



Concise title: Incipient road to extinction of a keystone herbivore in south-eastern Europe: Harting's vole (*Microtus hartingi*) under climate change

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Abstract

Climate forcing, which is blamed for the decennial decline in the dynamics of vole populations in Central and Northern Europe, may have similar effects in southern (Mediterranean) Europe, even more so since the region is especially vulnerable to global change. In the absence of population monitoring, we investigated the temporal development and geospatial pattern of the habitat of Harting's vole (*Microtus hartingi*) in southeast Europe (SEE) by relying on data regarding its presence, the most recent freely available geospatial datasets and state-of-the-art presence-only Species Distribution Modelling (SDM) techniques. Results indicate that (1) the potential habitat of Harting's vole was perhaps stable over the last 6000 years - modelling predictions are in conjunction with scarce fossil evidence, which points to repeated colonisations from Asia Minor punctuated by extinctions in SEE; (2) fragmentation of the potential habitat in SEE, which may have already begun in the Last Glacial Maximum, and will most likely continue in the near future; and (3) Harting's vole could disappear by the end of the century if more pessimistic climate change scenarios become reality. While climate change is suppressing the population dynamics of the keystone grass-eating voles from temperate and boreal ecosystems, it is about to annihilate their Mediterranean counterpart. This will result in a far more severe impact on community restructuring in the Mediterranean ecosystems than elsewhere. Long-term population monitoring is desperately needed in SEE to hone the ability to more accurately predict the impacts of climate change.

1 Introduction

Climate significantly influences the geographical distribution of species worldwide (Lomolino et al. 2009), therefore climate change is anticipated to have a profound impact at the species level. This is evident in changing body size and physiological parameters (Gardner et al. 2011), shifted phenologies (Richardson et al. 2013) and distributional ranges (Martinez-Meyer 2005; Scheffers et al. 2016; Dyderski et al. 2017), adjusted population abundances and dynamics (Cornulier et al. 2013) and accelerated extinction risks (Urban 2015). Recently, concerns have been raised regarding the dampening of the population cycles of Arvicolinae rodents across

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temperate and boreal Europe, with increasing intervals of low-amplitude vole populations. Grass-eating arvicolines (voles and lemmings) are keystone herbivores in agricultural and forest ecosystems; hence, their alternating population dynamics may have a cascading impact on trophic webs and the functioning of the ecosystem. Climate forcing is the most likely candidate to explain decennial trends in the dynamics of vole populations (Cornulier et al. 2013).

The pattern of cycle collapse in voles was retrieved via long-term population monitoring of small terrestrial mammals across western, central, and northern Europe (Cornulier et al. 2013). No comparable data are available from southern (Mediterranean) Europe although this region emerged as especially vulnerable to global change in climate change projection simulations (Giorgi and Lionello 2008). One may, therefore, anticipate the process, which is already unfolding in temperate and boreal Europe, also in the Mediterranean region, where in the absence of population monitoring, remains unnoticed. The presumption that a collapse of population cycles in this region is even more likely since the Mediterranean ecosystems put heavy pressure on grass-eating arvicolines (Kryštufek and Griffiths 1999) and not a single keystone vole from the study by Cornulier et al. (2013) occupies the Mediterranean region proper. Arid habitats of the eastern Mediterranean, however, are occupied by social voles (subgenus *Sumeriomys*) which are known for occasional population outbreaks (Pardiñas et al. 2017). One of these species, Harting's vole, attracted our attention for several reasons. It is the only social vole present in the European Mediterranean. Although the species occupies structurally simple habitats, its European range is highly fragmented (Kryštufek 1999). In addition, this vole is prone to high population oscillations, which have been noted as far back as by Aristotle (384–322 BC) in Thessaly, Greece (Harting 1893). Although the population biology of Harting's vole raised brief concerns during such excessively high population densities (e.g., Harting 1893; Ondrias 1965), this has never led to the establishment of a long-term monitoring of population oscillation. In the absence of relevant population data, we explored temporal dynamics in habitat suitability for Harting's vole within its European distribution. We postulate that a highly fragmented range makes this rodent an appropriate model for investigations of biogeographic dynamics under different climatic scenarios. We therefore employed species distribution models (SDMs) to predict the future of a keystone herbivore in an arid environment which is especially vulnerable to climate change (Giorgi and Lionello 2008). Approaches designed to habitat modelling have significant limitations and future projections cannot be subject to verification (Kerr and Dobrowski 2013). We therefore contrasted SDMs for three past time periods with the fossil evidence which is usually ample in arvicolines (Kowalski 2001). Concordance between these two proxies, or lack thereof, has been extrapolated to SDM projections obtained under different climate change scenarios.

2 Materials and methods

2.1 Model species

Harting's vole *Microtus hartingi* (Barrett-Hamilton, 1903) is a small (body mass 30–78 g) arvicoline rodent (Arvicolinae) occupying central and western Anatolia and the Balkans. In the past, this vole was amalgamated with Guenther's vole *Microtus guentheri* from eastern Anatolia and the eastern Mediterranean coast. Both species belong to a group of social voles (subgenus *Sumeriomys*) which is still in the ongoing process of speciation and abounds with cryptic species (Kryštufek et al. 2009). Harting's vole occupies well-drained upland habitats

and is absent from shallow skeletal soils which are too shallow for digging. Tunnels descend 20–45 cm below the surface to escape excessive heat during summer. The presence of the vole is further associated with graminoid vegetation although the grassland sites do not have to be extensive or contiguous (Ondrias 1965; our own unpublished observations).

2.2 Study area

The study area encompassed the Balkan Peninsula, also termed southeast Europe (hereafter SEE). This is an inverted triangle of land extending from central Europe to the eastern Mediterranean, being intermittently connected in the past to Asia Minor via the Bosphorus-Dardanelles straits and the Aegean island chain. Almost 70% of SEE is a high relief which imparts strong climatic contrasts and abrupt transitions in vegetation types. Due to the complexity of environments, its location in an important zone of faunal and floral transitions, and the refugial character over geologically recent Quaternary biogeographical dynamics, the SEE emerges on the continental scale as the top hot spot in biodiversity (Griffiths et al. 2004).

2.3 Harting's vole occurrence data

Occurrence data for Harting's vole were obtained from published sources, the collection of the Slovenian Museum of Natural History (Ljubljana), and our unpublished field notes. To eliminate taxonomic bias, we carefully assessed the reliability of the published evidence and re-identified museum vouchers. The presence of Harting's vole was documented in 102 localities in European Turkey, Greece, Bulgaria, the Former Yugoslav Republic of Macedonia (FYRM), and southernmost Serbia (Fig. 1). Approximately one third (= 29%) of the records (all from Greece) were based on owl pellet material. Furthermore, nearly all samplings were snapshots with specimens being recorded only once per site. The majority (= 68%) of localities have been sampled since 2000, and a mere 19% of the information predates 1980. Prior to analysis, the occurrence data were spatially filtered (Hijmans 2012; Boria et al. 2014) according to climate heterogeneity at a distance of 30 km in order to avoid spatial dependency by using the Spatially Rarefy Occurrence Data Tool within SDMtoolbox for ArcGIS (Brown 2014). Thus, 82 out of 102 localities were used in further analyses.

2.4 Ecogeographical (EG) variables

In order to identify and model the ecological niche of Harting's vole in the study area, ten EG variables (30 arc sec horizontal resolution, WGS84 coordinate system) were tested: (1, 2 and 3) all WORLDCLIM bioclimatic variables (z-standardised and converted to three PCA components explaining more than 85% of the variability in climate properties [Supplementary material 2]), (4) altitude, (5) longtime June NDVI mean [1999–2012], (6) longtime December NDVI mean [1999–2012], (7) land cover [year 2010], (8) distance to the nearest trees, (9) distance to a body of water and (10) distance to an urban area.

The bioclimatic variables (current, past and future) and altitude were gathered from the freely available WORLDCLIM database (www.worldclim.org/current). Land cover and longtime smoothed NDVI values corresponding to the mean NDVI over the period from 1999–2012 for summer (June 18) and winter (December 24) were purchased from the Land Cover CCI Climate Research Data Package (CRDP) which is a product developed by the Climate Change Institute of the European Space Agency (ESA CCI) (<http://maps.elie.ucl.ac>).

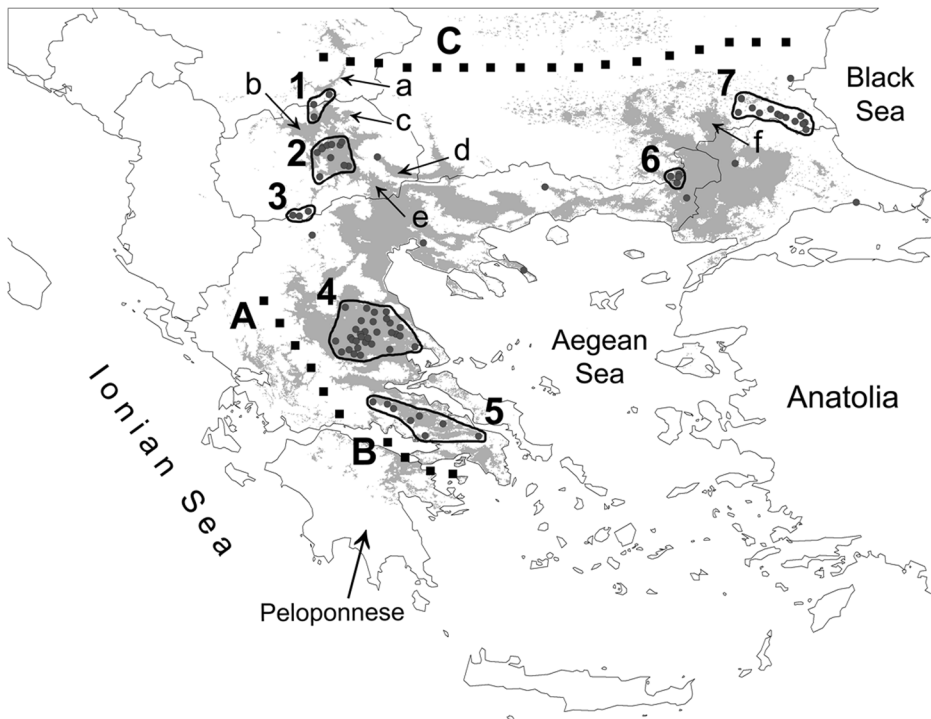


Fig. 1 Records of Harting's vole (dots) in SEE superimposed on the modelled suitable habitats (shaded grey). Dashed lines in bold show putative biogeographical barriers to the dispersal of Harting's vole. A – mountain ridge of the Albanian Alps and the Pindus Mts.; B – Isthmus of Corinth; C – mountain ridge of the Stara Planina. Main population fragments are bordered with solid lines. Arrows indicate potentially suitable habitats where there is most likely no presence of Harting's vole

[be/CCI/viewer/index.php](#)) (Supplementary Material 1). Distance variables (distance to urban area, distance to bodies of water and distance to the nearest trees), based on the ESA CCI land cover data, were calculated by applying the Euclidean distance algorithm within Spatial analyst tools in ArcGIS (ESRI 2010). Relationships between continuous environmental variables were tested using Pearson's correlation coefficients to determine correlated variables that could not be analysed within the same model ($r > 0.50$) (Thorne et al. 2012). The Chi-square statistics as well as Cramer's correlation coefficient were calculated to test and measure the strength of the relationship between the categorical land cover variable and other environmental variables using R statistical software (Development Core Team R 2008) (Supplementary Material 3). Accordingly, nine (9) EG variables were selected for final SDM development (the longtime June NDVI mean was excluded).

2.5 The time frame and magnitude of climate change

In order to evaluate the spatiotemporal range dynamics of Harting's vole based on bioclimatic properties captured in EG variables 1, 2 and 3 (PCA components), the following time windows and global climate models were taken into consideration: last interglacial (LIG) (Otto-Bliesner et al. 2006), last glacial maximum (LGM) (climate model CCSM4), mid-Holocene (MIDHO) (climate models CCSM4 and HadGEM2-ES), current conditions (Worldclim version 1), 2070

(climate models CCSM4 and HadGEM2-ES) with three selected scenarios (RCP2.6, RCP4.5 and RCP8.5), which assume an anthropogenic radiative forcing of about 2.6, 4.5 or 8.5 W/m², respectively, by the end of the twenty-first century relative to preindustrial conditions. The Community System Model (CCSM) and the Hadley Global Environmental model 2 – Earth System (HadGEM2-ES) were compared to identify possible variations and uncertainties in predicted habitat suitability (Supplementary Material 1).

Moreover, to illustrate the magnitude of change in climatic properties between the considered time windows (LIG to LGM, LGM to MIDHO, MIDHO to CURRENT and CURRENT to 2070) and to excuse the immense importance of climatic variables in modelling the potential distribution of Harting's vole through time and space in SEE; the Change Vector Analysis (CVA) was performed using the Terrset software package (Eastman 2016). CVA is frequently used for pairwise comparisons of multi-dimensional images with several spectral bands (Johnson and Kasischke 1998; Lilles et al. 2004). Here, the first two bioclimatic components (bio_pca1 and bio_pca2) in each time window were used as input bands. Difference images were created for each of the selected bands. These were then squared and then added together. The square root of the result represented the magnitude of the change vector where the units remained the same as in the input data. Thus, eleven (11) change magnitude images were produced showing geospatial information about the shifts in climatic conditions between the studied time windows (Fig. 3).

2.6 Ecological niche modelling

Comparative analyses were used to investigate the efficacy of various methods for modelling species distribution (Hernandez et al. 2006; Tsoar et al. 2007), showing that some modelling methods are more effective than others, but none has proven to be universal in all situations (Hernandez et al. 2008). In this study, Maximum Entropy modelling (Maxent) within the SDMtoolbox add-on for ArcGIS was applied (Brown 2014); it is a presence-only modelling technique that has frequently been used in ecological studies (Phillips et al. 2006; Phillips and Dudik 2008), and has been found to perform well in comparison to established modeling techniques (Elith et al. 2006) even on small samples (Hernandez et al. 2006). However, the SDMtoolbox approach for SDM development is known among GIS experts as one of the best by considering presence-only datasets.

After spatially rarefying our occurrence data, the background bias files were prepared with the Sample by the buffered MCP (minimum-convex polygon) tool in order to overcome the spatial bias problem of occurrence data (Barbet-Massin et al. 2012). To calibrate model parameters, we performed the geographically structured k-fold cross-validation test (spatial jackknifing; $k=3$) which evaluates the performance of spatially segregated independent localities. For further Maxent model optimisation, the Independent tests of model feature classes and regularisation parameters tool (RM = 0.5 to 5) (Boria et al. 2014; Radosavljevic and Anderson 2014), as well as the Automatic model selection tool were used. The latter chooses the best model by evaluating each model's: (1) omission rates (OR), (2) area under the ROC curve (AUC) value and (3) model feature class complexity. These three parameters are standard model quality measures in almost all SDMs. After the best model selection, we ran the final model with the SDMtoolbox using the occurrence points and the nine (9) selected EG variables. In order to obtain the spatiotemporal dynamics of the potential habitat of Harting's vole in SEE, past and future estimations were constructed by changing the EG variables describing climate properties (bioclimatic principal components 1, 2 and 3) for the

corresponding time periods. Finally, all binary models were produced by applying the equal training sensitivity and specificity logistic threshold value which has already been found to perform better than other commonly used thresholds (Liu et al. 2005; Thorne et al. 2012). Additionally, over-prediction correction for all binary outputs was carried out by applying the tool Clip models by buffered MCPs with SDMtoolbox. In order to evaluate the spatio-temporal distribution change of Harting's vole owing to climate change, distribution change maps were produced showing range expansion, no occupancy (absence in both), no change (presence in both) and range contraction (Fig. 3)

2.7 Potential habitat fragmentation of Harting's vole

As previously mentioned, the soft prediction maps produced (Maxent probability) for the potential habitat of Harting's vole for each time window were categorised using the equal training sensitivity and specificity logistic threshold value, thus identifying suitable and unsuitable habitat areas. Additionally, the Euclidean distance between these suitable areas was calculated for recent, past and future scenario time windows, using ArcGIS Spatial analyst tools (ESRI 2010) in order to evaluate the potential habitat structural connectivity (Chardon et al. 2003; Mühlner et al. 2010) and fragmentation (Tischendorf and Fahring 2000; Mühlner et al. 2010) of Harting's vole. From this perspective, the edge density parameter was also obtained to quantify the fragmentation process (McGarigal et al. 2002) of the potential habitat of Harting's vole by using the Patch Grid tool for ArcGIS (Rempel et al. 2012) (Fig. 4b).

3 Results

3.1 Climate change as a proxy for the potential distribution of Harting's vole

The mean AUC value for the best Maxent model in current environmental conditions was 0.808, which was considered "excellent discrimination" (Fig. 2a). The Jackknife test of variable importance showed that the strongest predictors for the potential habitat of Harting's vole were bioclimatic PCA components 2 and 1 (bio_pca2 and bio_pca1), followed

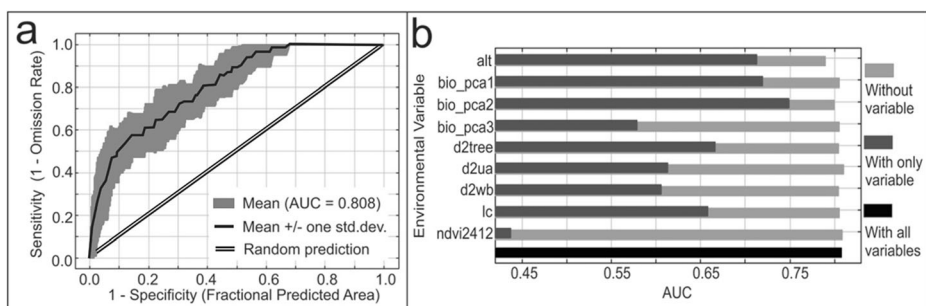


Fig. 2 Receiver Operating Characteristic (ROC) curve and the Area Under the Curve (AUC) values for training and test data (a). Results of jackknife tests of variable importance for training samples (b). Variable acronyms: alt – altitude; bio_pca1 – PCA component 1; bio_pca2 – PCA component 2; bio_pca3 – PCA component 3; d2tree – distance to the nearest trees; d2ua – distance to urban area; d2wb – distance to water bodies; lc – land cover; ndvi2412 – vegetation density in winter

by altitude (alt), distance to the nearest trees (d2tree), and land cover (lc). Vegetation density in winter (NDVI2412) seems to have a weak influence on the potential distribution of Harting’s vole (Fig. 2b). Climatic drivers play a key role in determining the geospatial extent of this species. From that perspective, past and future climate conditions can serve as a strong proxy for estimating the spatiotemporal dynamics of the potential habitat of Harting’s vole in SEE. Fig. 3a shows the magnitude of change in climatic conditions, captured in the bioclimatic components 1 and 2, among the considered time windows. Climate change was very intensive from LIG to LGM. Clear differences in change magnitude between the CCSM4 and HadGEM2-ES global climate models were evident in the LGM to MIDHO epoch. The southern part of the study area could have been more exposed to climate change during that period. Both models differ in the following time window as well. The magnitude of change in climate conditions from MIDHO to CURRENT times was less intensive in both models compared to previous periods. For the recent time window, Maxent retrieved suitable habitats scattered across the entire southern SEE. Sites where Harting’s vole was actually found were more restricted than suggested by predictive modelling. We tentatively identified seven fragments which were connected by habitats suitable for the vole but without evidence of its presence. In at least several such vacant regions, we failed to confirm the presence of the species despite repeated sampling over different years (as indicated by the arrows Fig. 1). Vacant habitats in SEE were obvious also along the periphery, i.e., in the west along the Ionian Sea, in the northeast in north Bulgaria and adjacent Serbia, and in the south in the Peloponnese (Fig. 1).

Future climate conditions will not be optimal for Harting’s vole. Significant variability in climate change magnitude, at current locations, is expected. In some areas, predominantly in the north-eastern part of SEE, the climate could remain stable whereas other currently occupied areas (in the southern part) will be faced with intensive climate change issues (Fig. 3b). If scenarios RCP4.5 or RCP8.5 are realised by the end of the century, climate conditions could be similarly or even more unsuitable for Harting’s vole in SEE, such as those during the LIG period.

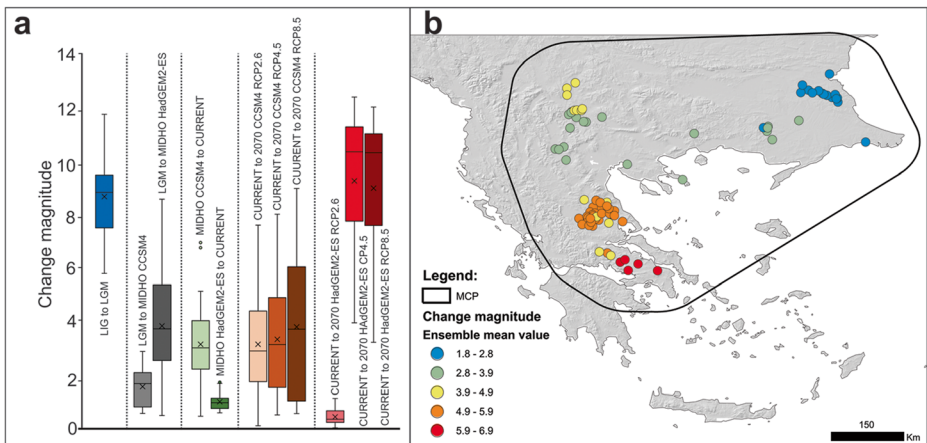


Fig. 3 Magnitude of climate change captured in the first two bioclimatic PCA components between considered time windows in current localities of Harting’s vole (a) and the geospatial pattern of the ensemble mean value of the change magnitude variable (b)

3.2 Spatiotemporal dynamics of the potential habitat of Harting's vole

The potential suitable habitat area shifted significantly over the observed time windows (Fig. 4). Climate conditions in the LIG time window could have restricted suitable areas for this small mammal in SEE (Figs. 4 and 5a). The availability of suitable areas that could be occupied increased from the LIG throughout the LGM and MIDHO to recent times and was perhaps stable over the last 6000 years (Fig. 5a). However, the distribution change maps (Fig. 4) and the range centroid movement indicate some northern displacement of potentially suitable habitat areas from the LGM to MIDHO and then a turn back to more southern localities in recent times according to both the climate models considered (CCSM4 and HadGEM2-ES). The distances between the identified potential habitats of Harting's vole in the MIDHO period (Fig. 5b), were similar to the recent situation with the given environmental conditions and the MIDHO potential habitat could only have been 175 km² smaller than today (HadGEM2-ES) or, in contrast, larger by 711 km², considering the CCSM4 model (Fig. 5a). The edge density parameter, which can provide an overall snapshot of habitat fragmentation on a regional scale shows that the habitat fragmentation process of Harting's vole could have started already in the LGM (Fig. 5b). Five out of six future projections indicate that suitable habitat for the Harting's vole could shrink or even completely disappear by the end of the century (Fig. 5a). Projections using CCSM4 show a more optimistic future development of potentially suitable areas in SEE compared to that using HadGEM2-ES (Fig. 4a). Surprisingly, the potential habitat centroid shift differs significantly between models; with CCSM4 there is an inland spatial shift of potential habitats, whereas with HadGEM2-ES there is a more southern or eastern dispersion (Fig. 3). Under RCP 4.5 or RCP 8.5, the potential habitat of Harting's vole in SEE is projected to become more fragmented or could even disappear (Fig. 5b).

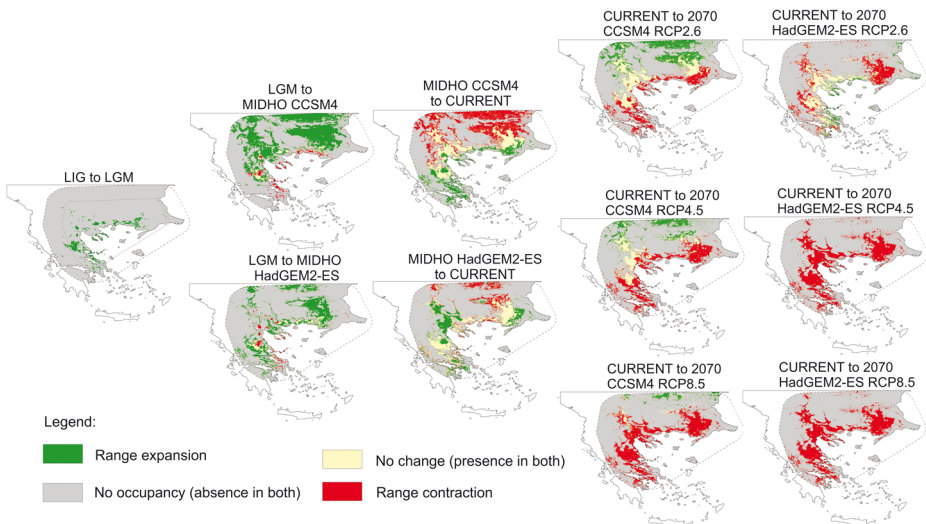


Fig. 4 Changes in the potential habitat area of Harting's vole among the considered periods by applying equal training sensitivity and specificity logistic threshold. The 2070 estimates depend on the greenhouse gas concentration pathway (RCP) scenarios and global climate models CCSM4 and HadGEM2-ES. Green indicates – range expansion, Red indicates – range contraction, Yellow indicates – no change (presence in both), Grey indicates – no occupancy (absence in both)

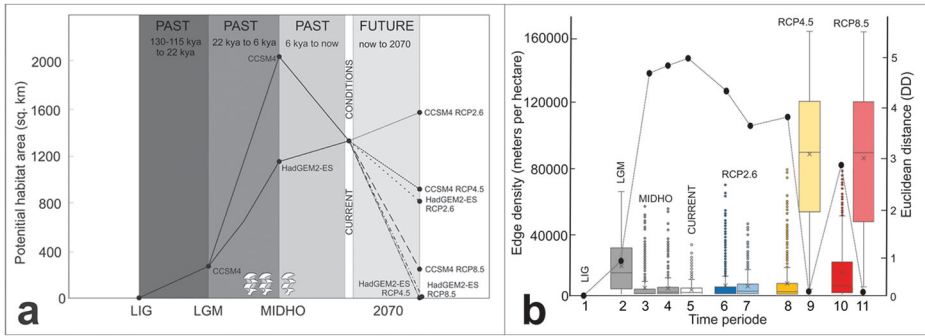


Fig. 5 Superficial development of potential habitat over time of Harting’s vole (a). Euclidean distance (in decimal degree) frequency distributions between identified the potential habitat of Harting’s vole area per time period and the edge density (metres per hectare) trend line (b). Acronyms: 1- Last interglacial; 2 – Last glacial maximum; 3 – Mid Holocene (CCSM4), 4 – Mid Holocene (HadGEM2-ES); 5 – Current conditions; 6–2070 CCSM4 RCP2.6; 7–2070 HadGEM2-ES RCP2.6; 8–2070 CCSM4 RCP4.5; 9–2070 HadGEM2-ES RCP4.5; 10–2070 CCSM4 RCP8.5; 11–2070 HadGEM2-ES RCP8.5). Symbols (2nd upper molar in inset a) summarise fossil evidence on the presence of Harting’s vole in SEE

4 Discussion

Our study showed that bioclimatic conditions are a strong determinant influencing the geospatial pattern of a keystone herbivore in SEE, and a good proxy which enables the estimation of the spatiotemporal range dynamics of Harting’s vole throughout past and future climate conditions. The results retrieved (1) the highly fragmented nature of this rodent’s range, (2) the vacant fragments of its potential habitat scattered throughout the region, and (3) the profound temporal dynamics in habitat suitability. We subsequently addressed potential gaps and omissions in our approach, which could bias the perception of temporal range dynamics in model species. Next, we explored a congruence between models for the past habitat suitability with hard evidence obtained through paleontological and molecular research. Finally, we focused on prospects for the species’ further existence considering the predicted increase in climate change, and last but not least, addressed the uncertainties and limitations of our study.

4.1 Range borders

Areas of potential habitat without a confirmed presence of Harting’s vole were apparent in our results, both inside the core area and along the periphery of occupied habitat fragments (Fig. 1). Peripheral absences are most likely genuine since Harting’s vole has not been reported from west-central Greece (Sterea Hellas), Peloponnese, and north Bulgaria (Pardiñas et al. 2017). Vacant habitats are evidently isolated from the core area by major biogeographical barriers: the Pindus Mts. to the west (line A in Fig. 1), the Stara Planina (or the Balkan Mts.) in the north (line C in Fig. 1), and the Isthmus of Corinth to the south (line B in Fig. 1). The narrow Isthmus of Corinth effectively filtered faunal exchange between the peninsular Peloponnese and the mainland Attica, turning the former into a biogeographical island (Griffiths et al. 2004).

The mountain ranges putatively posed an obstacle to the dispersal of Harting’s vole by densely forested slopes and ridges. Biogeographic barrier postured by contiguous forests is a

novelty in SEE and emerged at the Pleistocene-Holocene transition. During the late Pleistocene, the *Artemisia*-Chaenopodiaceae steppe was widespread vegetation in SEE while temperate forests expanded only at 10.5–9.5 kya (Eastwood 2004). Therefore, the large-scale distribution of Harting's vole in SEE can be attributed to historically young biogeographic factors.

4.2 Windows into past habitat suitability

Harting's vole most likely colonised SEE from Anatolia via the recurrent land corridor which permitted faunal exchanges between the two regions since the Middle Pleistocene (McHugh et al. 2008). The corridor was finally submerged by a significant rise in sea level at 7–5.3 kya (Kerey et al. 2004). Molecular evidence has indicated south-western Asia was the cradle for social voles (Kryštufek et al. 2009) and the group has been abundant in the fossil record from the Early Pleistocene (Goren-Inbar et al. 2000) onwards (Marder et al. 2011). On the other hand, there are merely four indisputable quaternary records of social voles in SEE (denominated either *M. guentheri* or *M. hartingi*), all within the current range of Harting's vole. Three records are from the Middle Pleistocene (Santel and von Koenigswald 1998; Kowalski 2001) and there is evidence regarding Harting's vole between the final Pleistocene (Palaeolithic) and the early Neolithic in Beotia, Greece (Wilczyński et al. 2016). The Beotian sample reveals a sharp increase in the vole's abundance from the Palaeolithic to the Mesolithic (Wilczyński et al. 2016) therefore perfectly matching our model which retrieved ample suitable habitat for Harting's vole in the mid-Holocene. Moreover, the period coincided with the onset of Neolithic agriculture (at 6–8 kya), which was characterised by an increase in open ground herbaceous habitats, a decrease in the density and diversity of woodland, and from around 4.5–2 kya onwards, the establishment of the present-day landscape (Eastwood 2004).

Absence from the fossil evidence of an abundant rodent such as the Harting's vole most likely signals its actual absenteeism throughout the upper Pleistocene. Repeated colonisation punctuated by extinctions is, therefore, a more plausible scenario than a single invasion from Asia Minor. The scenario benefits from independent support from a phylogeographic pattern, which suggests a fairly recent vicariance at the Bosphorus Straits (Thanou et al. 2012).

4.3 Future climate and habitat suitability changes

Projected future climate change is anticipated to result in decreased habitat suitability for Harting's vole by 2070. The velocity of habitat deterioration depends on the magnitude and direction of climate condition change. If the CO₂ emission declines substantially over the forthcoming years, then Harting's vole will even gain new potential habitats (Figs. 4 and 5a). This scenario, however, is highly unlikely, and there is every expectation that temperatures will continue to rise, perhaps at an accelerated pace (Loarie et al. 2009). The western cluster of suitable habitats will be drastically reduced in the area (Fig. 3) and severely fragmented (Fig. 4b) if the process continues unaltered into the 2080s and beyond.

Our results therefore suggest a collapse of the geographic range of Harting's Vole in SEE in a matter of decades. Because *Microtus* voles are poorly equipped to thermoregulate at high ambient temperatures (Rose and Birney 1985), climate change will likely pose an extra stress on the Harting's vole residing along the southern margin of arvicolines. The projected reduction and fragmentation of the potential habitat will most likely combine with the erosion of genetic diversity and inbreeding in small populations, and a higher risk of extinction from demographic stochasticity (Leigh et al. 2012). In the patchy and ephemeral

habitat of Harting's vole (Ondrias 1965), metapopulation persistence will be additionally affected by the rate of landscape change (Keymer et al. 2000). While climate change will expectedly suppress population dynamics of the keystone grass-eating voles from temperate and boreal ecosystems, it will simply annihilate their Mediterranean counterpart. This will result in a far more severe impact on community restructuring (Schmidt et al. 2012) in the Mediterranean ecosystems than elsewhere. Long-term population monitoring in SEE and beyond is urgently needed to hone the ability to predict the impacts of climate change on keystone species and the entire ecosystem.

4.4 Uncertainties and limitations

Climate change alone cannot entirely explain the range dynamics of this vole. Other environmental factors connected with human interference in the past and future definitely played and will continue to play a significant role as well. We attempted to consider at least some of those factors (land cover, distance to the nearest trees, and distance to an urban area) by predicting current suitable areas for Harting's vole. There is no doubt that future land-cover change, together with other anthropogenic activities will additionally influence the spatial distribution of Harting's vole and other key species in SEE, but this goes beyond the scope of the present study. The main outcome of our research is the message that in less than 80 years from the present day, human-induced climate change trends can potentially trigger the extinction of a keystone herbivore in SEE, whose population seems to have been stable for more than 6000 years. This can happen even without taking into consideration other significant factors of environmental change. In the ecosystem without the keystone small herbivore, the food web will be destabilised and a cascade of further extinctions can lead to severe biodiversity loss. There are still noticeable differences in climate change predictions between the freely available high spatial resolution climate data on the regional scale. Consequently, the variability is still high in the estimations of potential range contraction, range persistence and expansion. Of course, the results from SDMs are heavily dependent on the quality of information loaded in the spatial predictor variables. From that perspective, the SDMtoolbox has a major advantage compared to other frequently used SDM methods, because it offers a standardised protocol, which optimises the calibration process of the Maxent model and minimises typical and frequent user errors.

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