The effects of the Late Quaternary glacial–interglacial cycles on Anatolian ground squirrels: range expansion during the glacial periods?

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The present study aimed to understand how Anatolian ground squirrels, *Spermophilus xanthoprymnus* (Bennett, 1835), have responded to global climate changes through the Late Quaternary glacial–interglacial cycles. Accordingly, ecological niche modelling was used, together with molecular phylogeography. Using species occurrence data compiled from field observations and relevant sources and the maximum entropy machine learning algorithm in MAXENT, an ecological niche model was developed to predict the potential geographical distribution of *S. xanthoprymnus* under reconstructed past (the Last Interglacial, approximately 130 000–116 000 years ago and the Last Glacial Maximum, 21 000 years ago) and present (1950–2000) bioclimatic conditions. In addition, using cytochrome *b* mitochondrial DNA sequences deposited in GenBank and the Bayesian skyline plot in BEAST, demographic events (population fluctuations) were further assessed over the history of Anatolian ground squirrels. Combined ecological niche modelling and molecular phylogeography revealed that *S. xanthoprymnus*, itself also a temperate (mid-latitude) species, has responded to global climate changes through the Late Quaternary glacial–interglacial cycles in a fashion converse to that of most temperate (mid-latitude) species: its range expanded rather than contracted during the glacial periods and contracted rather than expanded during the interglacial periods. In other words, Anatolian ground squirrels have been in refugia during the interglacial periods, suggesting that the classical paradigm of glacial range contraction and interglacial range expansion for temperate species may not be as general as previously assumed. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **109**, 19–32.

ADDITIONAL KEYWORDS: ecological niche modelling – expansion-contraction model – global climate changes – Last Glacial Maximum – Last Interglacial – molecular phylogeography – *Spermophilus xanthoprymnus*.

INTRODUCTION

Understanding the geographical distribution of species has important implications for major issues in ecology, evolution, and conservation biology, such as which factors limit the geographical distribution of species and how species respond to global climate changes. A practical approach to understanding the geographical distribution of species is to use ecological niche modelling (Graham *et al.*, 2004). Ecological niche modelling relates georeferenced species occurrence data (i.e. a set of geographical coordinates where species of interest has been observed) to environmental data (i.e. a number of environmental variables obtained using a geographical information system-based approach) and creates models to predict the potential geographical distribution of species (Guisan & Thuiller, 2005). Under the assumptions of species–climate equilibrium and stability of ecological niches through time (Nogués-Bravo, 2009), these models can also be projected onto reconstructed past or projected future climate data to predict the potential geographical distribution of species at that time in the past or in the future (Peterson *et al.*, 2002; Hijmans & Graham, 2006; Waltari *et al.*, 2007).

The geographical distribution and genetic structure of temperate (mid-latitude) species have been

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strongly influenced by the climatic oscillations of the Late Quaternary (Hewitt, 1996, 1999, 2000, 2004). During the glacial periods, the climate was too cold and dry for the survival of most of these species in their current range. Thus, they survived these glacial periods in glacial refugia, usually at lower latitudes (glacial range contraction into refugia). During the interglacial periods, however, they recolonized new areas, usually at higher latitudes, from these glacial refugia (interglacial range expansion from refugia; Hewitt, 1996, 1999, 2000, 2004). This pattern of glacial range contraction and interglacial range expansion is known as the 'expansion–contraction' model (Provan & Bennett, 2008). This model has already been well documented in temperate species by molecular phylogeography (Hewitt, 1996, 1999, 2000, 2004), although it may not be appropriate for some of these species (e.g. Canestrelli & Nascetti, 2008). Ecological niche modelling has also been become widely used to understand further the response of species to global climate changes through the Late Quaternary glacial–interglacial cycles (Nogués-Bravo, 2009). In this respect, in mammalian species, many studies have used ecological niche modelling either alone (Waltari et al., 2007; Banks et al., 2008; Fløjgaard et al., 2009; Waltari & Guralnick, 2009) or together with molecular phylogeography (Carstens & Richards, 2007; Galbreath, Hafner & Zamudio, 2009; Jezkova et al., 2009; Vega et al., 2010).

Anatolian ground squirrels, *Spermophilus xanthoprymnus* (Bennett, 1835), are diurnally active, hibernating ground-dwelling squirrels that sleep and hibernate underground but forage aboveground in the steppes and alpine meadows of central lowland and eastern highland Anatolia and of adjacent Armenia and north-western Iran (Fig. 1; Kart Gür & Gür, 2010). Anatolian ground squirrels are mainly active from March to September and hibernate during the remaining months (Gür & Kart Gür, 2005; Kart Gür, Refinetti & Gür, 2009; Kart Gür & Gür, 2010). Along with being highly tolerant to dry conditions, *S. xanthoprymnus* also appears to be tolerant to cold seasonal conditions because it ranges from approximately 800 to 2900 m (Kart Gür & Gür, 2010). The geographical distribution of Anatolian ground squirrels is mainly in the central and north-eastern Anatolian climate zones, which are colder and drier than the other climate zones in Turkey (for the climate zones of Turkey, see Unal, Kındap & Karaca, 2003: fig. 5; for the geographical distribution of the species, see Fig. 1). The close correspondence between the two climate zones and the geographical distribution suggests that climate is one of the main factors that limit the geographical distribution of *S. xanthoprymnus* (Gür, 2007; Kart Gür & Gür, 2010). For this reason,

Anatolian ground squirrels may represent an ideal study system for ecological niche modelling.

The present study aimed to understand how Anatolian ground squirrels have responded to global climate changes through the Late Quaternary glacial–interglacial cycles, which is critical to predicting their likely responses to ongoing and future global climate changes and therefore can help guide management initiatives. If the classical paradigm of glacial range contraction and interglacial range expansion (i.e. the 'expansion–contraction' model; Provan & Bennett, 2008) broadly explains the response of temperate species to global climate changes through the Late Quaternary glacial–interglacial cycles, it is predicted that it should also be appropriate for *S. xanthoprymnus*, itself also a temperate (mid-latitude) species. To test this prediction, ecological niche modelling was used, together with molecular phylogeography (Richards, Carstens & Knowles, 2007). Using species occurrence data compiled from field observations and relevant sources and the maximum entropy machine learning algorithm in MAXENT (Phillips, Dudík & Schapire, 2004; Phillips, Anderson & Schapire, 2006; Elith et al., 2011), an ecological niche model (ENM) was developed to predict the potential geographical distribution of Anatolian ground squirrels under reconstructed past (the Last Interglacial, LIG, approximately 130 000–116 000 years ago and the Last Glacial Maximum, LGM, 21 000 years ago) and present (1950–2000) bioclimatic conditions. This approach allowed an evaluation of climate-driven range shifts (expansions or contractions) under the assumptions of species-climate equilibrium and stability of ecological niches through time (Nogués-Bravo, 2009). In addition, using cytochrome *b* (cyt *b*) mitochondrial (mt)DNA sequences deposited in GenBank (Harrison et al., 2003; Gündüz et al., 2007) and the Bayesian skyline plot in BEAST (Drummond et al., 2005), demographic events (population fluctuations) were further assessed over the history of *S. xanthoprymnus*. This approach also allowed an evaluation of climate-driven range shifts (expansions or contractions) under the assumption that range shifts should be accompanied by population fluctuations (Jezkova, Olah-Hemmings & Riddle, 2011). For example, if a species expanded or contracted its range at a certain time in the past, an increase or a decrease in the effective population size, respectively, would be detected at that time.

MATERIAL AND METHODS
ECOLOGICAL NICHE MODELLING

Species occurrence data were compiled from field observations (86 records) and the following sources
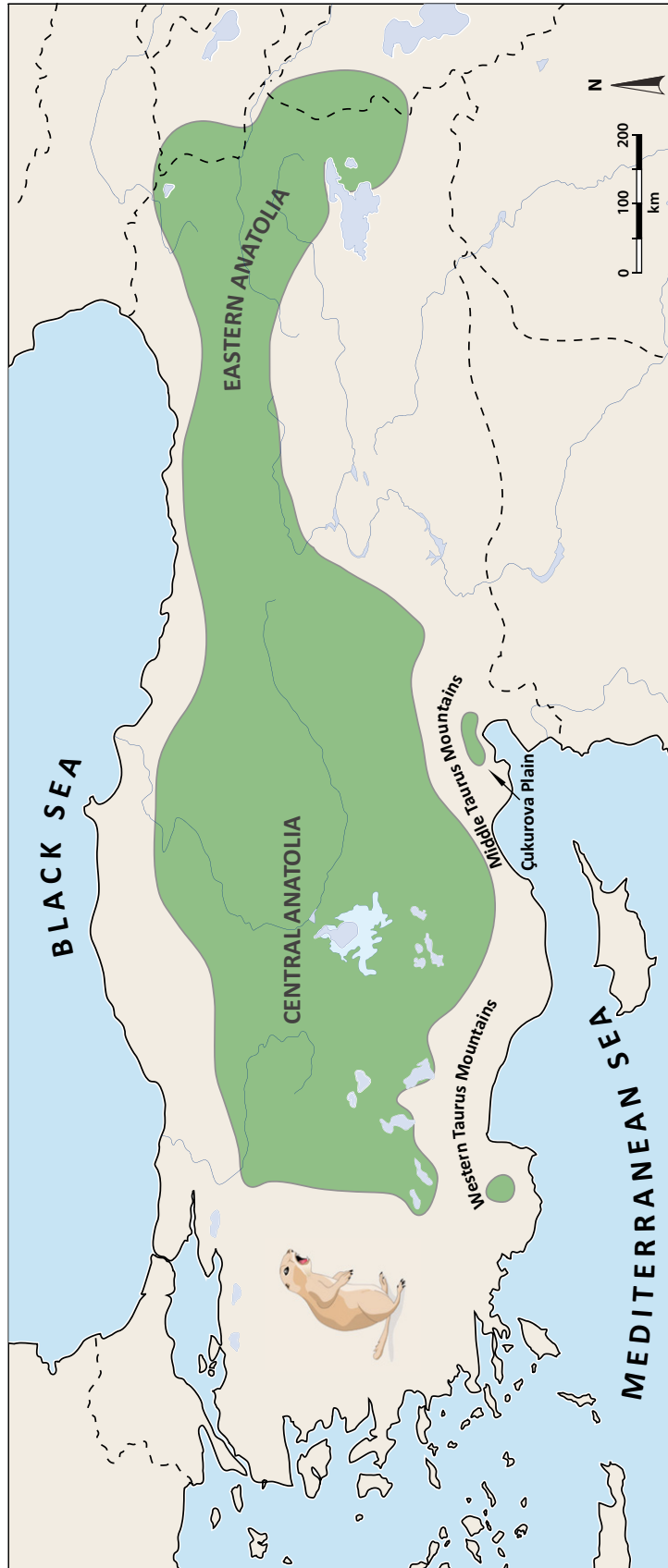
Figure 1. The geographical distribution (green shade) of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) in Turkey and adjacent countries (for literature citations, see Kart Gür & Gür, 2010).

(132 records): Osborn (1964), Mursaloğlu (1965), Kral (1975), Kaya & Şimşek (1986), Karaçay (2002), Kryštufek & Vohralík (2005), Gündüz *et al*. (2007), Özkurt *et al*. (2007), Aykut (2009), Gazyağcı, Aşan & Albayrak (2009), Kart Gür *et al*. (2009), Gür (2010), Holding (2011), GBIF (Global Biodiversity Information Facility; http://www.gbif.org), and TRAMEM (Anonymous Mammals of Turkey; http://www. tramem.org). The occurrence records with text-only locality descriptions were georeferenced using Google Earth, version 6.2 (http://www.google.com/earth). Because a low precision of the occurrence records can diminish the quality of ecological niche modelling (Graham *et al*., 2008), only those occurrence records with a precision of less than 5 km were considered. To correct for biased sampling effort and reduce spatial dependence, the occurrence records compiled were spaced at least 10 km apart by removing intervening ones (Pearson *et al*., 2007). Thus, a total of 169 occurrence records, covering almost all of the known geographical distribution of Anatolian ground squirrels, were used in ecological niche modelling (Figs 1, 2A). There were no occurrence records from southern Anatolia (i.e. in the western part of the western Taurus Mountains, the eastern part of the middle Taurus Mountains, and Çukurova Plain; Figs 1, 2A). Already, the species or biogeographical status of ground squirrel populations in these areas is unclear (Kart Gür & Gür, 2010). There were also no fossil occurrence records from the LIG and the LGM.

Bioclimatic data for three time periods were used: two past (the LIG, approximately 130 000– 116 000 years ago and the LGM, 21 000 years ago) and one present (1950–2000). Reconstructed LIG bioclimatic data are based on the Community Climate System Model, version 3 (CCSM; Otto-Bliesner *et al*., 2006). These bioclimatic data, obtained from the WorldClim–Global Climate Data (http://www. worldclim.org/past) at a spatial resolution of 30 s, were subsequently resampled to a spatial resolution of 2.5 min. Reconstructed LGM bioclimatic data are based on both the CCSM, version 3 (Collins *et al*., 2006) and the Model for Interdisciplinary Research on Climate, version 3.2 (MIROC; K-1 Model Developers, 2004). These bioclimatic data were obtained from the WorldClim–Global Climate Data (http://www. worldclim.org/past) at a spatial resolution of 2.5 min and have been previously used successfully in a similar study of 12 plant and animal species in the same region (Tarkhnishvili, Gavashelishvili & Mumladze, 2012). The present bioclimatic data are based on interpolation using a thin-plate smoothing spline of observed climate at weather stations from a large number of global, regional, national, and local sources, mostly for the period 1950–2000, with latitude, longitude, and altitude as independent variables (Hijmans *et al*., 2005a). These bioclimatic data were obtained from the WorldClim–Global Climate Data (http://www.worldclim.org/current) at a spatial resolution of 2.5 min.

Bioclimatic data include 19 bioclimatic variables derived from monthly temperature and precipitation values (for detailed descriptions of these bioclimatic variables, see Supporting information, Table S1; see also http://www.worldclim.org/bioclim). These bioclimatic variables represent biologically meaningful variables for determining the geographical distribution of species and therefore are commonly used in ecological niche modelling.

Ecological niche modelling was based on all 19 bioclimatic variables in the above-mentioned bioclimatic data (see below). All these variables were masked to include only 25° to 46°E and 35° to 43°N.

Using the maximum entropy machine learning algorithm in MAXENT, version 3.3.3k (http://www.cs. princeton.edu/~schapire/maxent) (Phillips *et al*., 2004, 2006; Elith *et al*., 2011), an ENM was developed within the above-mentioned mask to predict the potential geographical distribution of Anatolian ground squirrels under reconstructed past (the LIG, approximately 130 000–116 000 years ago and the LGM, 21 000 years ago) and present (1950–2000) bioclimatic conditions. Although MAXENT is relatively robust to correlations among bioclimatic variables, an ENM based on the four most significant bioclimatic variables (see Results) in predicting the present potential distribution of *S. xanthoprymnus* was also developed to test for model over-fitting (Galbreath *et al*., 2011; Wilson & Pitts, 2012). Both the ENMs gave qualitatively similar predictions for present bioclimatic conditions, suggesting that model over-fitting as a result of all 19 bioclimatic variables was not a critical issue (see Supporting information, Fig. S1).

MAXENT, which is among the most effective methods of ecological niche modelling (Elith *et al*., 2006), was run with the settings: auto features (feature types are automatically selected depending on the training sample size), create response curves (showing how the prediction depends on a particular bioclimatic variable), logistic output format, do MESS (multivariate environmental similarity surface) analysis (showing where novel bioclimatic conditions are encountered during projecting), regularization multiplier = 1, maximum number of background points = 10 000, extrapolate (extrapolating to bioclimatic conditions not encountered during training), do clamping (treating bioclimatic conditions not encountered during training as if they were at the limit of bioclimatic conditions encountered during training), maximum iterations = 500, convergence threshold = 0.00001, and fade by clamping (reducing the
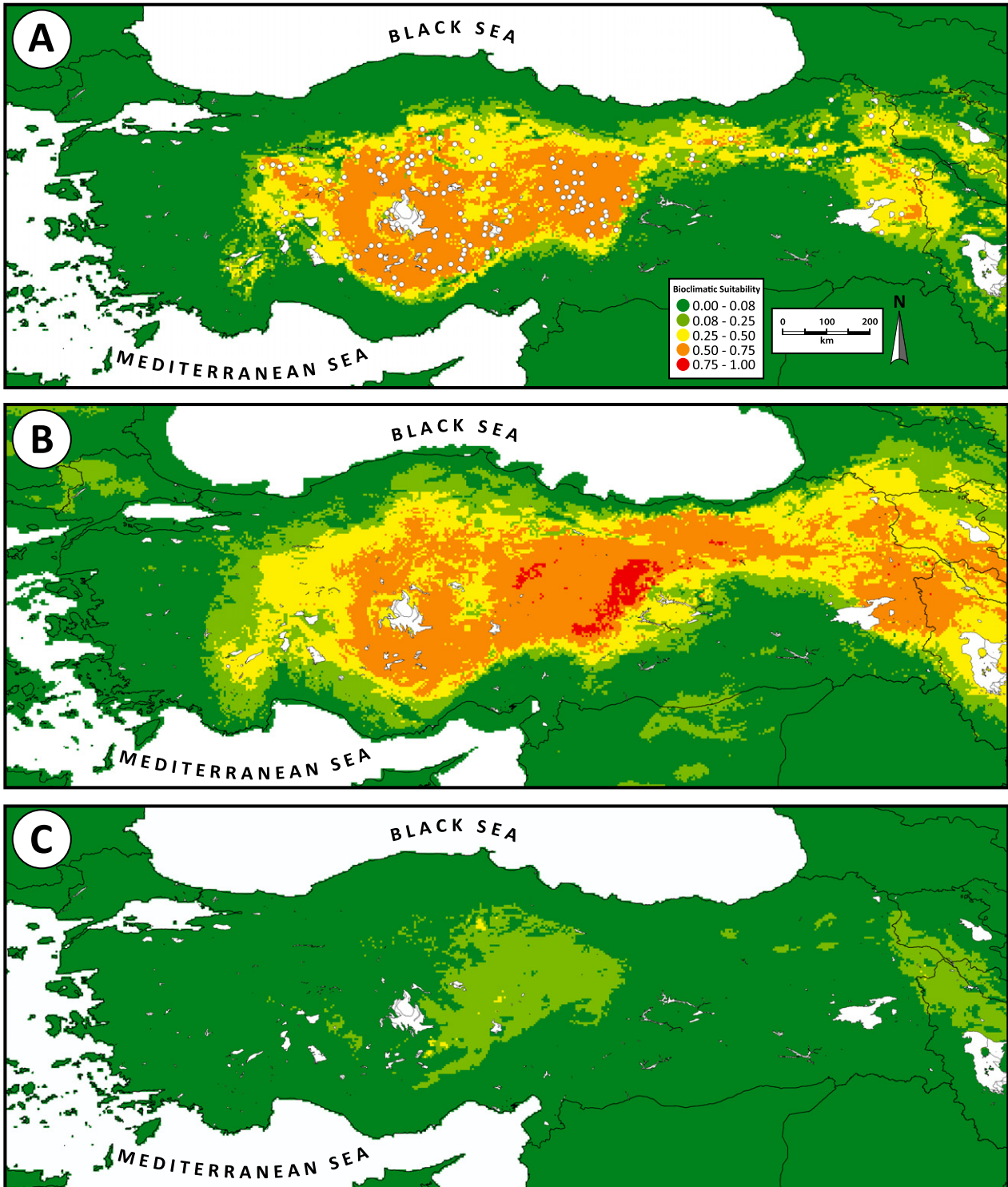
Figure 2. Ecological niche model (ENM) showing the potential geographical distribution of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) under (A) present (1950–2000) and (B, C) reconstructed past [(B) the Last Glacial Maximum, LGM, 21 000 years ago and (C) the Last Interglacial, LIG, approximately 130 000 to 116 000 years ago] bioclimatic conditions. The visible area in maps is 25° to 46°E and 35° to 43°N. A, open circles indicate the occurrence records. B, note that the LGM coastline differs from the present and the LIG coastlines because the sea level was lower in the LGM than both in the present and in the LIG, and also that the present borders of the lakes are shown (for the LGM borders of the lakes and the location of the Paleo–Konya Lake on the southern part of central Anatolia, see Doğan, 2010).

effect of projecting onto bioclimatic conditions not encountered during training). The default setting of the regularization multiplier provided the appropriate model complexity because the ENM performance did not differ [i.e. differences among the mean AUCs for test data (see below) ranged from 0 to 0.004], when setting the regularization multiplier at 0.05, 0.25, 0.50, 0.75, 1, 2, 5, and 10 (Richmond *et al.*, 2010; for further details about model complexity, see Warren & Seifert, 2011). Fade by clamping was performed because novel bioclimatic conditions were encountered during projecting (Elith, Kearney & Phillips, 2010). However, novel bioclimatic conditions encountered during projecting were not in terms of the four most significant bioclimatic variables (see Results) in predicting the present potential distribution of Anatolian ground squirrels (results not shown). Thus, novel bioclimatic conditions encountered during projecting were not a critical issue. A ten-fold cross-validation was also performed in which a different 90% of the occurrence records was used to train the ENM and 10% was used to test it for each of ten runs. Thus, each of the occurrence records was used to test the ENM once. It is important to note that the test omission rate was a good match to the predicted omission rate, suggesting that spatial dependence between test and training data was not a critical issue (Phillips, 2010). MAXENT provides estimates of the relative contributions of bioclimatic variables to the ENM through the percentage contribution and permutation importance. MAXENT also tests the ENM by computing the area under the receiver operating characteristic curve (AUC). An AUC > 0.5 indicates that the ENM performs better than a random prediction (AUC = 0.5). Conversely, an AUC < 0.5 indicates that the ENM performs worse than a random prediction. Given test data, MAXENT furthermore computes binomial probabilities (one-sided) for all 11 thresholds to test the null hypothesis that the test occurrence records are predicted no better by the ENM than by a random prediction.

MAXENT generates a continuous prediction of bioclimatic suitability of specific geographical locations for species occurrence and reports values ranging from 0 (least suitable) to 1 (most suitable; Phillips *et al.*, 2004, 2006; Elith *et al.*, 2011). To define bioclimatically suitable areas both in the past (the LIG and the LGM) and in the present, one out of 11 thresholds applied by MAXENT was chosen: the 'minimum training presence' threshold. This threshold was averaged across the ten-fold cross-validation runs (mean ± SD, range = 0.082 ± 0.026, 0.032–0.110). The 'minimum training presence' threshold was chosen because Anatolian ground squirrels do not have high dispersal ability and therefore are unlikely

to be observed in unsuitable habitats (Pearson *et al.*, 2007). Application of this threshold resulted in the prediction for present bioclimatic conditions largely in agreement with the known geographical distribution of *S. xanthoprymnus* (see Results).

Given one ecological niche modelling algorithm (MAXENT) and two reconstructed LGM bioclimatic data (the CCSM and the MIROC), two predictions for LGM bioclimatic conditions were obtained. These two predictions (i.e. logistic outputs) were similar and averaged to generate a final summary prediction for LGM bioclimatic conditions (Waltari & Guralnick, 2009).

All GIS operations were conducted using DIVA-GIS, version 7.5.0.0 (http://www.diva-gis.org) (Hijmans *et al.*, 2005b).

MOLECULAR PHYLOGEOGRAPHY

Anatolian ground squirrels are phylogeographically structured into five cyt *b* mtDNA lineages, labelled lineages 1 to 5 (Gündüz *et al.*, 2007). Gündüz *et al.* (2007) assessed the demographical history in five lineages and concluded that these lineages have signals of population expansion (fit with mismatch distribution, haplotypes with wide distributions, negative Tajima's *D* and Fu's F_S) using the mismatch distribution under the sudden expansion model (Rogers & Harpending, 1992) and Tajima's (1989) *D* and Fu's (1997) F_S statistics. The present study further assessed demographic events (population fluctuations) over the history of *S. xanthoprymnus* using cyt *b* mtDNA sequences (two cyt *b* mtDNA haplotypes from Harrison *et al.*, 2003 and 49 cyt *b* mtDNA haplotypes from Gündüz *et al.*, 2007) deposited in GenBank (http://www.ncbi.nlm.nih.gov/GenBank) and the Bayesian skyline plot in BEAST, version 1.7.2 (http://beast.bio.ed.ac.uk) (Drummond *et al.*, 2005). The Bayesian skyline plot, a coalescent-based approach, estimates the posterior distribution for effective population size at intervals along a phylogeny, thus allowing inferences of population fluctuations over time. This coalescent-based approach was performed for the complete Anatolian ground squirrel data but not for each lineage. This made the results of ecological niche modelling and molecular phylogeography more comparable because the ideal data were not available to develop an ENM and a Bayesian skyline plot (for possible caveats, see Ho & Shapiro, 2011) for each lineage.

The Markov Chain Monte Carlo (MCMC) analysis was run for 50 million iterations (sampled every 5000 iterations), of which the first 10% was discarded as the burn-in, with the settings: Hasegawa–Kishino–Yano (HKY) substitution model, estimated base frequencies, gamma site heterogeneity model with four

categories, two different clock models (strict molecular clock model and uncorrelated lognormal relaxed clock model), Bayesian skyline coalescent tree prior with ten groups, and piecewise-constant skyline model. These settings were created using BEAUti, version 1.7.2 (part of BEAST). The SD of the uncorrelated lognormal relaxed clock was estimated to be 0.178 (95% highest posterior density interval: –0.000 to 0.459), suggesting that the data were quite clock-like. Thus, in the MCMC analysis, the strict molecular clock model was used. The substitution model (HKY + gamma) was selected using MEGA, version 5.05 (http://www.megasoftware.net) (Tamura *et al.*, 2011). Given a divergence rate of 2% [a standard divergence rate for mammalian mtDNA (Avise, Walker & Johns, 1998) and also used for ground squirrel mtDNA (Gündüz *et al.*, 2007; Kryštufek, Bryja & Bužan, 2009)] per million year between cty *b* mtDNA sequences and a generation time of 1 year (Gür & Kart Gür, 2005; Kart Gür & Gür, 2010), a substitution rate of 1×10^{-8} per lineage per site per year was used for Anatolian ground squirrels (for exchange of divergence and substitution rates, see Schenekar & Weiss, 2011; http://www.uni-graz.at/zoowww/mismatchcalc/index.php). The MCMC analysis was repeated three times using different random number seeds to determine whether three independent runs were converging on the same distribution. After discarding the burn-in from each run, three independent runs were combined using LOGCOMBINER, version 1.7.2 (part of BEAST). The Bayesian skyline plot was created using TRACER, version 1.5 (http://tree.bio.ed.ac.uk/software/tracer). In all analyses, effective sample size for all parameters exceeded 200, suggesting that 50 million iterations were sufficient to assess population fluctuations over the history of *S. xanthoprymnus*.

The geographical distribution of cyt *b* mtDNA haplotypes from Anatolian ground squirrels was also assessed along with the predictions for reconstructed past (the LIG and the LGM) and present bioclimatic conditions to elucidate how five lineages may have colonized central lowland and eastern highland Anatolia, as well as adjacent Armenia and north-western Iran.

RESULTS

ECOLOGICAL NICHE MODELLING

For Anatolian ground squirrels, the ENM performed better than a random prediction. The AUC was close to 1 [AUC for training data (mean ± SD, range) = 0.932 ± 0.003, 0.928–0.937; AUC for test data (mean ± SD, range) = 0.885 ± 0.019, 0.842–0.905, based on the ten-fold cross-validation runs]. The

small SD for the mean AUC for test data suggested that the ENM performance was robust to variation in the selection of the occurrence records for training and testing. Furthermore, across all 11 thresholds and the ten-fold cross-validation runs, the test occurrence records were predicted significantly better by the ENM than by a random prediction ($P < 0.001$).

For three time periods (the LIG, the LGM, and the present), the logistic output of the ENM was reported (Fig. 2), which is a continuous prediction of bioclimatic suitability of specific geographical locations for Anatolian ground squirrels. The prediction for present bioclimatic conditions largely matched the known geographical distribution of *S. xanthoprymnus* (Figs 1, 2A), suggesting that Anatolian ground squirrels are at equilibrium or very near to equilibrium with climate and inhabit the steppes and alpine meadows within most areas with suitable bioclimatic conditions throughout Anatolia. Among bioclimatically suitable areas, those in the most eastern part of the study area (25° to 46°E and 35° to 43°N) are not known to harbour any populations of *S. xanthoprymnus*, although there are a few studies in these areas. Also, among bioclimatically unsuitable areas, those in southern Anatolia (i.e. in the western part of the western Taurus Mountains, the eastern part of the middle Taurus Mountains, and Çukurova Plain) are known to harbour a few populations of Anatolian ground squirrels (Figs 1, 2A). This last finding supported the suggestions of Kart Gür & Gür (2010): (1) the designation of ground squirrel populations in the western part of the western Taurus Mountains as *S. xanthoprymnus* may be suspicious because Taurus ground squirrels, *Spermophilus taurensis*, were recently recognized in southern Anatolia (i.e. in the eastern part of the western Taurus Mountains; Gündüz *et al.*, 2007; for the geographical distribution of both species, see Gür & Kart Gür, 2010: fig. 1) and (2) the presence of ground squirrel populations in the eastern part of the middle Taurus Mountains and especially in Çukurova Plain requires confirmation and, if confirmed, explanation.

When an ENM was also developed within the mask adjusted so as not to include southern Anatolia and then projected to the study area, the results did not change, supporting the suggestion that southern Anatolia was not within the present potential distribution of Anatolian ground squirrels (Figs 1, 2A; see also Supporting Information, Fig. S2).

The percentage contribution and/or permutation importance suggested that 'annual mean temperature' (Bio1), 'mean temperature of driest quarter' (Bio9), 'annual precipitation' (Bio12), and 'precipitation of warmest quarter' (Bio18) were the most significant bioclimatic variables in predicting the present potential distribution of Anatolian ground

squirrels (see Supporting information, Table S2). The response curves produced by models created using only one of these bioclimatic variables at a time indicated that *S. xanthoprymnus* prefers to inhabit areas where 'annual precipitation' is 270–550 mm, 'annual mean temperature' is up to 12 °C, 'precipitation of warmest quarter' is 10–140 mm, and 'mean temperature of driest quarter' is up to 21.5 °C (see Supporting information, Fig. S3).

The predictions for reconstructed past (the LIG and the LGM) and present bioclimatic conditions suggested that Anatolian ground squirrels survived the LIG in multiple interglacial refugia (one group in central lowland Anatolia and another group in eastern highland Anatolia and adjacent areas) and, afterwards, they substantially expanded their range from these interglacial refugia during the last glacial period (including the LGM; see also below) and slightly contracted their range into the present potential distribution during the present interglacial period (Fig. 2). However, the predictions for reconstructed past (the LIG and the LGM) and present bioclimatic conditions also indicated that *S. xanthoprymnus* did not experience altitudinal or latitudinal range shifts (median elevation, interquartile range = 1345, 1126–1587 m for the LIG; 1318, 1013–1768 m for the LGM; and 1393, 1086–1807 m for the present; for latitudinal shift, see Fig. 2) during the above-mentioned time period.

MOLECULAR PHYLOGEOGRAPHY

The Bayesian skyline plot suggested an increase in the effective population size starting before the LGM, during the last glacial period (115 000–12 000 years ago; Cowie, 2007), followed by a decrease in the effective population size starting after the LGM, largely during the present interglacial period. These population fluctuations followed a period of some stability in the effective population size, although this likely reflects a lack of demographic signal at deeper time scales (Fig. 3). Although the Bayesian skyline plot was based on a single mitochondrial locus and therefore the 95% highest posterior density interval was large (Fig. 3) and the assumption of panmixia may have been violated because Anatolian ground squirrels are phylogeographically structured, these findings were considered to be robust because they are consistent with those of ecological niche modelling in that *S. xanthoprymnus* substantially expanded its range from interglacial refugia during the last glacial period (including the LGM) and slightly contracted its range into the present potential distribution during the present interglacial period.

The geographical distribution of cyt *b* mtDNA haplotypes from Anatolian ground squirrels showed that four (lineages 2 to 5) out of five lineages inhabit central lowland Anatolia. Thus, during the last glacial period, lineages 2 to 5, or at least some of them, may
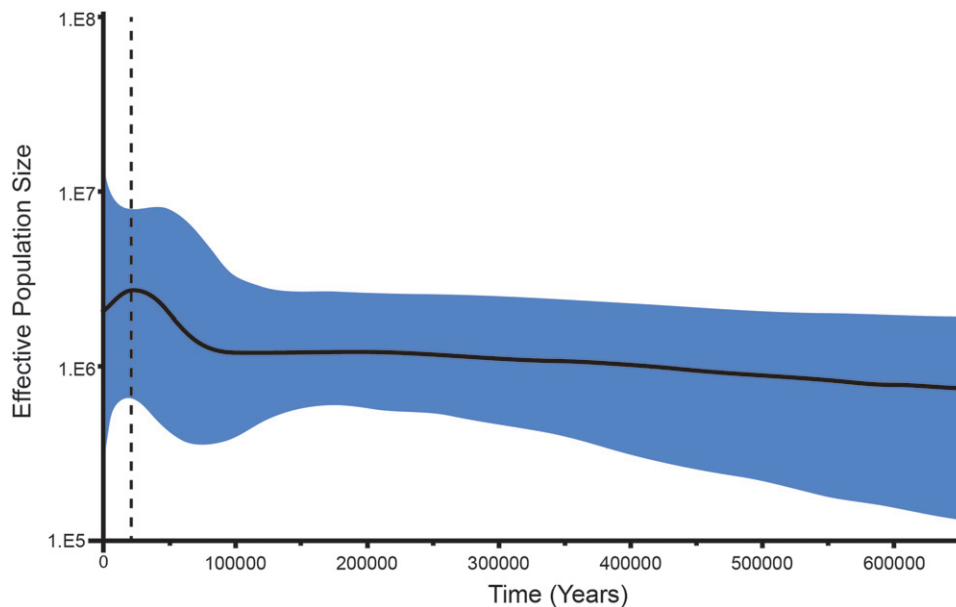

Figure 3. The Bayesian skyline plot for Anatolian ground squirrels (*Spermophilus xanthoprymnus*) showing the effective population size as a function of time. The central line represents the median value of the log₁₀ of the effective population size and the shaded area shows the 95% highest posterior density. The position of the Last Glacial Maximum (LGM, 21 000 years ago) is represented by the dashed vertical line.

have recolonized central lowland Anatolia from the interglacial refugia in the same region. Although these lineages in central lowland Anatolia partly overlap with each other, they do not at all overlap with lineage 1 in eastern highland Anatolia and adjacent areas. Thus, during the last glacial period, lineage 1 may have recolonized eastern highland Anatolia and adjacent areas from the interglacial refugia in the same region (Fig. 4).

DISCUSSION

The present study aimed to understand how Anatolian ground squirrels have responded to global climate changes through the Late Quaternary glacial–interglacial cycles. Accordingly, ecological niche modelling was used, together with molecular phylogeography (Richards, Carstens & Knowles, 2007), to test whether the classical paradigm of glacial range contraction and interglacial range expansion (i.e. the 'expansion–contraction' model; Provan & Bennett, 2008) for temperate species is also appropriate for *S. xanthoprymnus*, itself also a temperate species. The present study represents a first attempt to combine ecological niche modelling and molecular phylogeography for a species in Anatolia, in which high levels of intraspecific genetic differentiation are observed, and which is also an important source and refugium of genetic diversity for European biota (Bilgin, 2011).

The results of ecological niche modelling suggested that Anatolian ground squirrels have responded to global climate changes through the Late Quaternary glacial–interglacial cycles in a fashion converse to that of most temperate species: their range expanded rather than contracted during the glacial periods and contracted rather than expanded during the interglacial periods. In other words, *S. xanthoprymnus* has been in refugia during the interglacial periods. Thus, the classical paradigm of glacial range contraction and interglacial range expansion for temperate species (Hewitt, 1996, 1999, 2000, 2004) does not hold true for Anatolian ground squirrels and therefore may not be as general as previously assumed, at least at lower latitudes (Canestrelli & Nascetti, 2008) and in temperate species highly tolerant to cold seasonal and dry conditions. These results also supported the proposition of Stewart *et al.* (2010) suggesting that continental species, adapted to drier climate with greater seasonal variation, such as some Eurasian mammal species (e.g. ground squirrels, *Spermophilus s.l.*), have been in refugia during the interglacial periods. Thus, glacial range expansion and interglacial range contraction is not a pattern only for high-latitude (northern) and -altitude (alpine) species (Provan & Bennett, 2008).

The predictions for reconstructed past (the LIG and the LGM) bioclimatic conditions are more robust if the certain assumptions are met: species-climate equilibrium and stability of ecological niches through time (Nogués-Bravo, 2009). The geographical distribution of *S. xanthoprymnus* can be predicted successfully from present bioclimatic conditions, suggesting that Anatolian ground squirrels are at equilibrium or very near to equilibrium with climate. Thus, the assumption of species–climate equilibrium was confirmed. Indeed, of the most significant bioclimatic variables in predicting the present potential distribution of *S. xanthoprymnus*, 'annual mean temperature' (Bio1) and 'annual precipitation' (Bio12) affect the geographical distribution of the steppes in the Near East, including Anatolia (Atalay, 2002), and 'mean temperature of driest quarter' (Bio9) and 'precipitation of warmest quarter' (Bio18) (i.e. summer temperature and precipitation) affect plant productivity (food availability; Gür, 2007, 2010; Gür & Kart Gür, 2012), which influences life-history traits such as body mass, reproductive success, and survival of ground-dwelling squirrels (Van Horne, 2003). Although the assumption of stability of ecological niches through time could not be assessed, it appears to hold true for Anatolian ground squirrels because the results of molecular phylogeography were consistent with those of ecological niche modelling (see below).

Anatolian ground squirrels are phylogeographically structured into five cyt *b* mtDNA lineages that likely diverged 0.30–0.75 million years ago, with most population splits taking place 0.50–0.65 million years ago (Gündüz *et al.*, 2007). Gündüz *et al.* (2007) assessed the demographic history in five lineages and concluded that these lineages have signals of population expansion. Although Gündüz *et al.* (2007) did not directly estimate the time since population expansion, they suggested that *S. xanthoprymnus* survived the LGM in glacial refugia and recolonized Anatolia from these glacial refugia after the last glacial period. Gür (2010) suggested that, based on the pattern of geographical variation in body size of Anatolian ground squirrels and its relationship with environmental variables, these glacial refugia were located in habitats where summer precipitation was sufficiently high to allow accumulation of the fat reserves required to survive the prolonged winters under more extreme glacial conditions. Bilgin (2011) discussed intraspecific phylogeographical patterns of 29 plant and animal species (including *S. xanthoprymnus*) in and around Anatolia in terms of the classical paradigm of glacial range contraction and interglacial range expansion. However, it is interesting to note that the effective population size of Anatolian ground squirrels increased during the last glacial period
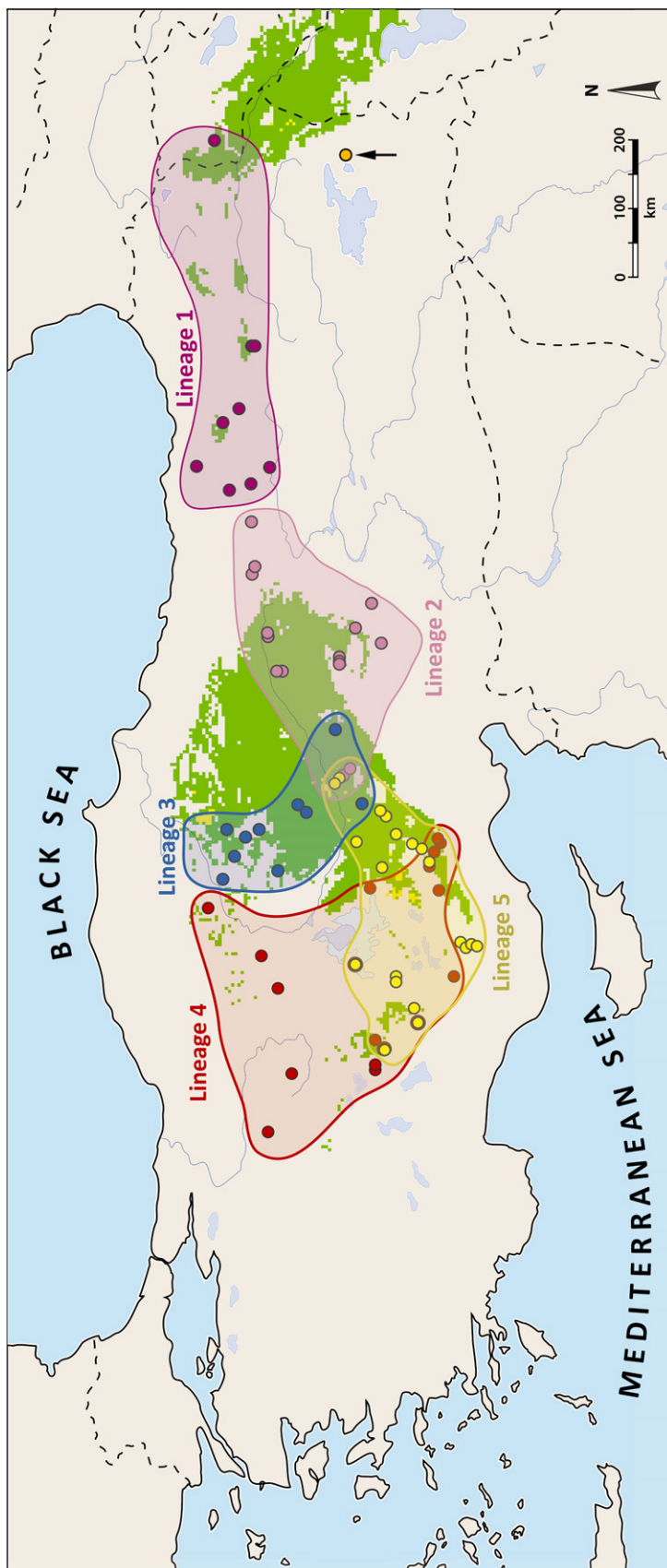
Figure 4. The geographical distribution of cytochrome *b* (cyt *b*) mitochondrial (mt)DNA haplotypes from five lineages (lineages 1 to 5) of Anatolian ground squirrels (*Spermophilus xanthoprymnus*). The locality codes and the number of sequences and haplotypes from each locality are provided in Gündüz *et al.* (2007): table 1 and fig. 1. The potential geographical distribution (green shade) under reconstructed past (the Last Interglacial, LIG, approximately 130 000 to 116 000 years ago) bioclimatic conditions is also shown (Fig. 2C). Note that the cyt *b* mtDNA haplotype shown by the arrow does not fall clearly within one of five lineages (Gündüz *et al.*, 2007).

(including the LGM) and decreased during the present interglacial period. Indeed, Kryštufek, Yiğit & Hutterer (2008) suggested that the population size of *S. xanthoprymnus* has been decreasing over the last 10 years, as a consequence of large-scale agricultural activities that result in habitat destruction and fragmentation. However, according to the evidence for the effects of the Late Quaternary glacial–interglacial cycles on Anatolian ground squirrels, ongoing global climate change has also been contributing to this population decrease (Maiorano *et al*., 2011). Thus, the results of molecular phylogeography were consistent with those of ecological niche modelling in that Anatolian ground squirrels expanded rather than contracted their range during the glacial periods and contracted rather than expanded their range during the interglacial periods.

During the glacial periods, the steppes of the Near East, including Anatolia, underwent an extensive expansion as a result of cold dry climatic conditions (Atalay, 1998). It is plausible that Anatolian ground squirrels have benefited from such an expansion of the steppes in Anatolia. Similarly, European ground squirrels, *Spermophilus citellus*, one of sister species of *S. xanthoprymnus* (another is Taurus ground squirrels), expanded their range as cold dry climatic conditions favoured the steppes in the south-eastern part of Europe during the glacial periods (Kryštufek, Bryja & Bužan, 2009).

In conclusion, the classical paradigm of glacial range contraction and interglacial range expansion for temperate species (Hewitt, 1996, 1999, 2000, 2004) does not hold true for Anatolian ground squirrels in particular, nor for temperate species highly tolerant to cold seasonal and dry conditions in general, and therefore may not be as general as previously assumed. Thus, it is these species that are of most immediate concern because they currently contract their range into interglacial refugia and face increased threat with further rises in global temperatures (Ashcroft, 2010). This conclusion demonstrates the utility of combined ecological niche modelling and molecular phylogeography for understanding the Late Quaternary refugial distribution of species (Carstens & Richards, 2007; Waltari *et al*., 2007).

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. The ecological niche model (ENM) showing the potential geographical distribution of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) under present (1950–2000) bioclimatic conditions. The visible area in maps is 25° to 46°E and 35° to 43°N. A, the ENM based on all 19 bioclimatic variables is shown. Open circles indicate the occurrence records. B, the ENM based on the four most significant bioclimatic variables ('annual mean temperature', Bio1; 'mean temperature of driest quarter', Bio9; 'annual precipitation', Bio12; and 'precipitation of warmest quarter', Bio18; see Supporting information, Table S2) is shown. Note that both the ENMs gave qualitatively similar predictions for present bioclimatic conditions.

Figure S2. The ecological niche model (ENM) showing the potential geographical distribution of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) under present (1950–2000) bioclimatic conditions. The ENM was developed within the mask (delineated by red line) adjusted so as not to include southern Anatolia and then projected to the study area. The visible area in maps is 25° to 46°E and 35° to 43°N. Open circles indicate the occurrence records.

Figure S3. The response curves produced by models created using only one of the four most significant bioclimatic variables ('annual mean temperature', Bio 1; 'mean temperature of driest quarter', Bio 9; 'annual precipitation', Bio12; and 'precipitation of warmest quarter', Bio18; see Supporting information, Table S2) in predicting the present potential distribution of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) at a time.

Table S1. Bioclimatic data used in ecological niche modelling.

Table S2. Estimates of the relative contributions of bioclimatic variables to the ecological niche model (ENM) through the percentage contribution and permutation importance. Values shown are means over the ten-fold cross-validation runs. The most significant bioclimatic variables in predicting the present potential distribution of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) are shown in bold. For abbreviations of bioclimatic variables, see Supporting information, Table S1; http://www.worldclim.org/bioclim.