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ORIGINAL PAPER

Do climate-driven altitudinal range shifts explain the intraspecific diversification of a narrow ranging montane mammal, Taurus ground squirrels?

Hakan Gür[1] · **Utku Perktaş**[2,3] · **Mutlu Kart Gür**[1]

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Abstract

Understanding how species have responded to strong climatic fluctuations accompanying glacial-interglacial cycles is critical to predicting their likely responses to future climate change, and therefore can help guide conservation strategies. Using molecular phylogeography and ecological niche modelling, we aimed to understand how a newly recognized cryptic montane mammal (*Spermophilus taurensis*, Taurus ground squirrels) has responded to global climate changes through the Late Quaternary glacial-interglacial cycles as a means to better predict their likely responses to future climate change. Accordingly, 51 cytochrome *b* mitochondrial DNA sequences from throughout the known distribution of Taurus ground squirrels were used to investigate the intraspecific diversification. Besides molecular phylogeography, ecological niche modelling was also employed to get insights into possible climate-driven altitudinal range shifts in the past (the Last Glacial Maximum, 22 kya and the Mid-Holocene, 6 kya) and in the future (2050). Taurus ground squirrels survived the Late Quaternary glacial-interglacial cycles by altitudinal migrations without large geographical displacements. As warming occurred from the Last Glacial Maximum to the Mid-Holocene to the present, the potential distribution of Taurus ground squirrels shifted towards higher altitudes, resulting in a smaller range in the present. As warming continues, the potential distribution of Taurus ground squirrels will continue to shift towards higher altitudes, resulting in a much smaller range in the future. Particular sources of concern are the synergistic effects of future climate change and anthropogenic impacts on Taurus ground squirrels and their montane environments.

Keywords Ecological niche modelling · Molecular phylogeography · Quaternary glacial-interglacial cycles · Range shifts · *Spermophilus taurensis*

Introduction

> "*The development of these huge ice sheets must have led to the destruction of all organic life at the Earth's surface*" (Agassiz 1840, *Études sur les glaciers, Studies of glaciers*).

Large continental ice-sheets in the Northern Hemisphere have grown and retreated many times throughout the Quaternary (the last 2.59 myr of the Earth's history). Times with and without large continental ice-sheets are known as glacial and interglacial periods, respectively

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✉ Hakan Gür
hakangur.ecology@gmail.com

[1] Anatolian Biogeography Research Group, Ahi Evran University, Kırşehir, Turkey

[2] Biogeography Research Laboratory, Department of Biology, Faculty of Science, Hacettepe University, Beytepe, Ankara, Turkey

[3] Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

(PAGES 2016). For example, the last 430 kyr has been dominated by 100-kyr glacial-interglacial cycles, of which a minor proportion (on average 20% or 10 to 30 kyr) was spent in interglacial periods. Glacial periods were colder and generally drier than interglacial periods (Jansen et al. 2007). Strong climatic fluctuations accompanying these glacial-interglacial cycles forced species to either move to locations that remain suitable, adapt to changing environmental conditions, or go extinct (Jansson and Dynesius 2002). Latitudinal and altitudinal range shifts are the most conspicuous and best documented responses of warm-adapted temperate and cold-adapted montane species to these climatic fluctuations, respectively. As warming has occurred since the Last Glacial Maximum, temperate and montane species shifted their range towards higher (northern) latitudes and altitudes, respectively (Bennett and Provan 2008; Stewart et al. 2010). These range shifts have left signals of high genetic diversity in refugia ("regions that a species inhabits during the period of a glacial/interglacial cycle that represents the species' maximum contraction in geographical range"; for detailed discussion of the refugium concept, see Stewart et al. 2010) and low genetic diversity in regions recently colonized from refugia (Hewitt 2000, 2004a, b). Currently, ongoing climate change is causing shifts in the geographic distributions of species globally, and has likely increased their vulnerability due to rapid changes in ecological conditions (Root et al. 2003; Parmesan 2006). Thus, understanding how species have responded to strong climatic fluctuations accompanying glacial-interglacial cycles is critical to predicting their likely responses to future climate change, and therefore can help guide conservation strategies.

Two species (*Spermophilus taurensis* Gündüz et al. 2007, Taurus ground squirrels and *S. xanthoprymnus*, Anatolian ground squirrels) of group-living, diurnal, hibernating, and pre-dominantly herbivorous, burrowing ground squirrels (the genus *Spermophilus* sensu stricto; Helgen et al. 2009) are native to the Asian part of Turkey, i.e. to Anatolia (Kart Gür and Gür 2010). Anatolian ground squirrels are nearly endemic to Anatolia, present in the central and eastern (especially northeastern) Anatolia, with minor range extensions into the western Armenia and northwestern Iran (Kart Gür and Gür 2010; Gür 2013). Taurus ground squirrels are endemic to the western Taurus Mountains (located along the southwestern Mediterranean coast of Anatolia), known only from Erenler Mountain and Geyik Mountains in the eastern part of these mountain ranges (Fig. 1), and parapatric with Anatolian ground squirrels at the northernmost limit of their range. They inhabit montane environments, at higher altitudes (> 1500 m), and have a small range and low genetic diversity (Gündüz et al. 2007; Özkurt et al. 2007; Kart Gür and Gür 2010; Thorington et al. 2012). Until recently, *S. taurensis* was included in *S. xanthoprymnus* (Gündüz et al. 2007). For this reason, in contrast to Anatolian ground squirrels (Kart Gür and Gür 2010), very little information exists on the physiology, ecology, and evolution of this newly recognized cryptic montane mammal. Thus, although Taurus ground squirrels are considered as 'least concern' by IUCN (Kryštufek et al. 2008),

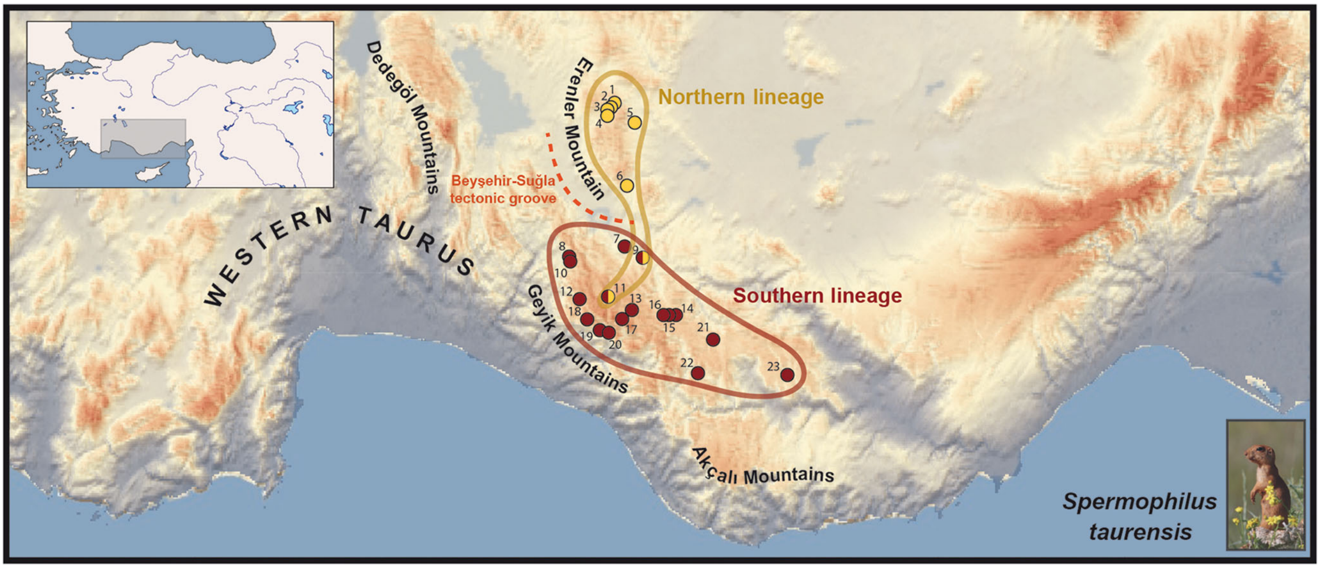

Fig. 1 Map of the southern Anatolia showing genetic sampling localities and the major topographical features mentioned in the text. Circles indicate sampling localities (including eight localities from Gündüz et al. 2007; see Table 1), and colors represent two different cyt *b* mtDNA lineages throughout the known distribution of Taurus ground squirrels (*Spermophilus taurensis*). Locality numbers correspond to those in Table 1. Warmer colors (more brown) depict areas of higher altitude. Basemap source: US National Park Service. Photograph source: Utku Perktaş

further studies (e.g. on modelling their responses to past and future climate changes) are needed to ensure their conservation.

The western Taurus Mountains are geologically located in the Alpine-Himalayan orogenic belt (Şengör and Yılmaz 1981), and a biogeographically interesting region (included in the Mediterranean basin biodiversity hotspot; Mittermeier et al. 2004, for further information, see http://www.cepf.net/resources/hotspots/Europe-and-Central-Asia), with high levels of species diversity and endemism (Davis 1971; Médail and Quezel 1997; Avcı 2005; Thompson 2005; Welch and Kirwan 2008; Parolly 2015; for taxon-specific examples, see e.g. Sevgili et al. 2006; Özüdoğru et al. 2015). This diversity and endemism may reflect a combination of past geological and climatic dynamics and topographic and climatic heterogeneities (Gür 2016; López-Pujol et al. 2016). For example, as in Mediterranean mountains (Hughes and Woodward 2017), the western Taurus Mountains were glaciated during the Late Quaternary (Sarıkaya et al. 2011; Sarıkaya and Çiner 2015, 2017). However, the western Taurus Mountains have also acted as refugia for Mediterranean species during glacial periods (Médail and Diadema 2009) because only the peaks of these rugged mountain ranges were glaciated (Sarıkaya et al. 2011; Sarıkaya and Çiner 2015, 2017). Despite their importance with respect to biodiversity, the western Taurus Mountains are an underexplored region of the Mediterranean basin biodiversity hotspot (Médail and Diadema 2009).

In this study, we aimed to understand how Taurus ground squirrels have responded to global climate changes through the Late Quaternary glacial-interglacial cycles and to predict their likely responses to future climate change. Thus, we used two key approaches that have been widely used together in recent biogeographic studies (Alvarado-Serrano and Knowles 2014; Perktaş and Gür 2015): molecular phylogeography (Avise 2000; Edwards et al. 2015) and ecological niche modelling (Elith and Leathwick 2009a; Peterson and Anamza 2015). Accordingly, by including available sequences from GenBank (Gündüz et al. 2007), 51 cytochrome b (cyt *b*) mitochondrial (mt)DNA sequences from throughout the known distribution of Taurus ground squirrels were used to investigate the intraspecific diversification. Besides molecular phylogeography, ecological niche modelling was also employed to get insights into possible climate-driven altitudinal range shifts in the past (the Last Glacial Maximum, 22 kya and the Mid-Holocene, 6 kya—two different time periods representing climatic extremes during the Late Quaternary) and in the future (2050). Owing to a small range of Taurus ground squirrels in montane environments, the late Quaternary glacial history of the western Taurus Mountains (see above), and previous findings on montane mammals (see Discussion), we hypothesized that this newly recognized cryptic montane mammal survived the Late Quaternary glacial-interglacial cycles by altitudinal migrations without large geographical displacements, and will shift their range towards higher altitudes as a result of future climate change.

Materials and methods

Ecological niche modelling

Species occurrence data were obtained across Erenler Mountain and Geyik Mountains from field studies/observations (19 records) and the following sources (12 records): Gündüz et al. (2007), Özkurt et al. (2007), Arslan and Arslan (2010), and TRAMEM (Anonymous Mammals of Turkey; www.tramem.org). These occurrence records are from the altitudes of 1357 to 2125 m and nine land-cover types. Natural grasslands and open spaces with little or no vegetation (sparsely vegetated areas and bare rocks) are the predominant cover types at higher altitudes (> 1650 m) and in the south (S1 Table). To correct for sampling bias and to reduce spatial autocorrelation (Boria et al. 2014; Brown 2014), the occurrence records were spatially filtered by reducing multiple records to a single record within 4 km distance, resulting in 24 records used for ecological niche modelling (Fig. 2). We filtered at 4 km because Taurus ground squirrels inhabit mountainous terrain with high topographic heterogeneity.

Bioclimatic data were downloaded from the WorldClim database (Hijmans et al. 2005; www.worldclim.org) for past (the Last Glacial Maximum, 22 kya and the Mid-Holocene, 6 kya), present (1960–1990), and future (2050, averaged across 2041–2060) conditions, and used at a spatial resolution of 30 arc-seconds (~ 1 km) to match approximately the resolution of the occurrence records. Past bioclimatic data are based on three general circulation model (GCM) simulations (CCSM4, MIROC-ESM, and MPI-ESM-P; for detailed information, see the WorldClim database). Future bioclimatic data are also based on three GCM simulations (CCSM4, MIROC-ESM, and MPI-ESM-LR) for the Representative Concentration Pathway (RCP) 4.5 (for detailed information, see the WorldClim database). The use of different GCM simulations enabled us to assess uncertainty in ecological niche modelling due to past and future bioclimatic data. Bioclimatic data include 19 bioclimatic variables derived from monthly temperature and precipitation values (for detailed descriptions of bioclimatic variables, see www.worldclim.org/bioclim). As in this study, if few occurrence records are available, it is good to first reduce the candidate predictor set using ecological understanding of the species (Elith and Leathwick 2009b). Thus, we chose a subset of eight bioclimatic variables on the basis of what is known about the ecology of ground squirrels (Morelli et al. 2012; Gür and Kart Gür 2012; Gür 2013; Kart Gür and Gür 2015). These included annual mean temperature and precipitation (BIO1 and 12), temperature and

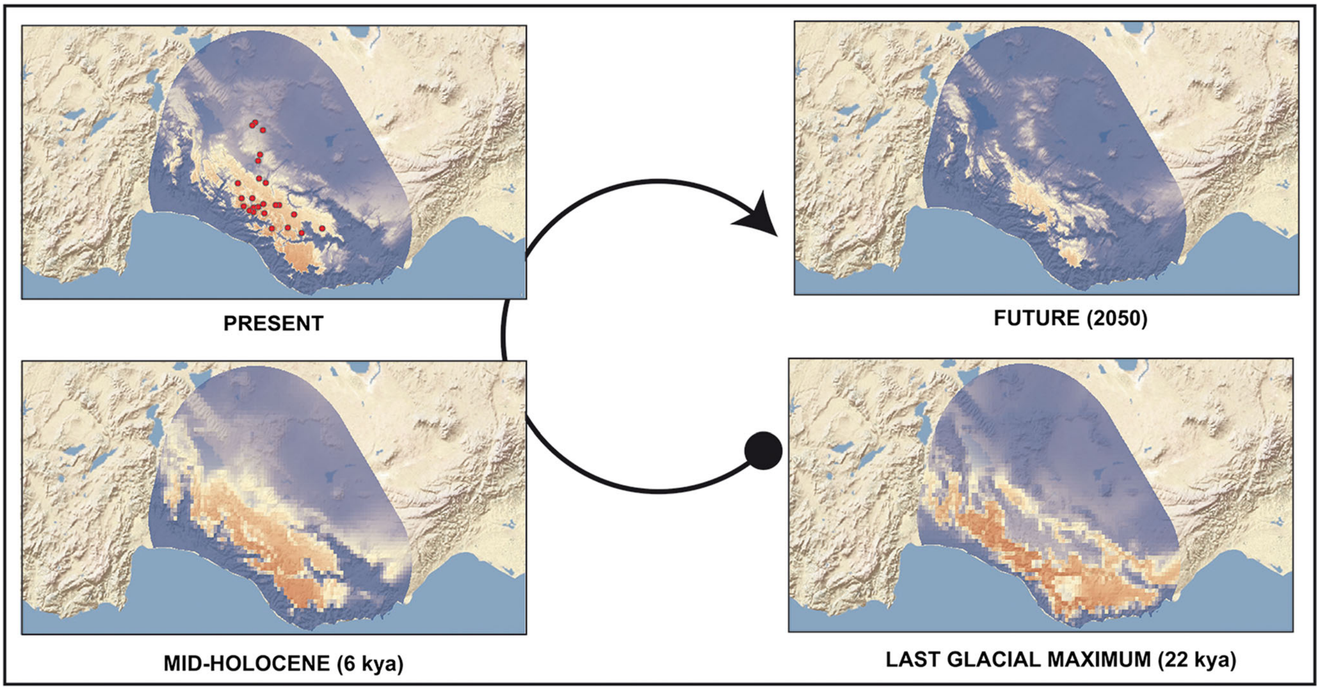

Fig. 2 Last Glacial Maximum (22 kya), Mid-Holocene (6 kya), present (1960–1990), and future (2050) predictions of the potential distribution of Taurus ground squirrels (*Spermophilus taurensis*). Red circles indicate 24 occurrence records used for ecological niche modeling. The predictions show a bioclimatic suitability gradient from low (blue) to high (red). Basemap source: US National Park Service

precipitation seasonality (BIO4 and 15), and mean temperature and precipitation of the warmest and coldest quarters (BIO10, 11, 18, and 19). Correlation structure among these bioclimatic variables in the study area (see below) appeared to be stable and consistent across time periods (Mantel test = $r \geq 0.977$, $P < 0.001$), suggesting that the model may be transferable to past and future bioclimatic conditions (Jiménez-Valverde et al. 2009).

To predict the potential distributions of Taurus ground squirrels under past, present, and future bioclimatic conditions, the maximum entropy machine learning algorithm in the software MaxEnt version 3.3.3 k (Phillips et al. 2006; Elith et al. 2011) was used, together with presence-only data (24 occurrence records) and eight bioclimatic variables, because it generally performs better, and is much less sensitive to sample size than comparable methods (Elith et al. 2006; Wisz et al. 2008). MaxEnt was run with the following settings. Since the known distribution of Taurus ground squirrels covers a small range in the eastern part of the western Taurus Mountains (Fig. 1), and is poorly described, a minimum convex polygon was created from the occurrence records to which a 100-km buffer was applied. This area (the study area) was used to randomly sample 10,000 background points. This might reduce issues associated with background selection and unoccupied or unknown occupied, suitable areas (Brown et al. 2016; see for a discussion on background selection, Elith et al. 2011; Merow et al. 2013). To map bioclimatic suitability, MaxEnt's logistic output (ranging from 0 to 1, with 0 indicating low and 1 indicating high suitability) was selected. To evaluate how bioclimatic variables affected the prediction, marginal response curves were used. The relative contributions of bioclimatic variables to the models (see below) were evaluated using the permutation importance. To optimize the model performance (for a discussion on features and regularization, see Elith et al. 2011; Merow et al. 2013), different models were tested, using all combinations of the following feature classes (as in Brown 2014) and regularization multipliers: (1) linear, (2) linear and quadratic, (3) hinge, (4) linear, quadratic, and hinge, and (5) linear, quadratic, hinge, product, and threshold, and 0.5 to 5 (in 0.5 increments). These models were developed using spatial jackknifing (or geographically structured k-fold cross-validation, $k = 3$), which tests evaluation performance of spatially segregated and independent occurrence records. They were calibrated with all permutations of the three spatial groups using the occurrence records and background points from two of the spatial groups, and then evaluated with the withheld group (Brown 2014). The best model was selected in the following order of preference (Brown 2014): (1) model with the lowest omission rate (to define bioclimatically suitable areas, the '10 percentile training presence' threshold was used), (2) model with the highest AUC [Area under the Receiver Operating Characteristic (ROC) Curve], and (3) model with the simplest set of feature classes. After the optimum model parameters were determined, a final model was developed using all the occurrence records together. This model was then projected to past and future bioclimatic conditions. Three predictions (logistic values) under three different GCM simulations were averaged to generate a final summary prediction for the past (the Last Glacial Maximum and the Mid-Holocene) and for the future (2050). Multivariate Environmental Similarity Surfaces (MESS) analysis was used to identify areas in which non-analog bioclimatic conditions were observed and to characterize the degree of extrapolation necessary (Elith et al. 2010). Clamping and extrapolation were performed because MESS analysis showed that projection into non-analog bioclimatic conditions was necessary. However, clamping, MESS, and the most dissimilar variable (the variable that is furthest outside its training range; Elith et al. 2010) maps, the MaxEnt's explain tool (exploring what drives a high or low prediction at any given site in geographic space; Elith et al. 2010), and response curves suggested that extrapolation might not be a critical issue.

BIO1, 10, and 11 are highly correlated with each other ($r \geq 0.964$), and BIO12 and 15 with BIO19 ($r \geq 0.925$). While multicollinearity among bioclimatic variables does not affect the predictive quality of the MaxEnt model, it does seriously limit any inference of the relative contribution of any correlated variables to the model (Elith et al. 2011; Merow et al. 2013; Brown 2014). To understand how multicollinearity affected variable selection, six further final models (labelled models 1 to 6) using the above-mentioned methodology, but all different sets of non-collinear bioclimatic variables ($r < 0.85$; Feldman et al. 2017), were developed. These models were compared by Akaike Information Criteria corrected for small sample sizes (AICc) using the software ENMTools version 1.4.4 (Warren et al. 2010). The model based on the lowest AICc score was selected as the model that would most accurately estimate the relative contributions of bioclimatic variables.

Niche overlap between cyt *b* mtDNA lineages was quantified using the software NicheA version 3.0 (Qiao et al. 2015) because it allows exploring distribution of occurrence records in environmental space even sample size is small (7 and 19 occurrence records for the northern and southern lineages, respectively; see Results). First, a principal components analysis was performed to reduce eight bioclimatic variables to three principal components, which explained 97% of variation. Then, a lineage's bioclimatic niche was defined as both the convex polyhedron (CP) and minimum volume ellipsoid (MVE) in three-dimensional environmental space (each dimension corresponds to a principal component). Niche overlap (of both CPs and MVEs) between lineages was quantified based on Jaccard's index (J). This index ranges from 0 (no overlap) to 1 (complete overlap).

To characterize landscape connectivity, first, the prediction for niche stability (higher values indicating higher stability) was created by summing three predictions for the Last Glacial Maximum, the Mid-Holocene, and the present (Pabijan et al. 2015). This prediction was first clipped to the spatial extent of geographic localities, and then inverted for use as friction layers; i.e. areas of high suitability throughout all three time periods were converted to areas of low dispersal cost. Then, least-cost corridors (LCCs) among geographic localities that share haplotypes from the same cyt *b* mtDNA lineage were calculated in three (high, mid, and low) classes by 'percentage of least-cost path (LCP) value' method. LCC class percentages of 5 to 2%, 2 to 1%, and < 1% were selected for, and LCC class weights of 1, 2, and 5 were applied to high, mid, and low classes, respectively. All weighted LCCs were summed to create the dispersal network (Chan et al. 2011; Brown 2014).

Except where otherwise indicated, we conducted all analyses using the software SDMtoolbox version 1.1c (Brown 2014) implemented in the software ArcGIS version 10.2.2.

Molecular phylogeography

We collected ear tissue samples from 31 Taurus ground squirrels across Erenler Mountain and Geyik Mountains (in total, 15 localities; Fig. 1 and Table 1). All individuals were trapped using treadle-style, wire-mesh live traps (Collapsible Traps with One Trap Door, Code: 202, Tomahawk Live Trap Company) baited with peanut butter, placed at burrow entrances (Gür and Kart Gür 2005; Kart Gür and Gür 2010), and then released to the field after collecting ear tissue samples. Tissue samples were taken using a 2-mm ear punch (Mouse Ear Punch, Kent Scientific Corporation).

Total genomic DNA was extracted from ear tissue samples using the DNeasy Blood and Tissue Kit (Qiagen). All DNA extraction steps were performed in a sterile laminar flow hood. We used the same primers and amplification conditions described in Gündüz et al. (2007) to sequence the cyt *b* mtDNA gene (1140 bp) in 31 individuals from 15 localities. Amplifications were conducted via PCR using a combination of two primers (L14727-SP and H15915-SP; Jaarola and Searle 2002). PCR reactions were conducted using fresh reagents and laboratory equipment. Hotstart Taq (GoTaq® Hot Start) was used in amplifications. The PCR protocol consisted of an initial 6-min denaturation step at 95 °C, 38 cycles of denaturation at 94 °C for 1-min, annealing at 49 °C for 1-min, and extension at 72 °C for 1-min 45 s, and a final 10-min extension step at 72 °C. Amplification products were visualized on agarose gels, and examined under ultraviolet light; negative controls were always 'blank'. For some samples, however, the same PCR protocol was repeated with an internal primer (L15162MO; Brunhoff et al. 2003) for a confirmation of previous amplification conditions against any contamination possibility. Cycle-sequencing reactions were conducted, and performed for both forward and reverse strands in a different laboratory, using a Big Dye terminator and the above-mentioned three primers. DNA strands were sequenced

Table 1 Sampling localities and genetic diversity of Taurus ground squirrels (*Spermophilus taurensis*), based on the cyt *b* mtDNA gene (1140 bp)

Locality number	Latitude	Longitude	*n*	Haplotype[b]	*h*	π
Northern population			12	3	0.621	0.00061
1[a]	37.742	32.108	2	ST1		
2[a]	37.725	32.092	2	ST1		
3	37.716	32.073	2	ST2		
4[a]	37.708	32.075	2	ST1,ST2		
5	37.667	32.206	2	ST2,ST3		
6	37.423	32.170	2	ST2		
Southern population			39	16	0.804	0.00159
7	37.188	32.158	3	ST4,ST5,ST6		
8	37.148	31.888	1	ST6		
9	37.146	32.244	3	ST2,ST6,ST7		
10[a]	37.142	31.892	5	ST6(4),ST8		
11	36.996	32.077	3	ST2,ST6,ST9		
12	36.987	31.939	3	ST10		
13	36.945	32.193	1	ST6		
14[a]	36.925	32.408	2	ST11		
15[a]	36.925	32.375	2	ST6,ST12		
16[a]	36.925	32.358	2	ST6,ST13		
17	36.910	32.144	1	ST6		
18[a]	36.908	31.975	3	ST6(2),ST8		
19	36.867	32.036	2	ST6		
20	36.856	32.081	2	ST14,ST15		
21	36.830	32.588	2	ST16,ST17		
22	36.699	32.515	3	ST16(2),ST18		
23	36.692	32.949	1	ST6		
Total			51	18	0.857	0.00258

Locality numbers correspond to those in Fig. 1

n, number of individuals; *h*, haplotype diversity; π, nucleotide diversity

[a] Available sequences from GenBank (Gündüz et al. 2007)

[b] Number of individuals with the same haplotype in parenthesis

on an ABI 3730xl (Applied Biosystems) automated sequencer.

Cyt *b* mtDNA sequences were aligned, and edited using the software Sequencher version 5.2. All cyt *b* mtDNA sequences were submitted to GenBank (www.ncbi.nlm.nih.gov/genbank), and are publicly available under accession numbers KY938046 to KY938076. To extend our analyses, 20 previously published cyt *b* mtDNA sequences from eight localities (in total, seven haplotypes) were downloaded from GenBank (accession numbers AM691690 to AM691696; Gündüz et al. 2007). Thus, 51 sequences from throughout the known distribution of Taurus ground squirrels were used for molecular phylogeography (Fig. 1 and Table 1).

The number of variable and parsimony informative sites and estimates of genetic diversity (including the number of haplotypes and haplotype and nucleotide diversities) were calculated using the software DnaSP version 5.10.01 (Librado and Rozas 2009).

A Bayesian-based phylogenetic tree was constructed using the software BEAST version 1.7.5 (Drummond et al. 2012). BEAST uses a Bayesian Markov chain Monte Carlo (MCMC) analysis, and samples possible evolutionary histories over many solutions, each weighted according to its posterior probability. One individual from each of two species of ground squirrels were used as outgroups: European ground squirrels, *Spermophilus citellus* (GenBank accession number FJ715461) and Anatolian ground squirrels (GenBank accession number AM691658). These species represent the sister taxa to Taurus ground squirrels (Gündüz et al. 2007). BEAST was run three times with the default settings, except the cases noted below. The MCMC analyses were set at 50 million chains (sampled every 5000 chains), of which the first 10% was discarded as the burn-in. The nucleotide substitution model was selected as the Tamura-Nei 93 (TN93) model, which was considered to describe the substitution pattern the best by Akaike Information Criteria corrected for small sample sizes (AICc) using the software MEGA version 7.0.14 (Kumar et al. 2016). These settings were created using BEAUti (part of BEAST). The MCMC outputs were combined using the software LogCombiner (part of BEAST), and assessed using the software Tracer version 1.5 (Rambaut and Drummond 2009). All parameters had effective sample size values above 1000. A consensus tree was generated using TreeAnnotator (part of BEAST), with a burn-in of 1000 trees. Finally, this tree with posterior probability values was visualized using the software FigTree version 1.3.1 (Rambaut 2014).

A median-joining haplotype network was also constructed using the software PopART v.1.7 (Leigh and Bryant 2015) because many of the underlying assumptions of traditional tree-building methods (fully bifurcating trees, complete lineage sorting) could be violated in intraspecific studies (Posada and Crandall 2001). PopART has the primary function of inferencing and visualizing genetic relationships among intraspecific sequences, and constructs a median-joining haplotype network using the algorithm described by Bandelt et al. (1999).

The analysis of molecular variance (AMOVA) was performed to partition genetic variation at two levels (defined based on the Bayesian-based tree and median-joining network) by the software GenAlEx 6.501 (Peakall and Smouse 2012): (1) between populations in Erenler Mountain and Geyik Mountains (i.e. the northern and southern populations, respectively; see Results), which almost entirely corresponded to cyt *b* mtDNA lineages, and (2) between subpopulations (western and eastern) within the southern population. The probability values estimated by 10,000 permutations were used to determine whether the partitioning of variance components was significant.

The patterns of genetic divergence among geographic localities were visualized using the software Genetic Landscapes GIS Toolbox version 10 (Vandergast et al. 2011) implemented in the software ArcGIS version 10.2.2. First, the number of nucleotide substitutions per site from averaging over all sequence pairs among geographic localities as the index of genetic divergence was calculated under the Tamura-Nei model using the software MEGA version 7.0.14 (Kumar et al. 2016). Then, pairwise values of genetic divergence were attached to the mapped midpoints between geographic localities, and a continuous surface (the patterns of genetic divergence; 1-km^2 grid cell size) was generated using a spatial interpolation algorithm, inverse distance weighted interpolation.

The time to divergence and migration rate between main populations (i.e. the northern and southern populations) were inferred using the software MDIV (Nielsen and Wakeley 2001). MDIV uses a Markov chain Monte Carlo (MCMC) analysis [to obtain the posterior estimates of the parameters of theta ($\theta = 2\ Nef\ \mu$), migration rate ($M = 2\ Nef\ m$), and time to divergence between two populations ($T = t/2\ Nef$), with N_{ef} being the female haploid effective size, μ the mutation rate, m the female migration rate, and t the number of generations], and is limited to two models of nucleotide substitution: Hasegawa-Kishino-Yano (HKY) and infinite sites. The nucleotide substitution model was selected as the HKY model. MDIV was first run using default search settings and default priors. Then, prior values for $T_{\max}$ and $M_{\max}$ were set to 50 and 2, respectively, because they produced consistent and well-behaved posterior distributions. MDIV was finally run for 2 million chains, of which 500,000 were discarded as the burn-in, and repeated three times with several random numbers to ensure convergence upon the same posterior distributions for each of the parameter estimates.

Results

Ecological niche modelling

We tested 150 different models based on different model parameters (feature classes and regularization multipliers) and training/test partitions (spatial jackknifing). The best model used feature classes of linear and quadratic and a regularization multiplier of 2, and performed better than a random prediction (training AUC = 0.911).

The bioclimatic variables that most contributed to the model were mean temperature and precipitation of the coldest quarter (BIO11 and 19; winter temperature and precipitation, respectively). Multicollinearity among bioclimatic variables did not affect variable selection (Table 2). For winter temperature, bioclimatic suitability increased with increasing values up to − 1 to − 2 °C, and then decreased. For winter precipitation, bioclimatic suitability increased with increasing values (S1 Fig).

Under present bioclimatic conditions, areas of high suitability (a threshold value of 0.256 or higher) were predicted across Erenler Mountain and Geyik Mountains, i.e. the known distribution of Taurus ground squirrels, but also in nearby montane regions (e.g. Dedegöl and Akçalı Mountains; Fig. 2), which could represent areas currently unoccupied due to non-climate-related factors or populations not yet detected. The altitude of these areas was 1686 ± 251 m (mean ± SD). Lowlands surrounding mountain ranges were areas of low suitability predicted (a threshold value of 0.256 or lower; Fig. 2) mainly due to high winter temperature and/or low winter precipitation. Thus, Beyşehir-Suğla tectonic groove (generally at the altitudes of 1100 to 1250 m) between Erenler Mountain and Geyik Mountains partly divided the known distribution of Taurus ground squirrels into two parts (northern and southern), which almost entirely corresponded to the geographic distributions of the northern and southern lineages (Figs. 1 and 2; see below). The northern part (hereafter also referred to as the northern population) was modelled as being lower suitability than the southern part (hereafter also

Table 2 The relative contributions of bioclimatic variables to the models, based on the permutation importance

Variables	Final model	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
BO1	0	59.9			42.6		
BIO4	0.5	1.2	5.1	1.2	11.4	16.4	5.8
BIO10	0		54.7			40.7	
BIO11	58.9			59.9			48.2
BIO12	0	0	0	11.3			
BIO15	0.1	36.9	37.6	27.2			
BIO18	0	1.9	2.6	0.3	3	3.2	1.4
BIO19	40.4				43	39.7	44.6
AICc		551.6	551.4	536.7	519.7	527.9	516.1
ΔAICc		35.5	35.3	20.6	3.7	11.8	0

referred to as the southern population; Fig. 2), with low suitability in Erenler Mountain mainly due to low winter precipitation (200 to 300 mm) and high suitability in Geyik Mountains mainly due to low winter temperature (around − 1 to − 2 °C) and/or high winter precipitation (300 to 400 mm). Jaccard's index (CP overlap = 0 and MVE overlap = 0.123) suggested a small overlap in bioclimatic niches of the northern and southern lineages (S2 Fig).

The GCM simulations (CCSM4, MIROC-ESM, and MPI-ESM-P) predict winter temperature averagely 5.0 °C and 0.7 °C colder and winter precipitation averagely 7 and 6% higher in the study area during the Last Glacial Maximum and the Mid-Holocene, respectively. Under these bioclimatic conditions, areas of high suitability were predicted generally across lowlands (at the altitude of 1146 ± 445 m) and mountain ranges (at the altitude of 1550 ± 305 m) during the Last Glacial Maximum and the Mid-Holocene, respectively. In these two time periods, Beyşehir-Suğla tectonic groove was bioclimatically suitable. These results suggest that as warming occurred from the Last Glacial Maximum to the Mid-Holocene to the present, the potential distribution of Taurus ground squirrels shifted towards higher altitudes, resulting in a smaller range in the present (the number of suitable pixels in the study area = 27,659, 31,632, and 20,887, respectively; Fig. 2).

The intersection of the predictions for the Last Glacial Maximum, the Mid-Holocene, and the present suggests that bioclimatically suitable areas throughout all three time periods were located mainly in Geyik Mountains (generally > 1250 m), except for higher altitudes (generally > 2000 m and > 1500 m in the southwestern and northeastern sides of these mountain ranges, respectively). Moreover, the prediction for niche stability indicates that stability was generally higher at higher altitudes and in the south, across Geyik Mountains (Fig. 3). Not surprisingly, the dispersal network suggests that landscape connectivity was generally higher in areas of high niche stability (Fig. 4).

The GCM simulations (CCSM4, MIROC-ESM, and MPI-ESM-LR) also predict winter temperature averagely 1.8 °C warmer and winter precipitation averagely 8% lower in the study area during the future (2050). Under these bioclimatic conditions, areas of high suitability were predicted across mountain ranges (at the altitude of 1927 ± 180 m). In this time period, Beyşehir-Suğla tectonic groove was much more apparent as an area bioclimatically unsuitable. These results suggest that as warming continues, the potential distribution of Taurus ground squirrels will continue to shift towards higher altitudes, resulting in a much smaller range in the future (the number of suitable pixels in the study area = 8703; Fig. 2).

Molecular phylogeography

We sequenced 1140 bp of the cyt *b* mtDNA gene for 31 Taurus ground squirrels sampled across Erenler Mountain and Geyik Mountains. 31 newly determined and 20 downloaded cyt *b* mtDNA sequences yielded 19 variable sites, of which 11 were parsimony informative. In total, 18 haplotypes were found, of which 11 were unique for this study (Table 1). The number of haplotypes and haplotype and nucleotide diversities were given in Table 1.

The Bayesian-based tree and median-joining network were similar to each other with respect to phylogeographic structure, and separated Taurus ground squirrels into two cyt *b* mtDNA lineages (northern and southern; Fig. 5). These lineages were strongly supported by high values of posterior probability in the Bayesian-based tree. The northern lineage was restricted to the northern population, i.e. to Erenler Mountain (with the exception of two individuals from two localities in Geyik Mountains), and the southern lineage to the southern population, i.e. to Geyik Mountains (Figs. 1 and 5). Moreover, AMOVA indicates that substantially more genetic variation between the northern and southern populations was observed than that within these populations (Table 3). The northern and southern lineages were separated from each other with four mutational steps (Fig. 5). The northern lineage had a small range (Fig. 1), and was comprised of three haplotypes

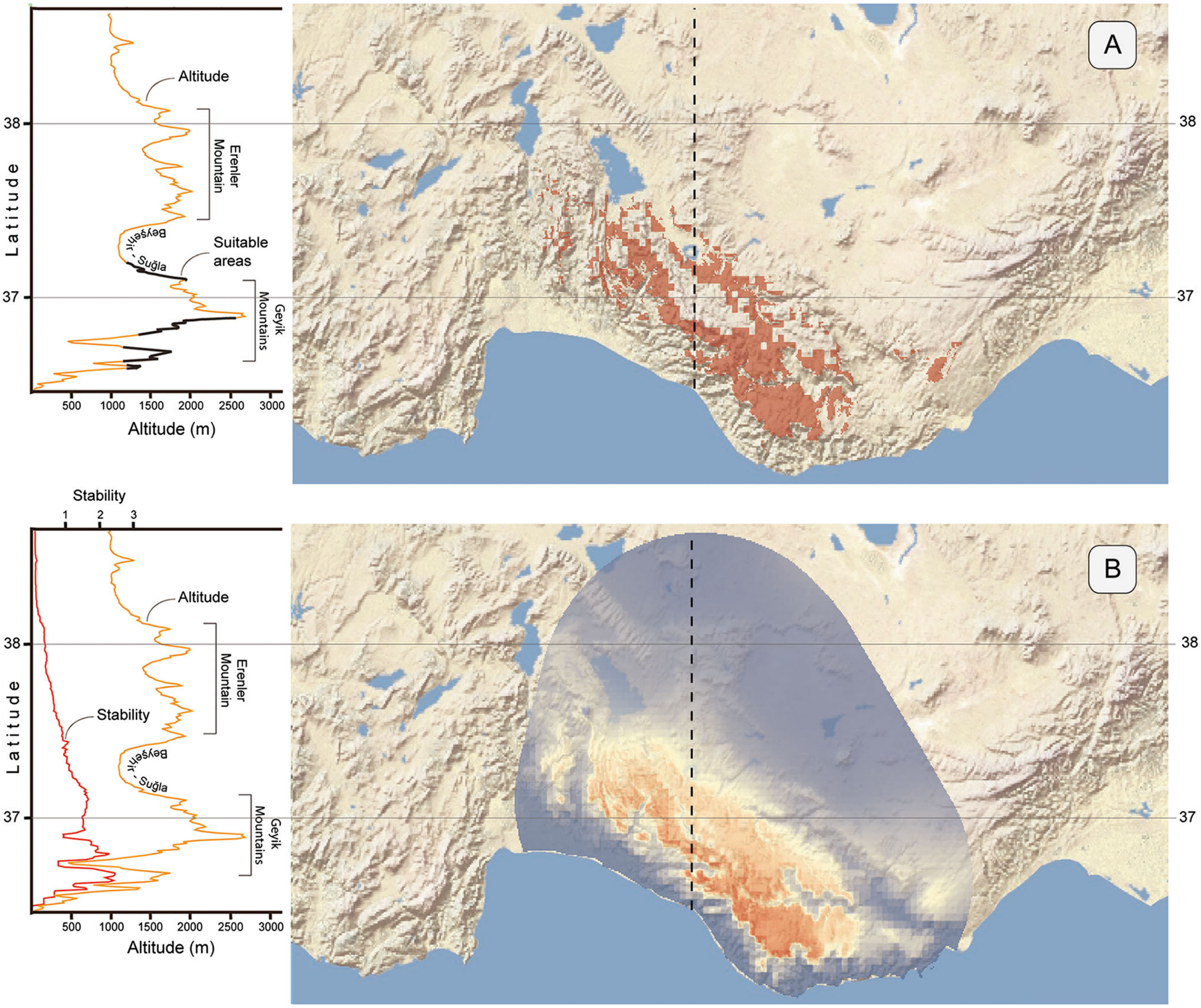

Fig. 3 **a** Bioclimatically suitable areas and **b** niche stability throughout all three time periods (the Last Glacial Maximum, 22 kya, the Mid-Holocene, 6 kya, and the present, 1960–1990) for Taurus ground squirrels (*Spermophilus taurensis*). In (**a**), brown shaded regions depict bioclimatically suitable areas. In (**b**), the prediction shows a niche stability gradient from low (blue) to high (red). Bioclimatically suitable areas and niche stability are also shown along a north-south transect (i.e. the dashed line) on the left. Basemap source: US National Park Service

(haplotype ST1 to ST3), which were separated from each other with a maximum of two mutational steps. Of these haplotypes, two were common (haplotype ST1 and ST2 with five and eight individuals, respectively), and one was private (haplotype ST3 found in only one locality; Fig. 5 and Table 1). The southern lineage had a large range (Fig. 1), and was comprised of 15 haplotypes (haplotype ST4 to ST18), which were separated from each other with a maximum of five mutational steps. Of these haplotypes, one was common (haplotype ST6 with 17 individuals), and 12 were private (each found in only one locality; Fig. 5 and Table 1). AMOVA indicates that, despite a genetic substructure within the southern population, substantially more genetic variation within the western and eastern subpopulations was observed than that between these subpopulations (Table 3). Not surprisingly, haplotype and nucleotide diversities were lower in the northern population than in the southern population (Table 1).

The visualized patterns of genetic divergence among geographic localities show that genetic divergence was generally low within both Erenler Mountain and Geyik Mountains (i.e. the northern and southern populations, respectively), and high between these mountain ranges (Fig. 6).

The maximum-likelihood estimates of the time to divergence and migration rate suggest a scenario of historical isolation ($T = 1.6$, 95% credibility interval = 0.8 to 49.9) with low level of gene flow ($M = 0.212$, 95% credibility interval = 0.016 to 0.972; less than one female migrant per generation) between the northern and southern populations (S3 Fig).

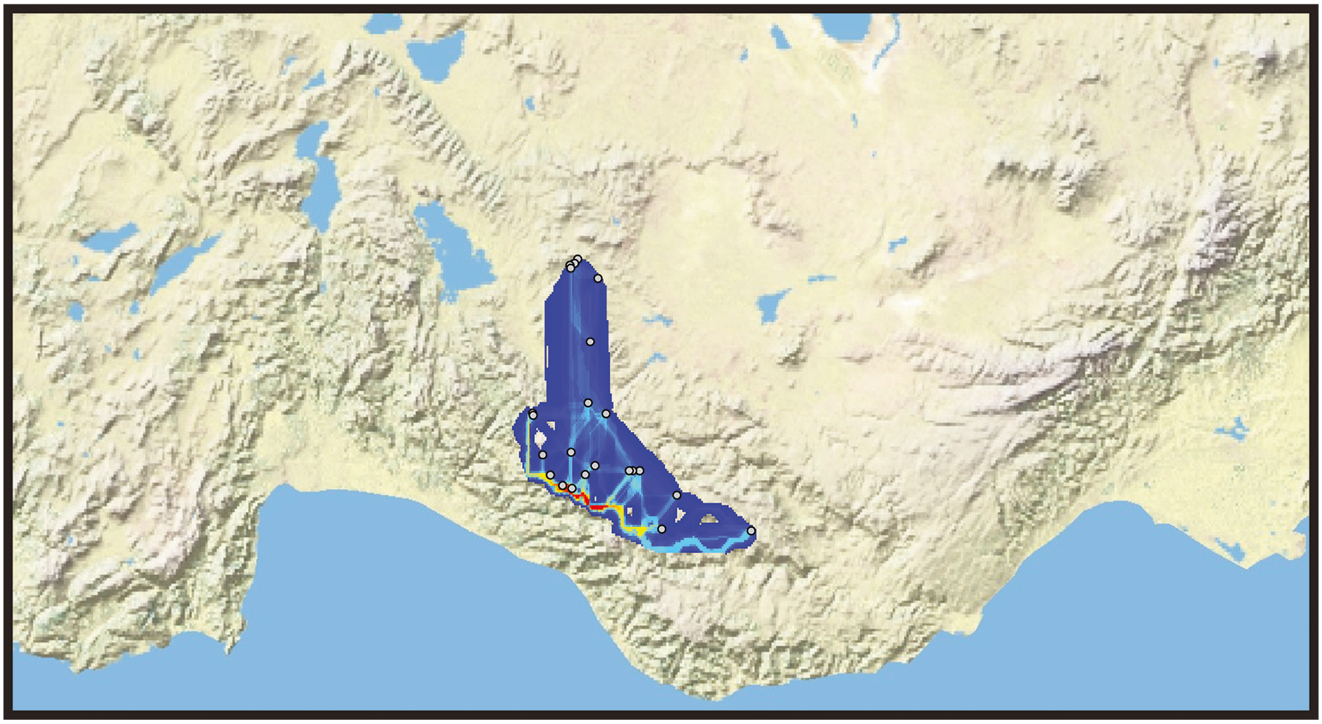

Fig. 4 The dispersal network for Taurus ground squirrels (*Spermophilus taurensis*). Gray circles indicate genetic sampling localities. Warmer colors (more red) depict areas of higher landscape connectivity. Basemap source: US National Park Service

Discussion

In this study, using molecular phylogeography (Avise 2000; Edwards et al. 2015) and ecological niche modelling (Elith and Leathwick 2009a; Peterson and Anamza 2015), we aimed to understand how Taurus ground squirrels have responded to global climate changes through the Late Quaternary glacial-interglacial cycles as a means to better predict their likely responses to future climate change. Thus, this study exemplifies the utility of integrating molecular phylogeography and ecological niche modelling (Alvarado-Serrano and Knowles 2014; Perktaş and Gür 2015). For example, the least cost path (LCP) calculation coupled with these two approaches has been applied to reveal landscape connectivity, which is crucial in understanding historical dispersal and resulting gene flow among populations affected by global climate changes through the Late Quaternary glacial-interglacial cycles (Pabijan et al. 2015; Perktaş et al. 2015). Moreover, this study extends our understanding of the Quaternary dynamics and evolutionary history of Taurus ground squirrels and therefore the biogeography of the western Taurus Mountains, a biogeographically interesting, but under-explored region of the Mediterranean basin biodiversity hotspot (Médail and Diadema 2009). However, in this study, there are also some caveats: sample size was limited (24 occurrence records), and a single genetic locus was used. Hernandez et al. (2006) showed that models built with few occurrence records are still useful, encouraging for modeling rare species, and MaxEnt (Phillips et al. 2006; Elith et al. 2011), the algorithm used for ecological niche modelling in this study, performs well across different sample sizes. Moreover, although a single genetic locus (the cyt *b* mtDNA gene, maternally inherited, and therefore reflecting the maternal history of populations) was used, the results of ecological niche modelling and molecular phylogeography were highly consistent with each other (e.g. about population structure). Thus, we believe that our results are worthy of reporting. However, future studies based on a more complete sampling and multiple genetic loci are also needed to accurately understand the Quaternary dynamics and evolutionary history of Taurus ground squirrels.

Our results suggest that the potential distribution of Taurus ground squirrels is limited by high winter temperature and/or low winter precipitation. Similarly, high winter temperature is negatively related to the persistence of a montane, hibernating mammal (Belding's ground squirrels, *Urocitellus beldingi*) along the trailing edge of its range, with a higher rate of extirpations at lower altitudes, potentially owing to snowcover loss (Morelli et al. 2012). In the southwestern Anatolia, high temperature and/or low precipitation during winter are likely to lead to reduced snowcover, at lower altitudes. Reduced snowcover may result in montane mammals losing their buffer against low temperatures, and could cause to depletion of fat

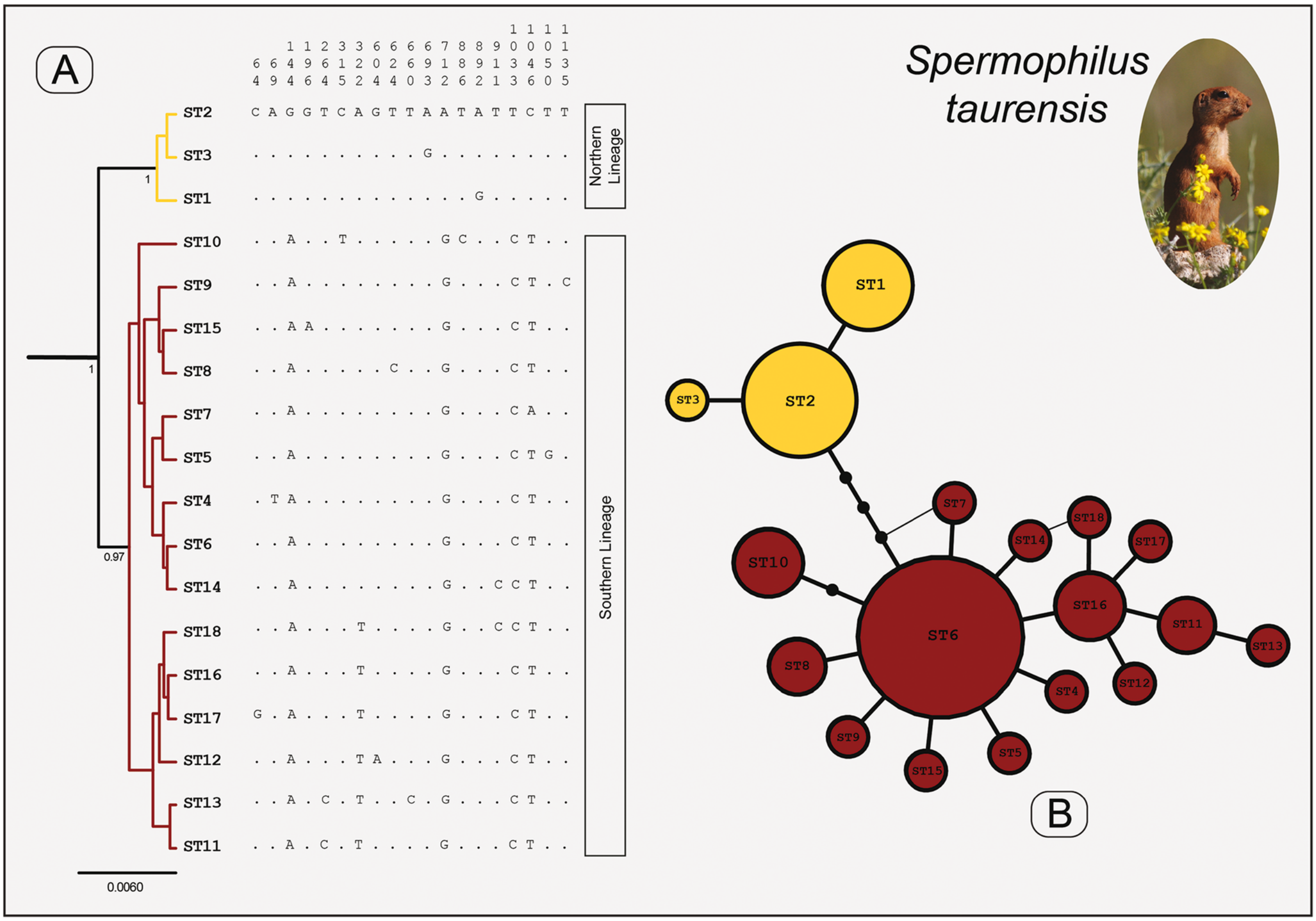

Fig. 5 **a** The Bayesian-based tree (variable sites also shown with sequence positions given above) and **b** median-joining network for Taurus ground squirrels (*Spermophilus taurensis*). Colors represent two different cyt *b* mtDNA lineages. In (**a**), two species (*S. citellus* and *S. xanthoprymnus*) were used as outgroups (they are excluded from the shown tree); posterior probabilities are shown next to nodes; and dots indicate a same nucleotide compared to the first reference sequence. In (**b**), the circle size reflects the frequency of haplotypes. Photograph source: Utku Perktaş

reserves and therefore over-winter starvation, especially for hibernating mammals (Morelli et al. 2012). These variables may also limit the potential distribution of Taurus ground squirrels by structuring the vegetation. Geyik Mountains (included in the Mediterranean basin biodiversity hotspot; Mittermeier et al. 2004) where natural grasslands and open spaces with little or no vegetation are the predominant cover types are generally higher and

Table 3 Summary of AMOVA

Level	Source	df	SS	MS	Var	%	PhiPT	*P*
Northern and southern populations[a]	Among populations	1	35.162	35.162	1.873	71	0.706	0.000
	Within populations	49	38.250	0.781	0.781	29		
Western and eastern subpopulations within southern population[b]	Among populations	1	2.377	2.377	0.091	10	0.095	0.006
	Within populations	37	31.981	0.864	0.864	90		

df, degree of freedom; *SS*, sum of square; *MS*, mean square; *Var*, estimated variance component; %, percent of variance component; *PhiPT*, statistic calculating population differentiation; *P*, probability value

[a] For the northern and southern populations, see Table 1

[b] The eastern subpopulation: locality 14, 15, 16, 21, 22, and 23; the western subpopulation: other localities within the southern population. For locality number, see Table 1

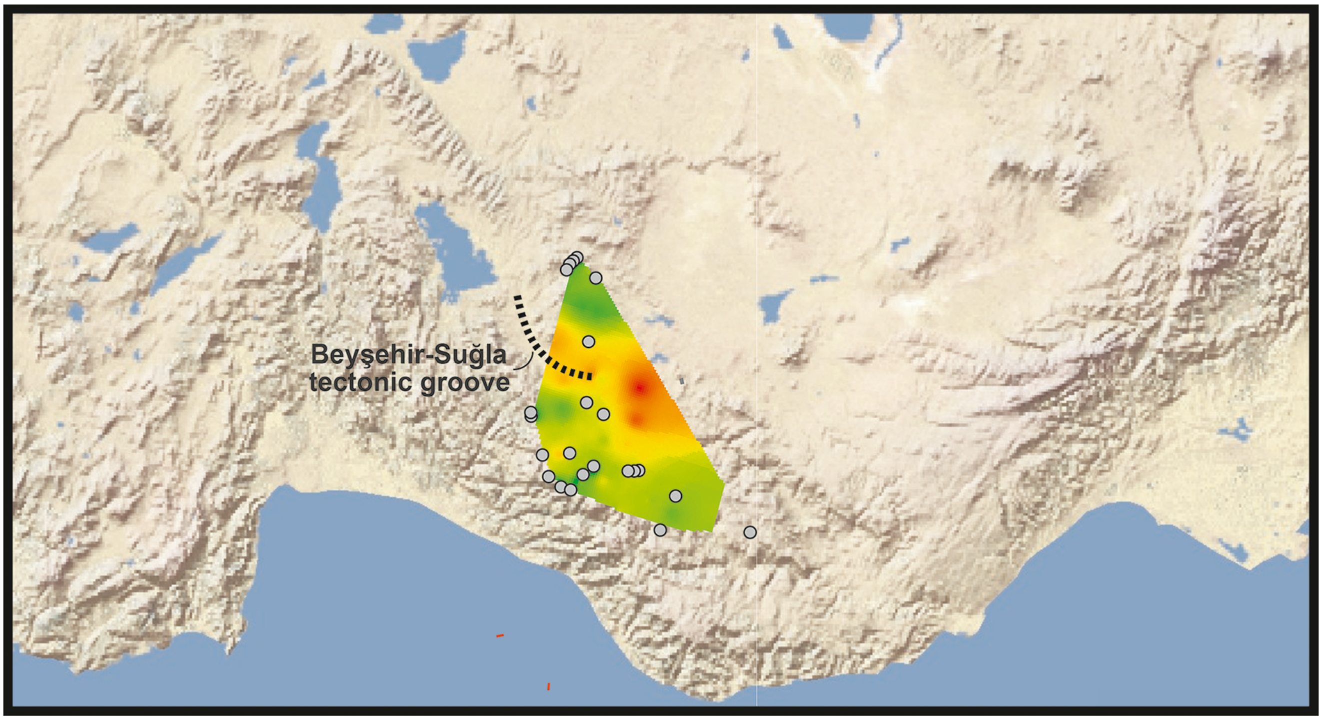

Fig. 6 The visualized patterns of genetic divergence for Taurus ground squirrels (*Spermophilus taurensis*). Gray circles indicate genetic sampling localities. Warmer colors (more red) depict areas of higher divergence. Basemap source: US National Park Service

therefore colder and snowier than Erenler Mountain (included in the Irano-Anatolian biodiversity hotspot; Mittermeier et al. 2004).

As in Mediterranean mountains (Hughes and Woodward 2017), the western Taurus Mountains, to which Taurus ground squirrels are endemic, were glaciated during the Late Quaternary (Sarıkaya et al. 2011; Sarıkaya and Çiner 2015, 2017). The Last Glacial Maximum was 8 to 11 °C colder and 1.5 to 2 times higher precipitation in this region, the southwestern Anatolia (Sarıkaya and Çiner 2015). For example, the advance and retreat of piedmont glaciers in the Namaras Valley of Geyik Mountains occurred at $> 19.1 \pm 3.4$ kya and 18.0 ± 1.0 kya. These glaciers expanded down to an altitude of c. 2000 m, and reached a length of c. 4 km (Çiner et al. 2015). In these mountain ranges, the equilibrium line altitude has risen from 2500 to 3400 m since the Last Glacial Maximum (Sarıkaya and Çiner 2015, 2017). As hypothesized, our results suggest that Taurus ground squirrels survived these Late Quaternary glacial-interglacial cycles by altitudinal migrations without large geographical displacements. Such altitudinal migrations are common for montane mammals (Graham 1986; Waltari and Guralnick 2009). As warming occurred from the Last Glacial Maximum to the Mid-Holocene to the present, the potential distribution of Taurus ground squirrels shifted towards higher altitudes, resulting in a smaller range in the present. Thus, lowlands (i.e. Beyşehir-Suğla tectonic groove) between Erenler Mountain and Geyik Mountains, also a biogeographic boundary between the Irano-Anatolian and Mediterranean basin biodiversity hotspots, partly divided this range into two parts (the northern and southern populations). Taurus ground squirrels had a relatively shallow phylogeny, and were composed of two geographically structured cyt *b* mtDNA lineages (northern and southern). As it is understood, these lineages were geographically associated to mountain ranges, with the northern lineage in Erenler Mountain (with the exception of two individuals from two localities in Geyik Mountains) and the southern lineage in Geyik Mountains, and had a small overlap in their bioclimatic niches. Accordingly, the patterns of genetic divergence were spatially coincident with areas of low suitability between these mountain ranges. The time to divergence and migration rate suggested a scenario of historical isolation with low level of gene flow between these populations. These MDIV results should be interpreted cautiously because they are based on a single genetic locus, and MDIV assumes a stable effective size since divergence and equal effective sizes in the two populations. All these suggest that populations on different mountain ranges experienced alternating periods of connectivity and isolation through the Late Quaternary glacial-interglacial periods, respectively. Alternating periods of connectivity and isolation during altitudinal migrations caused by the Late Quaternary glacial-interglacial cycles also explain the intraspecific diversification of other montane mammals (e.g. Harrison et al. 2000; Galbreath et al. 2009).

Taurus ground squirrels had a small range and low genetic diversity (this study; Gündüz et al. 2007). Much higher genetic diversity was found for European ground squirrels (Říčanová et al. 2013) and Anatolian ground squirrels (Gündüz et al. 2007), the wide-ranging sister taxa of Taurus ground squirrels (Gündüz et al. 2007; for the range maps, see Thorington et al. 2012). A role of climate-driven range shifts as a driver of divergence through the Late Quaternary glacial-interglacial cycles was also supported for these species (Gür 2013; Říčanová et al. 2013). Within Taurus ground squirrels, the narrow-ranging northern population from areas of low niche stability in Erenler Mountain had lower genetic diversity than the southern population in Geyik Mountains. This is consistent with a generalized pattern of reduced genetic diversity for populations occurring on both increasingly small and isolated islands (Ditto and Frey 2007) and/or in areas where the Late Quaternary glacial-interglacial cycles would have made the region less inhabitable or uninhabitable during particular periods (Alvarado-Serrano and Knowles 2014). Médail and Diadema (2009) identified 52 refugia in the Mediterranean bioclimatic region, of which one corresponds to the region where Geyik Mountains are located, and argued that these refugia represent climatically stable areas. Accordingly, landscape connectivity was generally higher across Geyik Mountains.

Montane species are especially vulnerable to global climate changes because they have geographically isolated, small ranges, and unique adaptations to montane environmental conditions (Johnston et al. 2012). Thus, montane environments represent one of the most sensitive ecosystems to global climate changes. Moreover, endemism increases with increasing altitude in the western and central Taurus Mountains, making higher altitudes of these mountain ranges outstandingly important in terms of conserving the high-mountain diversity (Parolly 2015). As expected and hypothesized, our results suggest that as warming continues, the potential distribution of Taurus ground squirrels will continue to shift towards higher altitudes, resulting in a much smaller range in the future. Future projections for other montane mammals also gave similar results (e.g. Johnston et al. 2012). All these are consistent with that montane species are shifting their range towards higher altitudes as a result of ongoing climate change (Parmesan 2006). With an upward shift of life zones, anthropogenic impacts (transhumance, shifts in land-use systems, overgrazing) may even reach higher up in the future (Parolly 2015). Thus, particular sources of concern are the synergistic effects of future climate change and anthropogenic impacts on Taurus ground squirrels and their montane environments.

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Author contributions U.P. conducted laboratory studies; H.G. conducted ecological niche modelling analyses; H.G and U.P. conducted molecular phylogeography analyses; H.G, U.P., and M.K.G. contributed to the interpretations of the results; and H.G. prepared and edited the manuscript, with input from all authors.

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