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European Ground Squirrels at the Edge: Current Distribution Status and Anticipated Impact of Climate on Europe's Southernmost Population

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Abstract: The European ground squirrel (*Spermophilus citellus*) is an endangered semifossorial small mammal of grassland/agricultural ecosystems. In the last few decades, the species' population has declined throughout its range in Europe. The Greek populations represent the southernmost limit of the species' range and are notably small, scattered, and located mainly in human-modified areas. The goal of the present research is to understand the environmental and anthropogenic variables associated with its distribution in the Mediterranean habitats, assess possible drivers of observed local extinctions, and propose conservation and land-use management actions in light of near-future climate change scenarios. We used presence records since 2000 across all known populations (107 colonies) and maximum entropy conditional probability models (MaxEnt) to calculate both the habitat suitability (bioclimatic variables) and habitat availability (anthropogenic/land-use variables) within the European ground squirrel's historical range in northern Greece. We report a projected 39% to 94.3% decrease in habitat suitability by 2040–2060 due to climate change. Based on our findings, we provide guidance by proposing nascent conservation actions to protect the few existing colonies in Greece via improved land management practices and identify in situ climate refugia that could be prioritized as sites for future reintroductions.

Keywords: *Spermophilus citellus*; maximum entropy modeling; species distribution modeling; climate change refugia

1. Introduction

Agriculture in Europe underwent significant transformations since the middle of the 20th century. Intensification of farming practices due to increased mechanization, together with rapid industrial, urban, and transportation network development, has led to a homogenization of farmlands and the fragmentation of natural and semi-natural habitats, especially in lowland areas [1–6]. At the same time, the shift of human activities near cities was followed by a decline in traditional pastoral activities, with extensive grazing reducing or replaced by intensive grazing [7]. Furthermore, the abandoned grasslands became gradually encroached by shrubland or forest, especially at mountainous landscapes [8,9].

While some wildlife species have benefited from these land-use changes [10–13], the overall biodiversity of European agroecosystems has decreased, threatening a range of grassland species due to habitat loss or degradation and a reduction in habitat connectivity [3,6,14]. Moreover, human-induced global warming is likely to cause shifts in the distribution of many species in the near future [15]. Species with narrow niche breadth could be more susceptible to such changes due to their limited geographic range and low dispersal capacity [15,16]. Identifying currently available and future suitable habitats for these species is key to developing effective conservation priorities for them.

The European ground squirrel (*Spermophilus citellus*) is one such narrow niche breadth species that inhabits natural and anthropogenic grasslands of central and southeastern Europe. Its populations have been declining across its range due mostly to the conversion of suitable habitat to intensively cultivated fields and urban areas and the abandonment of grazing areas [17–21]. A group-living, semifossorial, and mostly herbivorous rodent, the European ground squirrel hibernates in individual burrows from early fall to early spring, depending on the altitude and latitude [22,23]. It is considered an ecosystem engineer and keystone species of grasslands, as its burrowing activity aerates the soil, increases plant composition, and creates microhabitats for other species, while being an important prey for raptors [19,24–27]. The species is listed as endangered in the IUCN Red List Data Book [28] and is protected by the European framework (Bern Convention—Appendix II, Directive 92/43/EEC—Annexes II and IV).

The Greek populations of the European ground squirrel constitute the species' southern distributional limit, having adapted to the Mediterranean climate [23]. The populations occur in three discrete sub-regions at the north of the country, with most colonies being concentrated in central Macedonia and fewer in western Macedonia and Thrace [29,30]. Surveys over the last decade have documented significant reductions, both in the overall range (62.4%) and the number of active colonies (74.6%), compared to records at the end of the previous century [30]. Moreover, the remaining colonies are isolated and significantly smaller in size compared to older records [30]. While some previously unknown populations were discovered during the latest surveys, large areas of the species' historical range remain unoccupied. Climate change is an especially pertinent threat for the Greek populations, given their presence at the southern edge of the species' range. Predictions for anticipated climate changes by 2100 in the Mediterranean region include a 2–5 °C temperature rise, depending on the season, and an overall decrease in precipitation [31,32]. Rising ambient temperatures could affect the circannual rhythms of the species during hibernation, resulting in a loss of body mass that, in turn, will likely negatively affect individual fitness [33,34]. Improving our understanding of current and future European ground squirrel habitat suitability would be key for prioritizing conservation actions and areas that are likely to yield long-term benefits to the species in the face of anticipated climate changes.

Ecological niche modeling (ENM) is a well-established approach for predicting both the distribution of a species across a geographical area, where presence information is limited or imperfect [35], and for assessing the relation of environmental (biotic, abiotic, bioclimatic) and anthropogenic parameters and the species' habitat suitability [36–39]. The maximum entropy algorithm (MaxEnt; [40–42]) is a popular ecological niche modeling method for endangered species, including ground squirrels [43–50], as it has high prediction accuracy, even with relatively small datasets, and it requires only presence data [37,51–54]. These characteristics make it an ideal tool for the European ground squirrel dataset that we have developed.

In this study, we first used all available data on the historical and current distribution of the European ground squirrel in Greece to infer the species' current habitat availability (i.e., suitable land-use/habitat) and habitat suitability (i.e., bioclimatically suitable areas) using MaxEnt ecological niche models, and to assess which parameters limit its distribution. Second, we examined possible anthropogenic and environmental causes for the observed local extinctions of European ground squirrel colonies. Third, we used the current habitat suitability model values to predict the effect of climate change on the species' potential distribution in the near future (2040–2060) under a variety of possible scenarios, with the aim of identifying priority areas for conservation within its historical range (i.e., in situ climate change refugia). Lastly, we examined the results from the above analyses to produce a list of targeted conservation actions for the European ground squirrel in Greece, which we hope will help reverse the very real prospect of the species' country-wide extinction.

2. Materials and Methods

2.1. Study Area

The study area extended across the administrative regions of Western Macedonia, Central Macedonia, and Eastern Macedonia and Thrace in northern Greece (41.44° N, 26.12° E to 39.95° N, 21.41° E; Figure 1), which enclose the historical range of the European ground squirrel in the country. The geomorphology of the area is complex, including mountain ranges, alpine plateaus, and lowland valleys. The mean elevation is 485 m (range 0–2918 m). Main land-uses in the lowlands are monoculture agriculture, settlements, and industrial developments, while mid-to-higher elevation areas are characterized by semi-natural and natural environments. The climate is typical Mediterranean with hot semi-arid to cold semi-arid summers in lowlands and humid subtropical and continental in mountainous areas [55]. The mean annual precipitation is 561.3 ± 108.7 mm (range 411−1071 mm), occurring mainly during the winter months. The mean monthly temperature of the coldest quarter is 3.5 ± 1.9 °C (range −6.1 to 8.8 °C), while in the warmest quarter it is 21.7 ± 2.6 °C (9−25.3 °C) [56]. The European ground squirrel shares its habitat with common small mammal species of the Talpidae, Soricidae, Cricetidae, and Muridae families, as well as the European hedgehog (*Erinaceus europaeus*) and the European hare (*Lepus europaeus*). Potential natural mammalian and avian predators include the least weasel (*Mustela nivalis)*, stone marten (*Martes foina*), red fox (*Vulpes vulpes*), European wild cat (*Felis silvestris*), Golden eagle (*Aquila chrysaetos*), and buzzards (*Buteo* spp.) [27]. Domestic dogs and cats are also present across the range, especially in lowland agricultural areas near settlements.

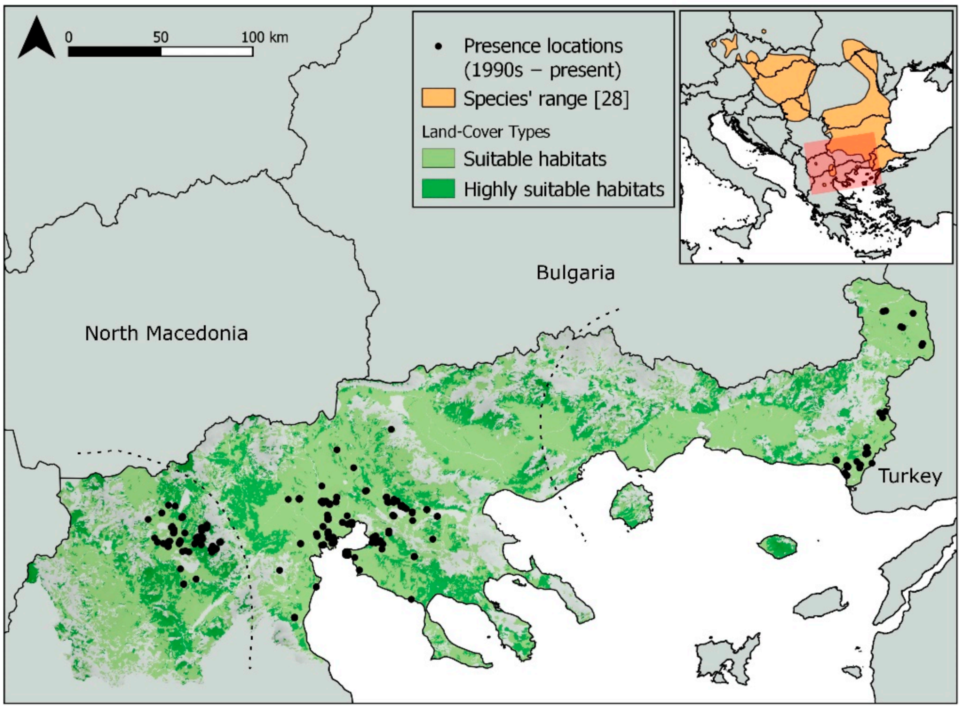

Figure 1. The distribution of the presence records (1990−2021) of *Spermophilus citellus* in Northern Greece. The suitable habitats of the species in the study area are schematically marked in green (light green for suitable and dark green for highly suitable habitats, please see Table 1 for more details), and the unsuitable habitats are in grey. Habitat suitability was assessed based on ecological criteria from [17,19]. Dashed lines separate the three sub-populations of Western Macedonia (**left**), Central Macedonia (**center**), and Thrace (**right**).

Table 1. Bioclimatic, environmental, and anthropogenic variables considered in either or both of the *Spermophilus citellus* ecological niche models (model 1: habitat availability 100 m resolution; model 2: habitat suitability 4500 m resolution). Note: asterisks mark models in which a given variable was used in the final model.

Model	Category	Variable	Type	Source	Initial Resolution
1 *	Environmental—Abiotic	Elevation	Continuous	https://land.copernicus.eu (EU-DEM v1.1)	25 m
1 *,2 *	Environmental—Abiotic	Slope	Continuous	Developed using the EU-DEM v1.1 layer and the QGIS Slope function	25 m
1 *	Environmental—Abiotic	Aspect	Continuous	Developed using the EU-DEM v1.1 layer and the QGIS Aspect function	25 m
1 *	Environmental—Abiotic	Tree cover density	Continuous	https://land.copernicus.eu (Tree Cover Density 2018)	10 m
1 *	Environmental—Abiotic	EGS suitable land-cover	Categorical	https://land.copernicus.eu (Corine Land Cover 2018) (Reclassified/suitable: 2–4, 9, 12–14, 19–22, 35, 37, 38; highly suitable: 6, 10, 11, 15–18, 26, 28, 32)	100 m
1 *	Anthropogenic—Abiotic	Soil imperviousness (soil sealing)	Continuous	https://land.copernicus.eu	10 m
1 *	Anthropogenic—Abiotic	Road density	Continuous	https://geodata.gov.gr; converted tarred roads to 50 m interval point layer, and applied heat map/kernel density estimation function in QGIS (200 m radius/quartic kernel shape)	Vector
2	Environmental—Biotic	Normalized difference vegetation index (NDVI)—20-year mean (1999−2019)	Continuous	https://land.copernicus.eu	1000 m
2	Bioclimatic—Abiotic	(Bio1) Annual mean temperature	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio2) Annual mean diurnal range	Continuous	https://www.worldclim.org/	4500 m
2 *	Bioclimatic—Abiotic	(Bio4) Temperature seasonality SD	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio7) Annual temp range	Continuous	https://www.worldclim.org/	4500 m
2 *	Bioclimatic—Abiotic	(Bio8) Mean temp of wettest quarter	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio9) Mean temp of driest quarter	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio10) Mean temp of warmest quarter	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio11) Mean temp of coldest quarter	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio12) Annual precipitation	Continuous	https://www.worldclim.org/	4500 m
2 *	Bioclimatic—Abiotic	(Bio15) Precipitation seasonality (CV)	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio16) Precipitation of wettest quarter	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio17) Precipitation of driest quarter	Continuous	https://www.worldclim.org/	4500 m
2 *	Bioclimatic—Abiotic	(Bio18) Precipitation of warmest quarter	Continuous	https://www.worldclim.org/	4500 m
2	Bioclimatic—Abiotic	(Bio19) Precipitation of coldest quarter	Continuous	https://www.worldclim.org/	4500 m
2	Anthropogenic—Biotic	Population density	Continuous	https://ec.europa.eu/eurostat	1000 m
2 *	Environmental—Abiotic	Soil bulk density	Continuous	https://esdac.jrc.ec.europa.eu (LUCAS Database)	500 m
2 *	Environmental—Abiotic	Soil texture (USDA classification)	Categorical	https://esdac.jrc.ec.europa.eu (LUCAS Database)	500 m

2.2. Species Data

We compiled presence records of the European ground squirrel across the species' historical range in Greece, as indicated in Youlatos [29], from technical reports, interviews, photographs, and field surveys. The oldest records were from the mid-90s, whereas most were from the last decade (2011−2021). The 2427 records obtained (Figure 1) refer to active burrow entrances or observations of individual animals. All were validated for this project [30] and have exact coordinates. In addition, we compiled 403 records of species absence, which were used to correct for sampling bias during ecological niche modeling (MaxEnt). All absence data correspond to true absences validated in the field. The presence records were spatially filtered by randomly retaining a single record per 100 m and 4500 m grid cells, resulting in 425 and 85 presence records for inferring habitat availability (i.e., suitable land-use/habitat) and habitat suitability (i.e., suitable bioclimatic areas) models, respectively (as defined by Gür [44]).

2.3. Ecological Niche Modeling Variables

The variables for inferring the European ground squirrel's habitat availability were used at a resolution of 100 m, while those used for modeling habitat suitability were at a 4.5 km resolution. We resampled variables available at a higher resolution to one of a model using the nearest-neighbor-joining method. Variables were masked to the extent of the study area (three administrative regions of northern Greece) and converted to ASCII format, as required by the MaxEnt software. To reduce the risk of model overfitting due to variable collinearity, which can affect the model transferability spatially or temporally [57], we kept only one of the highly correlated variables (Pearson correlation coefficient $r > 0.7$ or $r < -0.7$). All file conversions and data processing were performed using Quantum GIS v.3.16.14 [58].

In total, seven variables were considered for the habitat availability (100 m resolution) models: two anthropogenic (road density, soil imperviousness) and five environmental (elevation, slope, aspect, tree cover density, European ground squirrel suitable land cover). The land-cover types were categorized into suitable and highly suitable, representing artificial/arable land and land-uses with special management (i.e., airports, pastures)/permanent crops/semi-natural and natural land-cover types respectively, based on what is known about the species' ecology [17,19] and our field observations. Nineteen variables were considered for the habitat suitability (4500 m) models: 14 bioclimatic variables (WorldClim database version 2.1; [56]), 1 anthropogenic (population density), and 4 environmental (20-year mean normalized difference vegetation index (NDVI), soil bulk density, soil texture, and slope). We excluded 5 of the 19 available WorldClim bioclimatic variables from the analysis based on preliminary tests of collinearity, consideration of recent variables included in ecological niche models for the European ground squirrel and its congener, namely, the Anatolian ground squirrel (*Spermophilus xanthoprymnus*) [43,44], and an emphasis on seasonal mean or range rather than min–max values. Details of the source, initial resolution, and model for which a variable was considered are provided in Table 1.

We also downloaded future bioclimatic data for the study area for the period 2041−2060 (near future) from the Coupled Model Intercomparison Project Phase 6 (CMIP6) based on three global climate models (BCC-CSM2-MR2, CNRM-CM6-1, CanESM5; representing long-term average Earth surface temperature rises, resulting from a doubling of atmospheric CO_2, of 3 °C, 4.3 °C, and 5.6 °C respectively) and three combinations of shared socio-economic pathways (SSP) and representative concentration pathways (RCP) by 2100 (SSP2/RCP4.5, SSP3/RCP7.0, SSP5/RCP8.5). The SSPs 2, 3, and 5 represent different narratives of global and regional efforts to combat climate change (SSP2—medium challenges to mitigation and adaptation, SSP3—high challenges to mitigation and adaptation, SSP5—high challenges to mitigation, low challenges to adaptation) (see [59]). The RCPs 4.5, 7.0, and 8.5 refer to slowly declining, slowly rising, and rising CO_2 emissions (for more information refer to https://www.carbonbrief.org/, accessed on 10 January 2022). Using different global models and SSP/RCP scenarios, we captured the uncertainty of the anticipated climate change pathways in the future European ground squirrel ecological niche models.

2.4. Model Implementation and Processing

We used the software Maxent 3.4.4 [42], available from https://biodiversityinformatics.amnh.org/open_source/maxent/, accessed on 15 December 2021), to model the habitat suitability and availability of the European ground squirrel throughout the historical range of the species in Greece and to examine the species' response in relation to the environmental, bioclimatic, and anthropogenic parameters considered. We opted for the use of MaxEnt because it shows good predictive performance, even with small presence datasets, and it does not require real absence data [60]. It is, therefore, suitable for our dataset. Moreover, MaxEnt was shown to produce similar results to more complicated "black box ensemble models" [61].

Since there have been significant concerns raised against using MaxEnt software's default feature classes and regularization parameter options (e.g., [62]), we used the ENMVeval R package [63] to run a combination of model settings (i.e., "tuning"). We tested 36 candidate models for both the habitat availability (100 m resolution) and the habitat suitability (4500 m resolution) modeling process by combining five feature classes (linear; linear and quadratic; hinge; linear, quadratic, and hinge; linear, quadratic, hinge, and product) and nine regularization multiplier values (1 to 5 in 0.5 increments). We used a fixed set of non-correlated environmental, anthropogenic, and/or bioclimatic variables. To address possible survey biases of our dataset for the habitat availability models, we defined the background extent (within which 10,000 background points would be randomly selected) as a polygon enclosing a 10 km buffer around our presence and absence points [64]. This was not done for the habitat suitability models, as the grid cell resolution of 4500 m limited the number of available background points. Therefore, in this case, we used all of the study area as the background extent. Model evaluation statistics were calculated by using the random k-fold methods, which partitioned the data into "bins" (k = 5) for training and testing for cross-validation. To identify the model with the optimal model settings, we used the model with the lowest Akaike information criterion [65] corrected for small sample sizes (AICc) value, which penalizes for model overfitting. In order to evaluate the model, we chose two metrics: the average of the area under the receiver operator curve (AUC) [51] and the continuous Boyce index (CBI) [66,67]. Higher AUC values denote models that discriminate better between conditions at occurrence locations withheld for testing and those at background points [63]. Values close to 0.5 are as informative as random models. We considered models with AUC > 0.9 as excellent, 0.8−0.9 as good, 0.7−0.8 as fair, and <0.7 as poor [68]. However, the usefulness of using only AUC for accuracy measurement has been criticized when true absence data are not available [69]. The CBI is considered more appropriate for the evaluation of presence-only models, as in our case, as it only requires presences [67]. The CBI values range from −1 to +1, with positive values indicative of the model output being positively correlated with the true probability of presence, values near zero the output being not different from a random model, and negative values the output being negatively correlated with the true probability of presence, i.e., counter predictions [70].

Once we had determined the optimal set of model settings, we ran the selected model in the MaxEnt GUI using ten cross-validated replications with no threshold values and the same bias file (in the case of habitat availability); the remaining settings were left at default values. We selected jackknife testing to assess each variables' contribution to the model and selected for response curves to be produced to assess how each variable affected the European ground squirrel's ecological niche model. We used MaxEnt to map habitat suitability/availability using a Cloglog output, with values of 0.0 to 1.0 indicating low to high suitability/availability, respectively. In the case of the habitat suitability model, we also projected the model results onto future conditions, in addition to the current ones across the study area, by providing the MaxEnt software with the predicted variable layers for the 2040−2060 period. In total, nine future habitat suitability maps were projected for the European ground squirrel; one for each of the three global climate models and three SSP/RCP scenario combinations. We averaged the three model results for each SSP/RCP scenario, as per Gür [44], using QGIS. Finally, we categorized the habitat suitability/availability maps into five classes (also as per Gür [44]): very low suitability (<0.2), low suitability (0.2−0.4), moderate suitability (0.4−0.6), high suitability (0.6−0.8), and very high suitability (>0.8). This was done to facilitate interpretation and reporting. We considered areas with values ≥0.6 as suitable (or available) for the European ground squirrel. We identified areas suitable for the species both at present and under all future climate scenarios (2041−2060 period) as in situ climate change refugia [71].

2.5. Drivers of Colony Extinction

To examine possible drivers of colony extinction, we assigned colonies as either active or inactive based on the presence or not of the species during the 2019−2021 field visits. We excluded from the analysis colonies that were not visited. A colony was defined as the total number of the burrow entrances, which were loosely distributed in a location, creating aggregations of several individuals that live and interact in the same area [72,73]. We used binomial regression models (link—logit) in R (v.4.1.2; [74]) with active and inactive colonies (0 and 1) being the response variable. We considered all the ecological, anthropogenic, and bioclimatic variables as potential predictor variables considered in the MaxEnt ecological niche models; these were calculated as their mean value within a 1 km buffer from the centroid of each colony, considering the maximum dispersal of the species [75]. In addition, we considered the percent cover by areas modeled as having habitat availability of 60% and above, and the percent change in the number of free-ranging small ruminants over the past 20 years (available at the prefecture level). The latter variable was included to examine whether a reduction in grazing livestock and the ensuing abandonment of traditional grazing areas could explain the observed decline in the number of colonies at the landscape level. We first ran univariate models and compared them against the null (intercept only) model in order to select an optimal set of informative variables while also managing the model complexity. We used the Akaike information criterion (AIC) [65] for the model selection. Among the correlated variables, we kept the one with the lowest univariate model AIC for further consideration. Once a final set of fixed variables was selected, we ran all possible multivariate combinations, again using the AIC for the model selection.

3. Results

3.1. Ecological Niche Modeling

We considered an equal number (36) of candidate models of varying model settings when assessing the European ground squirrel's current habitat availability (model 1, 100 m resolution). The final habitat availability model used aspect, elevation, slope, road density, soil imperviousness, tree cover, and suitable land-cover (categorical) for the European ground squirrel as input variables. The model was developed using linear, quadratic, and hinge feature classes, and a regularization multiplier of 1.0 (Supplementary Table S1). No other model had $\Delta AICc \leq 2$. The average test AUC value for the ten replicates was 0.82 ± 0.02 and the CBI value was 0.94 ± 0.02.

The univariate response curves of most variables were either bell-curved or linear, with no truncations or significant differences in shape with the marginal curves (Supplementary Figure S1). The available habitat for the species is typically in south-facing, lowland, slightly sloped (<3°), and treeless areas within human-modified landscapes (i.e., moderate-to-high road density, low-to-moderate soil imperviousness). An exception was natural grasslands at a higher elevation. All variables, except soil imperviousness and aspect, contributed significantly to the final model (i.e., >10% contribution and/or permutation importance; see Table 2). While, according to the model habitat, availability extends over 11.3% of northern Greece, only 43.8% of those areas (5%, 2119 km^2) were within the suitable habitat areas, which accounted for approximately one-fifth of the suitable areas. A large part of the available vs. suitable area disparity certainly stemmed from the difference in the resolution of these models, but it was apparent that current human landscape modifications (buildings, road infrastructure, mining) and land-use practices had reduced the available habitat to a fraction of the European ground squirrel's historical potential. The largest clusters of available habitats are found at the Axios River valley and agricultural areas east of the city of Thessaloniki (Central Macedonia), and the alpine meadows of Mount Vermio (Western Macedonia) (areas 2 and 1 in Figure 2, respectively). Mount Vermio is home to the sole European ground squirrel mountainous population in Greece. While the model predicts habitat availability at several additional mountains and roadless [76] plateaus (e.g., Grammos, Kaimaktsalan, Krystallopigi, Menikio, Sfika), none were within suitable habitat according to the bioclimatic and soil model. The available habitat at the Evros Delta (Thrace) is highly fragmented.

Table 2. Percentage contribution (Pc) and permutation importance (Pi) values of variables used to predict the distribution of available (model 1) and suitable habitats (model 2) of *Spermophilus citellus.*

Variables	**Model 1: Habitat Availability**		**Model 2: Habitat Suitability**	
	Pc (%)	**Pi (%)**	**Pc (%)**	**Pi (%)**
Road density	30.9	26.7	–	–
Elevation	29.1	25.7	–	–
EGS suitable land-cover	14	16	–	–
Tree cover density	12.7	9.5	–	–
Slope	8.8	18.4	52.5	29.8
Aspect	2.4	1.5	–	–
Soil imperviousness	2.1	2.3	–	–
Precipitation seasonality (Bio15)	–	–	22.4	34.7
Soil texture	–	–	11.1	6.1
Soil bulk density	–	–	7.2	3.6
Precipitation of warmest quarter (Bio18)	–	–	4.4	18.7
Temperature seasonality SD (Bio4)	–	–	1.5	3.3
Mean temp of wettest quarter (Bio8)	–	–	0.9	3.7

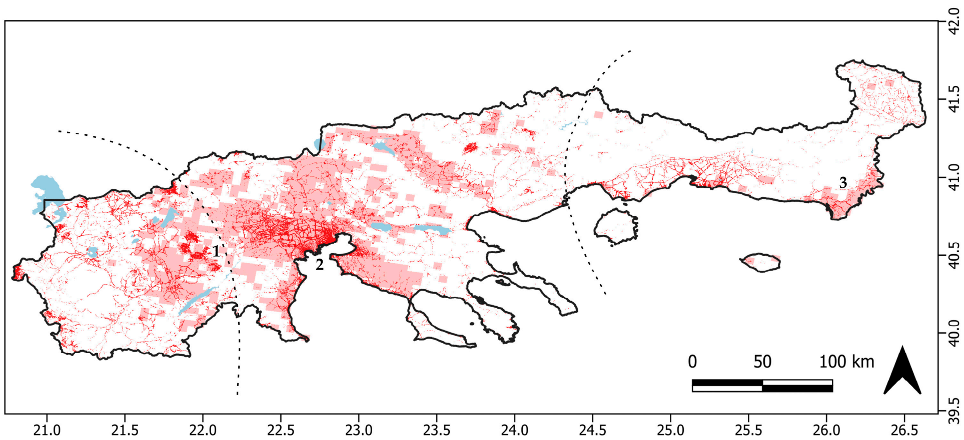

Figure 2. Map of *Spermophilus citellus* current habitat availability (dark red, resolution 100 m) and habitat suitability (light red, resolution 4.5 km) across the species' historical range. The dashed lines separate the three sub-populations (Western Macedonia, Central Macedonia, and Thrace), while the numbers indicate the main available habitats of the species in (**1**) Mount Vermio, (**2**) Axios River valley and eastern Thessaloniki, and (**3**) Delta Evros River.

We considered 36 candidate models of varying model settings to assess the European ground squirrel's current habitat suitability (model 2, 4.5 km resolution) within the species' historical range. The final habitat availability model used slope, soil bulk density, soil texture (categorical), temperature seasonality (Bio4), mean temperature of the wettest quarter (Bio8), precipitation seasonality (Bio15), and precipitation of warmest quarter (Bio18) as input variables. The model was developed using linear and quadratic feature classes and a regularization multiplier of 1.0 (Supplementary Table S1). No other model had ΔAICc ≤ 2. The average test AUC value for the ten replicates was 0.76 ± 0.05 and the CBI value was 0.73 ± 0.15.

The univariate response curves of most variables were also either bell-curved or linear without truncations and differed in overall shape from the marginal curves only for temperature seasonality (Bio4) (Supplementary Figure S1). The model showed that areas most suitable for the European ground squirrel were flat (or with slope <5°) with silt clay-loam or clay-loam soil of high bulk density, with cold winters (i.e., wettest quarter) and dry summers (i.e., warmest quarter), and low variation in seasonal precipitation. Slope, precipitation seasonality, summer precipitation, and soil texture were the variables that contributed the most to the final model (see percent contribution and/or permutation importance in Table 2).

Based on the MaxEnt model, the currently suitable areas (predicted suitability ≥ 0.6; ~20 km^2 grid area at the equator) for the European ground squirrel extend over 25.3% of northern Greece (10,327 km^2) (Figure 2). The distribution of suitable habitat coincided broadly with the three known sub-populations in Greece: Western Macedonia, Central Macedonia, and Thrace, with a clear and extended (100−300 km) discontinuity in habitat suitability between the populations of Central Macedonia and Thrace. There were also no suitable areas at the western edge of the study area, with the city of Kozani and surrounding areas being the westernmost limit, which matched the known historical distribution of the species.

Under the future climate change scenarios, the European ground squirrel's suitable habitat will significantly contract (range 39% to 94.3%) by 2041−2060 (Figure 3), affecting all three sub-populations. There are no predicted areas of habitat suitability expansion. Conservatively, i.e., under the most pessimistic scenario, the climate refugia for the European ground squirrel within its historical range in Greece will be limited to along the Axios River in Central Macedonia and the delta of the Evros River in Thrace. In Western Macedonia, suitable habitats will be fragmented near Mount Vermio and semi-mountain areas near the city of Ptolemaida.

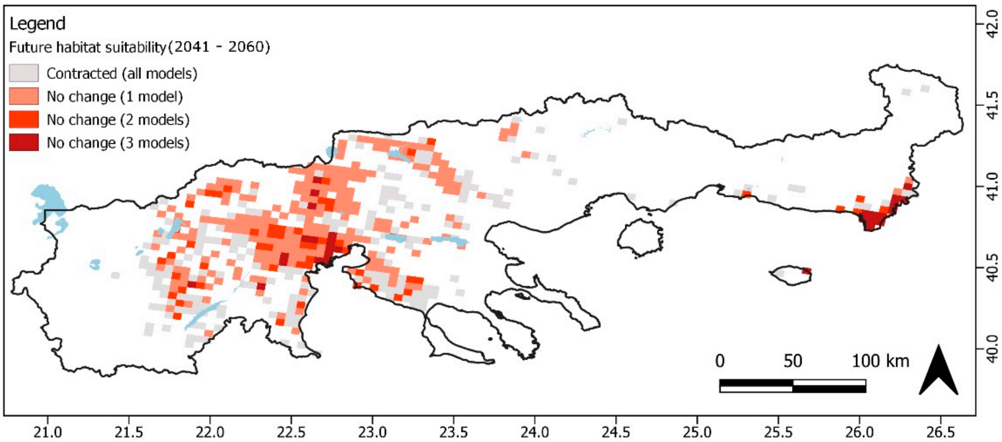

Figure 3. Near-future (2041−2060) *Spermophilus citellus* predicted habitat suitability contraction (grey) and persistence (light to dark red) under three future scenarios (SSP/RCP 2−4.5, 3−7.0, 5−8.5; mean suitability of BCC-CSM2-MR2, CNRM-CM6-1, CanESM5 global climate models ≥0.6). Dark red grid cells denote areas predicted to remain suitable for the species under all future scenarios and can therefore be considered most likely to be climate refugia. Map resolution: 4.5 km.

3.2. Drivers of Colony Extinction

For this study, we analyzed data from 107 colonies (Figure 1 and Supplementary Table S2). Most (68.2%) were within agricultural landscapes consisting of a mosaic of arable land, permanent crops, and pastures. One in five colonies (19.63%) was located in artificial areas (e.g., discontinuous urban fabric, industrial or commercial units, airports, sports leisure facilities, and construction sites). The remaining colonies were at wetlands (8.4%), where the species lives in elevated, well-drained areas (e.g., canal banks, flood zone dikes), and semi-natural grasslands (3.7%). While most of the colonies were on public lands (57%), less than one-third of the total (29%) were within the Natura 2000 network of protected areas. During the 2019−2021 surveys, only 37 (34.6%) of the colonies were still active.

The model that best explained the characteristics of colonies that went extinct over the past two decades consisted of two environmental variables: soil imperviousness and percent cover by high suitability habitat (see Table 3). Both variables were significant ($p < 0.001$) and had a negative relation to a colony's probability of extinction. Nevertheless, there was significant unexplained variance ($\chi^2 = 13.621$, df = 8, $p = 0.09$), which suggests that we were unable to effectively explain the drivers of local extinction.

Table 3. Model estimates and significance of environmental variables for the extinction of *Spermophilus citellus* colonies.

Variables	Estimate	SE	z-Values	Pr (>∣z∣)
Intercept (β)	1.555	0.337	4.613	<0.0001
Soil imperviousness	−0.0813	0.029	−2.754	<0.001
High suitability habitats	−3.639	1.260	−2.887	<0.001

4. Discussion

Our results provide the most complete assessment to date of the conservation status of the European ground squirrel population at its southernmost range, combining data from multiple sources to incorporate all known colonies since the mid-1990s. The reported colony extinction rate over the past two decades, combined with the low habitat-availability-to-habitat-suitability ratio and significant forecasted habitat suitability contraction by 2041−2060, build a bleak picture of the species' prospect for survival. Nevertheless, the study also provided the information required for prioritizing actions, areas, and land-uses for the urgently needed conservation efforts to save the species from extinction.

The large unexplained variance in causes of colony extinction suggests that additional, not tested, variables may be responsible, and/or that the drivers of the observed rapid decline may not be universal or detectable at the spatial scale examined. While the area occupied by a colony was not an important predictor of extinction, in many cases, the colonies were not monitored frequently enough (or at all) to be able to document population trends leading to extinction. Considering that many of these colonies had very small populations (<20 adult animals) at the time of last count [30], stochasticity (e.g., due to weather, predation, disease) alone could explain their eventual demise [77,78]. In fact, outright habitat loss or overall land-use change was rarely observed to be the case of a colony's extinction during field visits. Given the European ground squirrel's low vagility and fragmented distribution of colonies, even at the last strongholds of the species in Central and West Macedonia, the possibilities of recolonizing these areas are very low [79]. The limited connectivity and natural emigration between colonies (and even more between sub-populations) could have already led to genetic isolation and inbreeding depression, which, in turn, affected the population fitness [80]. An important first step to protecting the few remaining colonies is the adoption of a regular, statistically robust, monitoring protocol that is not limited to population counts, but that extends also to measuring genetic variation and parasitic charge. This will allow for the early identification and reduction of threats. Such small-scale monitoring projects have already been launched in 2020 within two national parks in Central Macedonia (Axios Delta National Park and Koroneia and Volvi National Park), but it is important that they secure long-term funding and that they are expanded to all colonies.

Perhaps counterintuitively, most of the colonies assessed for the study (87.5%) were within human-modified landscapes, even adjacent to human settlements or industrial areas, while colonies in highly suitable (natural) habitats, such as grasslands and sclerophyllous vegetation with sparse trees, were few and more likely to go extinct. Field surveys during

2019−2021 showed one in ten collapsed colonies having dense tallgrass vegetation with no signs of grazing or mowing. The importance of grazing in maintaining open abandoned fields is known [81,82], and Greece has experienced significant declines in the number and size of extensive grazing herds [7,9]. Abandonment of rural land has been linked to a decline in farmland species and biodiversity [83–86], and this may be the cause for at least some of the observed extinctions within European ground squirrel natural habitats. The systematic management of natural or semi-natural grasslands is needed, ensuring that areas with European ground squirrel colonies are either mowed or grazed frequently enough to maintain a suitable food vegetation structure [87,88]. For such a measure to be sustainable, areas with the European ground squirrel's presence should be recognized as high-value farmland (HNVF) to increase the viability of extensive livestock farming [89,90]. Moreover, the national grazing management plans currently under development should explicitly take into account the presence of grazing-dependent species, such as the European ground squirrel.

The prevalence of the remaining colonies in areas near human settlements indicated the current dependence of the species on human activities [30,50]. Human-managed areas provide short grass, steppe-like habitats that could be an important factor for the survival of colonies and their connectivity [18,50,91–93]. Therefore, in addition to actions aimed at grasslands, European-ground-squirrel-friendly practices should be adopted in agricultural areas. Agri-environmental management schemes promoted by the Common Agricultural Policy (CAP) [94,95] aim to substantially enhance or restore farmland species' habitats. Such efforts need to be long-term and adapted to local conservation needs [96]. Measures that could be beneficial to the European ground squirrel are, among others, low or no pesticide and fertilizer use, no plowing of fallows fields until October if the fields are to be cultivated next year, no burning of fallow vegetation, vegetation cut at least once annually (preferably before June), maintenance of unploughed strips at the edge of fields, intercropping, and the selection of crops that do not require dressed seeds [95,97]. Studies of another endangered, fossorial, small mammal, namely, the European hamster (*Cricetus cricetus*), also indicated that increasing the crop variety and farmland habitat mosaic improved the density and fitness of hamster populations [98,99]. The European ground squirrel could serve as a "flagship species" for farmland biodiversity (as they are charismatic and attractive to the public [100] and a keystone species), contributing toward sustainable agricultural landscapes.

Our results also showed an important role of roads in European ground squirrel habitat availability. Lowland areas (e.g., within the Axios River and Evros River deltas, and areas east of Thessaloniki) are, on the one hand, significant clusters of available habitats, but on the other, fragmented by considerable road networks. Despite the negative effects of roads on wildlife [101,102], the grass strips along roads could act as corridors for the expansion and connectivity of nearby colonies. It is important that such dispersal corridors are identified to take measures for reducing roadkill risk (e.g., speed bumps, signposts, fencing) and maintaining suitable vegetation along them (e.g., via mowing, planting appropriate grass/forbs, and ensuring sufficient soil drainage). Similar measures have been suggested for providing "stepping-stone" habitats along rivers [50]. Another measure for lowland habitats could be to improve the quality of abandoned, underutilized, or undeveloped plots around settlements and industrial infrastructure, where several colonies persist, albeit with a small number of individuals, in order to provide more suitable microhabitats for nesting and foraging of the populations [103]. In these areas, the invasive plant silverleaf nightshade (*Solanum elaeagnifolium*) abounds. This North American toxic invasive species is frequently encountered within European ground squirrel colonies in Central Macedonia and, to a lesser extent, in the colonies of Western Macedonia and Thrace [104]. It is considered a pest that outcompetes native species of the Mediterranean [104,105]. Based on our field observations, European ground squirrels feed on shoots, leaves, flowers, and seeds of the silverleaf nightshade, potentially affecting (negatively or positively) its spread. We do not fully understand the effect of the plant's toxins on the European ground squirrel's physiology or the vegetation composition, which are concerns that have been documented for other invasive plant species [106]. More studies are needed to assess the need, or not, to control this and other invasive plants within European ground squirrel colonies [107].

Contrary to the high level of habitat fragmentation reported for lowland areas, semi-mountainous and mountainous areas contain large tracts of roadless [76], available habitat for the European ground squirrel. Unfortunately, most of these areas do not appear to be suitable habitats according to the bioclimatic model. Nevertheless, surveys should be undertaken there in the near future. In Western Macedonia, the incongruence between available and suitable habitats for semi-mountainous areas near the cities of Kozani and Ptolemaida is due to the large-scale open-pit mining fueling the soon-to-be-closed coal energy production plants. Although there is no information on whether the species was present in these areas, we propose that the planned restoration activities for the mines should explicitly take into consideration the potential for these areas' natural or assisted recolonization by the European ground squirrel, as it could help increase the connectivity of the Western Macedonian sub-population.

Another land-use development of concern for the population of Western Macedonia is the proposed construction of wind farms in the Mount Vermio area that contains in its entirety the sole mountainous population of the country. While the impact of the construction and operation of wind farms on European ground squirrels is not yet well understood [47,108–110], we consider that measures to protect this high-altitude-adapted population and its large, fragmented, natural alpine environment (without invasive plant species) should be a conservation priority for the species. A solution would be to either move the wind farms to areas that exclude the land of current colonies and their potential connection corridors outside the Natura 2000 (GR1210001) [111] or to require the construction and operation companies to adhere to specific operation protocols that will mitigate all impact on this unique population and safeguard its long-term conservation.

According to our future habitat suitability projections for the European ground squirrel, there will be contractions in the broader Mount Vermio region, which is one more reason that the population there should be protected. The high-altitude adaptation of this population could be key in captive breeding programs aimed at establishing additional high-altitude colonies within the historical range of the species [112]. The most conservative future climate change scenarios predict the larger-in-size climate change refugia for the European ground squirrel to be in the lowland areas of the Axios River and Evros River delta regions. While the former area still supports some large colonies, the Evros population is in critical condition, with just a handful of small colonies persisting. It is imperative that they are urgently protected on the ground, with measures aimed at buffering them from stochastic events (e.g., flooding, food scarcity, possibly predators, and accidental eradication due to land-use changes). Similar future range contraction to lowland areas due to climate change was also reported for other ground squirrels, such as the Anatolian ground squirrel (*Spermophilus xanthoprymnus*) [44]. However, our study's findings disagree with the predicted suitable habitat expansion of the European ground squirrel in Greece reported by Demirtaş [43]. That study examined the past, present, and future distribution of the European ground squirrel across Europe, including the southern lineage containing the Greek populations. Only six locations from the country were used. Since our study was based on a much larger dataset, we believe that our predictions are likely more realistic, while acknowledging the considerable uncertainty that climate change predictions inherently contain.

Overall, our results identified three areas that incorporate (a) the genetic variation of the Greek sub-population [Rammou et al., in preparation], (b) both lowland and mountain population adaptations, and (c) most remaining individuals [30]. These are the Axios River valley, the Evros River delta, and the Mount Vermio alpine meadows. Therefore, we propose these three areas to be the focal areas where the core breeding of populations will sustain and probably expand the species' current distribution, while they will constitute future climate refugia as well. These focal areas could furthermore receive via translocation individuals from very small colonies (<10 animals; 21 of 37 known colonies) occurring in less favorable habitats and faced with a high probability of extinction. At this point, Bulgarian, Czech, Slovakian, Polish, and Hungarian specialists have accumulated over 30 years of expertise on population reinforcement conservation activities [75,112–117]. However, before any translocation or population reinforcement takes place in Greece, a national legal framework (Species Action Plan) is required in order to align all conservation activities with national and EU directives, such as the CAP strategic plan and the Habitat Directive (92/43/EEC). This is especially important, as many European ground squirrel populations are outside the protected area network, with many in public lands managed by different public bodies (e.g., municipalities, airports, archaeological sites, military facilities), for which a national management plan is needed in order to expedite and facilitate cross-agency collaborations.

5. Conclusions

This study reiterated the importance of developing species-specific conservation approaches, especially for populations at the edge of a species' range, which are most likely to be affected by anticipated climate changes. Our analysis shows that the status of the European ground squirrel's southernmost population is deteriorating, with most known colonies having been lost over the past decade. While the species persists in all three of the previously reported sub-populations in West Macedonia, Central Macedonia, and Thrace, our ecological niche model predicts habitat suitability contraction in the next twenty to forty years across all of these regions. The species' forecast climate refugia are in need of different conservation interventions. The already scattered lowland colonies in Central Macedonia (Axios River valley) and Thrace (Evros River delta) face increased isolation, and therefore future conservation efforts should emphasize maintaining or establishing sub-population connectivity. On the other hand, the sole remaining mountainous colony on Mount Vermio (West Macedonia) occurs in good quality natural habitat, though it requires protection of its habitat from forest encroachment and proposed large-scale energy production developments. Halting the observed population decline of all colonies is a universal priority, however, which will involve maintaining, and eventually expanding, habitat availability and identifying colony-specific drivers of extinction. For each planned activity, the trade-offs of the prioritization process should be considered (see conservation triage [118]). Such coordinated and well-planned actions require a currently lacking national action plan for the species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land11020301/s1, Table S1: Model evaluation statistics of model 1: habitat availability (100 m resolution) and model 2: habitat suitability (4.5 km resolution) with delta AICc values of $\leq$2. The variables are referred to as FC, feature classes (L—linear, Q—quadratic, H—hinge; RM, regularization multiplier; AUC_{DIFF}, the difference between training and testing AUC; validation AUC, the validation set to estimate prediction error for model selection; OR_{10}, 10% training omission rate; AICc, the Akaike information criterion corrected for small sample sizes; delta AICc, the difference between the lowest AICc and each AICc; N.coef, the number of coefficients. Figure S1: Marginal (above group of diagrams) and univariate (below group of diagrams) response curves of the variables that were used in the habitat availability ecological niche model 1 (left) and habitat suitability ecological niche model 2 (right). The numbers of categorical variables indicate suitable land-cover for EGS: 0, the unsuitable habitats; 1, the suitable habitats; and 2, the highly suitable habitats, according to our classification, and for soil texture: 3, silt clay-loam; 5, sandy clay-loam; 6, clay-loam; 9, loam; and 12, sandy loam, according to USDA classification (for more details, please see Section 2.3 of Materials and Methods). Table S2: Area characteristics (property, Corine land-cover, and protection status) of the present and absent colonies of *Spermophilus citellus* in three sub-populations in Greece that were used in the analysis.

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and D.Y.; data curation, D.-L.R. and C.A.; writing—original draft preparation, D.-L.R. and C.A.; writing—review and editing, D.-L.R., C.A., D.M., G.B., A.G., T.K. and D.Y.; visualization, D.-L.R. and C.A.; supervision, D.Y.; project administration, D.Y.; funding acquisition, D.-L.R., C.A. and D.Y. All authors have read and agreed to the published version of the manuscript.

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