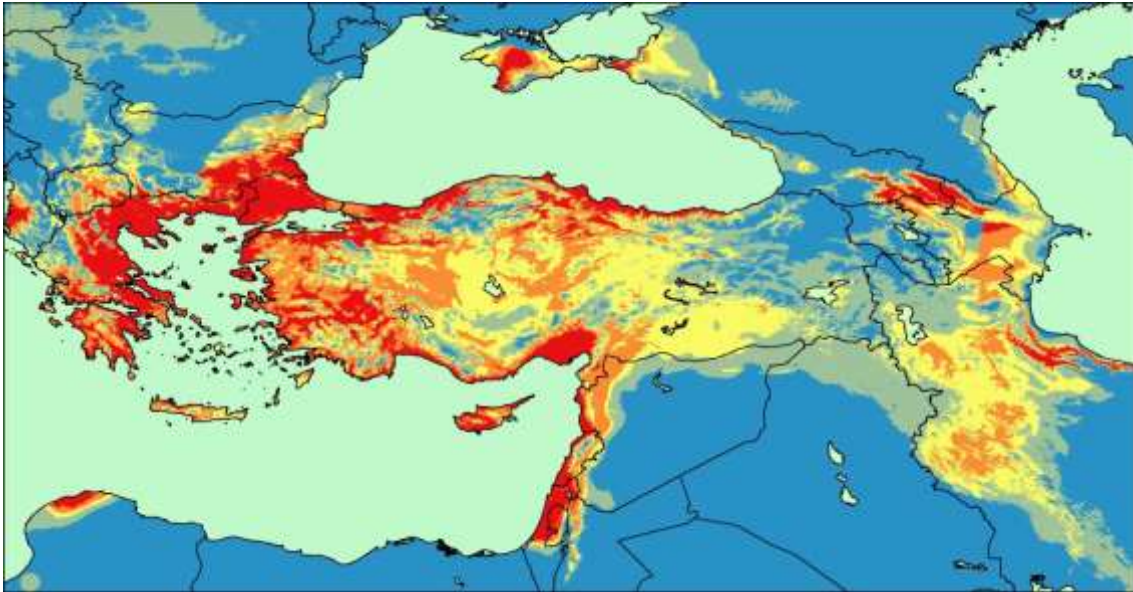


206

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

210 ***Future Potential Geographical Distribution of *M. macedonicus****

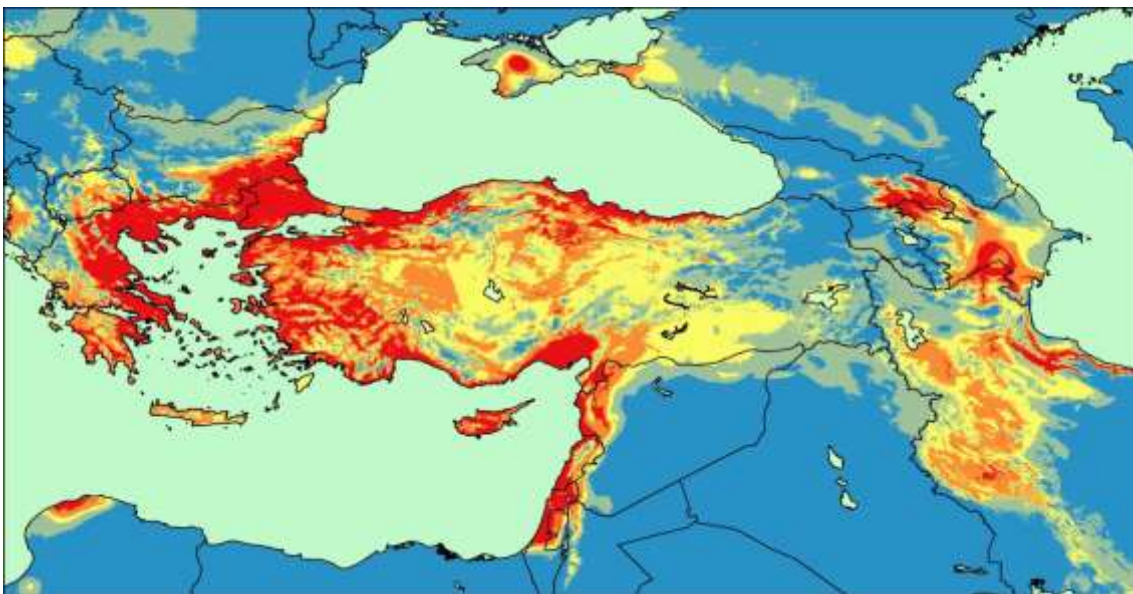
211 The predicted potential geographical distributions under RCP 4.5 and RCP 8.5 climate change scenarios
212 for 2070 are shown in Figures 5 and 6. Both scenarios closely resemble each other. However, in the future
213 model with RCP 4.5, 72.0% of the habitat was unsuitable and 28.0% suitable, broadly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



220

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

224



225

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

229 **Discussion**

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

239 Our MaxEnt results strongly suggest that precipitation is an important variable shaping the range of this
240 species and that the Macedonian mouse is adapted to biomes with a particular annual precipitation regime
241 characterised by warm, hot, dry summers and cool, wet winters. The mean temperature of the driest and
242 coldest quarters of the year also appeared crucial and are likely related to the physiological requirements
243 of *M. macedonicus*, including its capacity for natural hypothermia (Schubert et al. 2010). Studies
244 conducted on the house mouse (*M. musculus domesticus*), a close relative of the Macedonian mouse,
245 indicate that *M. m. domesticus* exhibits hypothermic responses to overnight fasting (Hudson & Scott
246 1979) and low ambient temperatures (Tomlinson et al. 2007). Moreover, physiological studies on the
247 house mouse have shown that daily torpor is not restricted to starvation conditions and depends on the
248 environment (Schubert et al. 2010). Our Jackknife test results support the ENM analyses, suggesting that
249 physiological activity may shape the distribution of the species.

250 The results of ENM based on current bioclimatic variables demonstrate that the Macedonian mouse is a
251 species adapted to relatively mesic habitats in the Mediterranean climate zone, with moderate and fairly
252 constant humidity and warm-hot temperature levels. Studies of nonshivering thermogenesis capacity in
253 the Macedonian house also conclude that it is a mesic species (Haim et al. 1999; Shabtay et al. 2000). *M.*
254 *macedonicus* often occupy the same habitat as other mesic species, such as *Apodemus flavicollis*
255 (Melchior, 1834), *Apodemus uralensis* (Pallas, 1811), and *Apodemus mystacinus* (Danford & Alston,
256 1877). Moreover, the Macedonian mouse is also a relatively eurytopic species, coexisting with similar
257 taxa such as *Apodemus sylvaticus* (Linnaeus, 1758) and *Apodemus witherbyi* (Thomas, 1902) (Kryštufek
258 & Vohralik 2009).

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

278 Our LGM range prediction is compatible with previous studies on molecular and morphological variation
279 in *M. macedonicus* (Hewitt 1996; 1999; Orth et al. 2002; Çolak et al. 2006; Macholán et al. 2007),
280 which suggest that separate glacial refugia were located in the south of the Caucasus and the Black Sea,
281 southern Turkey and the Levant. Populations from the Levant have been considered to belong to a
282 separate subspecies (*Mus macedonicus spretoides*) (Orth et al. 2002), which diverged from *M.*
283 *macedonicus macedonicus* ca. 300,000 BP (Macholán et al. 2007). Time to a most recent common
284 ancestor for *M. macedonicus macedonicus* populations in Europe, and Asia has been suggested to be in
285 the order of 160,000 years, meaning that population subdivision over multiple glacial cycles has been
286 essential in generating the genetic diversity seen in this mouse today (Macholán et al. 2007). Our
287 bioclimatic model for the LGM provides an important tool for further exploration of the genetic structure

288 of Macedonian mouse populations, suggesting, as it does, other areas where the species is likely to have
289 persisted during glacial episodes. Our ENM results showed that the LGM model significantly differed
290 from the present and future models. Because the sub-climate type in LGM was different from today.
291 Although we showed that the Levant population had a broader distribution in the LGM period, it did not
292 provide enough knowledge to indicate a separate subspecies. However, this foresight may become
293 prominent with more regional analyzes. The two corridors indicated by the LGM map show that the
294 Caucasian and Iranian populations separated from the main population after LGM. Moreover, this
295 separation will be evident in the near future. However, other climate methods and molecular data need to
296 support this prediction. Future climate change scenarios showed significant geographical range
297 differences between the current and future periods, especially in the central Anatolian Peninsula, the
298 Aegean Sea and Black Sea coasts, and northwest Iran. These regions are expected to be drier and
299 experience less precipitation under continued global climate change. However, these analyses also
300 identified several potentially suitable future areas including in eastern Georgia and central Azerbaijan.
301 Such regions were located at lower altitudes than those in western Georgia and northern Azerbaijan,
302 which become unsuitable for *M. macedonicus* under the future IPCC scenarios. Under both scenarios, the
303 range of the Macedonian mouse is likely to retreat in more arid regions such as central Anatolia, the
304 Turkey-Syria border region, and northwest Iran, but it seems likely to expand its distribution range into
305 central Iran and Azerbaijan. Such an observation for this mesic species is consistent with the suggestion
306 that coniferous forests are likely to undergo a contraction in the eastern Mediterranean over the same
307 period (Zeydanlı et al. 2011), and predicted reductions in the potential distributional areas of a variety of
308 taxa in the region in the future (Perktaş et al. 2015; Gür et al. 2017; Malekian & Sadeghi 2019; Öricü
309 2019; Walas et al. 2019).

310 In summary, our study has evaluated habitat suitability and the potential geographical distribution of *M.*
311 *macedonicus* throughout its range in the Balkans, Anatolia, the Levant, Russia, Transcaucasia, and Iran
312 using Maximum Entropy Modelling based on bioclimatic variables and known occurrence records.
313 Models for past (LGM), current, and future climatic scenarios were robust and pointed to the importance
314 of a suite of precipitation and temperature variables in determining the 'species' range. Modelled
315 distribution during the LGM is consistent with the view that the species survived cold periods in multiple
316 glacial refugia and suggests the existence of additional refugial areas to those proposed to date based on

317 genetic studies. Shifts in the 'species' range are predicted under both modelled future climate change
318 scenarios, with population losses and gains suggested across its distribution. Our findings provide a sound
319 framework to explore Macedonian mouse range dynamics in more detail and highlight the relatively
320 limited shifts in the distribution of this species during changing climates – something which is in sharp
321 contrast to the situation with similar taxa further north in Eurasia.

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325 **Declarations**

326 **Conflict of interest**

327 The authors declare that they have no conflict of interest

328 **Ethical approval**

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

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465

466 **Figure Legends**

467

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

471

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

475

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

480

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

484

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

488

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

492

493 **Supplementary Material**

494 Table S1. Occurrence records of Macedonian mouse