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Projecting Current and Future Habitat for the European Ground Squirrel Using MaxEnt Modeling under Climate Change

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Abstract. Climate change and human activities are changing the places where different species live more and more quickly. The European ground squirrel (Spermophilus citellus) is a species at risk, and it plays a very important role in keeping grassland environments healthy. But right now, we still do not know clearly where this threatened species lives now and where it will live in the future as the climate changes. This study combined data from many different sources and used an improved Maximum Entropy (MaxEnt) model (the test AUC value is more than 0.87) to carefully study the current situation and future changes of the good living areas for this species. The results found that the number of people living in an area and isothermality are the main environmental factors that affect where this species lives. Future guesses show that the good living areas for it will keep getting smaller. This is especially true under the high-pollution SSP5-8.5 scenario. By the end of the century, this might lead to a total loss of more than 20% of its suitable living areas. At the same time, there will be a big drop in the number of high-quality living areas for the species. It is projected that the area where this species lives will have a big move to the north. This study points out that we badly need active and flexible management methods to protect this species. The species can survive only if the world works to cut greenhouse gases. The results give important scientific support for creating specific ways to protect the species.

Keywords: European ground squirrel, MaxEnt, Habitat suitability, Climate change

1. Introduction

Climate change has become a main cause of loss of different living things. It greatly increases the chance that species will disappear by changing where they live, how they interact with each other, and how ecosystems work. Even a small rise in the world's average temperature (like 1.5°C) can make extinction rates go up a lot. But climate changes in specific regions—such as more frequent extreme weather events and changed rainfall patterns—often have more direct and strong effects on how populations grow or shrink [1,2]. Species that only live in certain biogeographical areas, like temperate Europe (the region with mild weather in Europe), are especially at risk from these climate-led changes. This is because they often have narrow living needs and specific habitat requirements, making them more likely to disappear than species that live in many places [3].

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The European ground squirrel (Spermophilus citellus) is a typical example of this vulnerability. This at-risk species lives in open grasslands in Central and Southeastern Europe. It relies on specific small-scale habitat conditions, such as short plants and soils that let water flow away easily [4]. As an animal that eats plants, its feeding activities have a significant influence on the structure of vegetation [5-7]. More importantly, it acts as an "ecosystem engineer": its burrowing activities greatly change soil properties, how nutrients move, and small-scale land shapes. In this way, it creates living spaces for other species [8,9]. Besides, as a key food source for many endangered predators, it plays a necessary role in keeping the food web stable [10-13]. So, whether its populations can survive affects more than just the species itself. It also has a big impact on the structure and function of local ecosystems.

But the European ground squirrel's need for a narrow range of environmental conditions—such as specific requirements for light, soil drainage, and low water levels—makes it very sensitive to climate change [6]. Specifically, rising temperatures may go beyond what its body can bear. At the same time, changed rainfall patterns increase the risk of burrow flooding. This directly threatens the survival and reproductive success of each individual [14]. Also, human activities like the expansion of farming and the growth of cities are causing habitat loss and fragmentation [6,15]. Even though it was listed as Endangered on the IUCN Red List in 2023, the current conservation measures have not been enough to reverse population declines [6]. There is a key lack of knowledge: we don't have clear, space-related predictions of how climate change and human activities may work together to cause future habitat loss. This gap seriously stops the development of active and effective conservation strategies.

Species distribution models (SDMs) are a powerful tool to fill this knowledge gap [16]. While SDMs—especially the Maximum Entropy (MaxEnt) model—have been widely used to predict current and possible distributions, and to plan conservation for many threatened species, their use in predicting how the European ground squirrel's distribution will change under global change is still limited. Importantly, most existing studies on other species have not fully combined many types of drivers (like climate, land shape, soil, and human-related factors) or optimized model parameters. This may lead to underestimating the uncertainty in future habitat projections [14,17,18]. Besides, understanding how habitats will change differently under different Shared Socioeconomic Pathways (SSPs) is essential for developing flexible, adaptive conservation strategies. But there are still not many comparative studies on this.

So, this study aims to measure the current and future patterns of suitable habitats for the European ground squirrel using an integrated modeling framework. Specifically, we first use an optimized MaxEnt model that includes climate, land shape, soil, and human-related variables. We use it to simulate its current distribution and find key environmental drivers. Then we predict possible changes in its distribution for 2050 and 2090 under multiple Shared Socioeconomic Pathways. The findings provide important scientific evidence for developing targeted climate-adaptive conservation strategies for this endangered species.

2. Methods

2.1. Occurrence data and environmental variables

Species occurrence data for the European ground squirrel were downloaded from the Global Biodiversity Information Facility (GBIF) in June 2025 (GBIF, https://www.gbif.org; GBIF Backbone Taxonomy). The initial dataset comprised 6,641 records, with a temporal range spanning 1893–2025. To maximize model reliability, a rigorous data cleaning protocol was applied: (1) all

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records lacking latitude/longitude coordinates were removed; (2) records clearly located outside the geographical boundaries of Europe (e.g., points in oceans or North Africa) were excluded based on the species' known distribution. The final number of occurrence points used for modeling was 4,999 (As shown in the Figure 1).

Environmental variables were selected based on their potential relevance to the ecology of the European ground squirrel (e.g., burrowing, hibernation, and foraging) and data availability [6,17]. We collected four major classes of variables (Table 1): (1) 19 bioclimatic variables representing thermal and moisture regimes; (2) four topographic variables (elevation, slope, roughness, Topographic Position Index) describing landform characteristics; (3) two soil property variables (clay content, bulk density) relevant to burrowing suitability; and (4) anthropogenic pressure (population density) and land use/land cover (LULC) data. The LULC variable was reclassified into seven groups (water, forest, grass, barren, crop, urban, and ice) to reduce overdispersion and then calculated as percentages of each LULC type at a coarser spatial resolution (e.g., 5 km).

The future distribution model of the European ground squirrel used the same variables as the historical model. We downloaded data for each variable under Shared Socioeconomic Pathways (SSP) 1, 2, and 5 for 2050 (middle of the 21st century) and 2090 (end of the 21st century). SSP1, 2, and 5 represent different narratives of global and regional efforts to combat climate change: SSP1 (low challenges to mitigation and adaptation), SSP2 (medium challenges to mitigation and adaptation), and SSP5 (high challenges to mitigation, low challenges to adaptation). Future climate data from three Global Climate Models (GCMs) were considered to reduce uncertainty through averaging: BCC-CSM2-MR, HadGEM3-GC31-LL, and IPSL-CM6A-LR [17]. All variables for the current and future periods were resampled to a unified 5 km spatial resolution using the average method and masked to the extent of Europe (31° West to 70° East, 27° North to 82° North) to ensure spatial comparability.

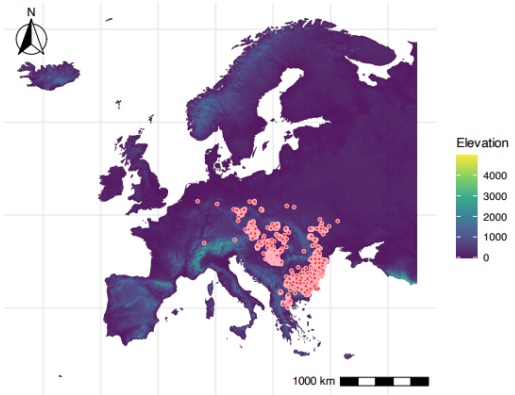


Figure 1. Occurrence plot of the European ground squirrel in the study area

Table 1. Environmental variables used in the model

Class	Variable	Description	Spatial resolution	Source
Climate	BIO1	Annual Mean Temperature	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO3	Isothermality (BIO2/BIO7) (×100)	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)

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Table 1. (continued)

Climate	BIO4	Temperature Seasonality (standard deviation ×100)	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO5	Max Temperature of Warmest Month	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO6	Min Temperature of Coldest Month	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO7	Temperature Annual Range (BIO5-BIO6)	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO8	Mean Temperature of Wettest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO9	Mean Temperature of Driest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO10	Mean Temperature of Warmest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO11	Mean Temperature of Coldest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO12	Annual Precipitation	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO13	Precipitation of Wettest Month	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO14	Precipitation of Driest Month	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO15	Precipitation Seasonality (Coefficient of Variation)	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO16	Precipitation of Wettest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO17	Precipitation of Driest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO18	Precipitation of Warmest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Climate	BIO19	Precipitation of Coldest Quarter	~5 km	WorldClim (https://www.worldclim.org/data/worldclim21.html)
Terrain	Elevation		~5 km	https://www.earthenv.org/topography
Terrain	Slope		~5 km	https://www.earthenv.org/topography
Terrain	Roughness		~5 km	https://www.earthenv.org/topography
Terrain	Topographic Position Index (TPI)		~5 km	https://www.earthenv.org/topography
Anthro pogenic	POP	Population density	~5 km	History: World Population Hub (https://hub.worldpop.org/project/categories?id=18) Future: https://figshare.com/articles/dataset/Projecting_1_km-grid_population_distributions_from_2020_to_2100_globally_under_shared_socioeconomic_pathways/19608594/3
Land use	LULC	water, forest, grass, barren, crop, urban and ice	~5 km	ESA CCI LC for the year of 2000 (https://maps.elie.ucl.ac.be/CCI/viewer/download.php) LC-SSP-RCP scenarios for the future (https://zenodo.org/records/4584775)
Soil	Clay	Clay content (mass %)	~5 km	SoilGrid250_v2 (https://soilgrids.org)
Soil	Bulk	Bulk density of the fine earth fraction (kg / m³).	~5 km	SoilGrid250_v2 (https://soilgrids.org)

2.2. MaxEnt modelling and model optimisation

We used the Maximum Entropy (MaxEnt) model to predict where the species lives. The main idea of this model is to find the maximum entropy probability distribution. This distribution is the closest to being balanced. It follows the rules from environmental variables at the species' known living places. In this way, the model gives a reliable estimate of the species' living needs and possible

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distribution [19]. The MaxEnt model is especially good for studies that only have data on where the species is present. It also stays stable even when the sample size is small. So it is a perfect tool for predicting the distribution of rare species or those with limited data, like the European ground squirrel.

To reduce the chance of overfitting in the MaxEnt model and make it more applicable, we used a strict variable selection process. High correlation between variables makes these problems worse. First, we calculated Pearson correlation coefficients (r for short) between every two environmental variables. If two variables were highly correlated ($|r| > 0.7$), we kept the one that made more sense in terms of ecology. Then, we did a Variance Inflation Factor (VIF) analysis. We used the 'vifstep' function from the R software package 'usdm'. We set a strict rule: VIF must be less than 7. We removed variables with high correlation step by step until all met this rule. In the end, we chose 19 variables for the next modeling step. All of their VIF values were below 7. These variables are: Isothermality (BIO3), Temperature Annual Range (BIO7), Mean Temperature of Wettest Quarter (BIO8), Mean Temperature of Driest Quarter (BIO9), Precipitation of Driest Month (BIO14), Precipitation Seasonality (BIO15), Precipitation of Coldest Quarter (BIO19), Elevation, Slope, TPI, Clay, Bulk, POP, Water, Forest, Grass, Barren, Urban, and Ice.

We used a systematic way to adjust the model. We used the R package 'ENMeval' to find the best combination of regularization multiplier (RM) and feature class (FC). Our goal was to balance the model's complexity and its ability to predict, and to avoid overfitting. To make the model work as well as possible, we tested all possible combinations of RM and FC. For RM, we used values from 0.5 to 5.0, increasing by 0.5 each time. For FC, we included L, Q, H, P, T and their combinations—there were 27 settings in total. We evaluated how well the model worked with block spatial cross-validation. This method divides the study area into four separate spatial blocks. We used two main criteria to choose the model. One was AICc (Akaike Information Criterion corrected for small sample sizes). The other was AUC (Area Under the Receiver Operating Characteristic Curve) from the test data. We preferred models with low AICc and high test AUC. This helped balance the model's complexity and its predictive ability. The best final model settings were RM = 0.5 and FC = LQHP. With these settings, we ran the model 50 times using bootstrap replicates. In each run, 75% of the data was used for training the model, and 25% was used for testing. We report the model's performance as the average test AUC plus or minus the standard deviation from the 50 runs. Besides, we did a jackknife test to find out how important each variable was. We also drew response curves. These curves help show the connection between key variables and the predicted habitat suitability. At last, we made a map showing the average habitat suitability for the European ground squirrel.

3. Analysis

The continuous habitat suitability values (0–1) produced by the MaxEnt model were divided into four suitability classes. This was done to help explain results and make conservation plans. The four classes are: Unsuitable (< 0.2), Low suitability (0.2–0.5), Moderate suitability (0.5–0.7), and High suitability (> 0.7). This way of setting thresholds took into account two key things. One is the probability distribution of the points where the species is known to live. The other is the common methods used in this area of study. Then, the area covered by each of these four suitability classes was calculated in detail. For future predictions, we first used the optimized model for each of the three SSP scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5). These model runs were carried out under three different GCMs (BCC-CSM2-MR, HadGEM3-GC31-LL, IPSL-CM6A-LR). Then, we computed the average of the projection results from the three GCMs for each SSP scenario. This step was to

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lower the uncertainty that comes with using just one climate model. And this average gave the final suitability maps for 2050 and 2090 under each SSP scenario. We also calculated two important things for each future time point (2050 and 2090) and each SSP scenario. One is the changes in the area of each suitability class. The other is the percentage of change when compared to the current distribution of suitable habitats.

4. Results

4.1. Model performance and key drivers

The optimized MaxEnt model showed very good ability to predict habitat suitability, and it effectively described the living requirements of the European ground squirrel. The final model used linear, hinge, product, and threshold feature classes. Its regularization multiplier was set at 0.5, which successfully balanced the model's complexity and how well it fits the data. Through spatial block cross-validation, the model got a high average test AUC of 0.876 ± 0.001 (As shown in the Figure 2). This result means its prediction accuracy was much better than random guesses. The very small standard deviation of the AUC values showed that the model worked stably when applied to different spatial parts. Also, the Akaike Information Criterion corrected for small sample sizes (AICc) was low. This proved that the model did not have the problem of overfitting while still keeping a strong ability to tell suitable habitats apart from unsuitable ones.

The analysis of variable importance showed that human-related influence mainly shapes where the European ground squirrel lives (As shown in the Figure 3). Key climate factors also have important effects on its distribution. Specifically, human population density was the most influential factor, contributing 23.0%. This shows the species is closely linked to habitats changed by humans, such as the edges of farmlands and pastures. Among climate variables, Temperature Annual Range (BIO7) contributed 20.9%. It means the species is very sensitive to the range of temperature changes that happen over a year in its living areas. Next was Isothermality (BIO3), which contributed 18.9%. This further emphasizes how important temperature stability is for the species. This metric represents the ratio of daily temperature variation to annual temperature variation. Besides, Precipitation of the Coldest Quarter (BIO19) had a notable influence, with an 8.4% contribution. It suggests that wet conditions during winter may be a factor that limits the species' survival. All these factors together point to the great importance of keeping burrow stability and a suitable microclimate. These are the core reasons that determine whether a habitat is suitable for the species. This includes avoiding burrow collapse caused by frost heave, too much water in the soil, or direct human disturbance.

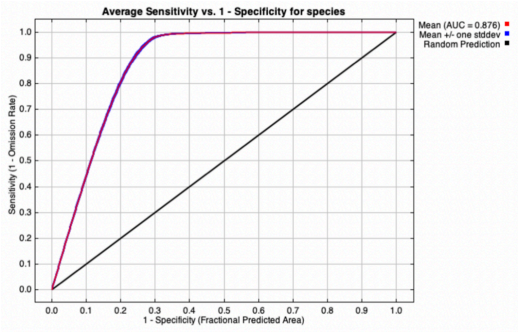


Figure 2. Average sensitivity and specificity curve of model testing results

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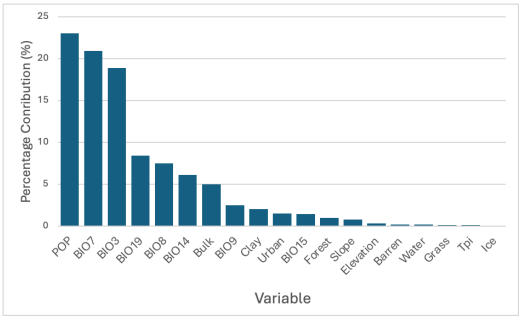


Figure 3. Variables included in modeling the current distribution of the European ground squirrel and their contributions to the model

4.2. Current distribution of suitable habitat

The model showed that the currently suitable habitats for the European ground squirrel are distributed differently in various areas (As shown in the Figure 4). An obvious focus of these habitats lies in Central and Southeastern Europe (As shown in the Figure 4b). The total area of suitable habitats (with suitability over 0.2) is about 1 million square kilometers. This area makes up around 13.83% of Europe's total land area. It is worth noting that highly suitable habitats (suitability over 0.7) are very rare. They cover only 0.61% of Europe's land, which is approximately 140,000 square kilometers. These highly suitable habitats are closely grouped around the Carpathian Mountains. They form clear key areas in central Romania, northern Hungary, and northeastern Serbia. Moderately suitable habitats (0.5–0.7) and low-suitability habitats (0.2–0.5) spread out from these core areas. They especially extend towards the northern Balkans.

Analysis at the national level showed clear conservation priorities. Romania, Hungary, and Bulgaria are the most critical countries for protecting the European ground squirrel (As shown in the Figure 5). Together, they hold more than 60% of the total highly suitable habitats across Europe. Specifically, Romania has the largest area of highly suitable habitats. It accounts for nearly 30% of the European total. Hungary and Bulgaria come right after Romania in this regard. Moderately suitable habitats are mainly found in Slovakia, Serbia, Romania, Moldova, North Macedonia, Hungary, and Bulgaria. Low-suitability habitats are more widely spread. There are significant areas of such habitats in Moldova, North Macedonia, Czechia, and Croatia. This layered distribution pattern makes it clear that cross-border conservation efforts are necessary. It also highlights the importance of focusing conservation resources on these core countries where the species mainly lives.

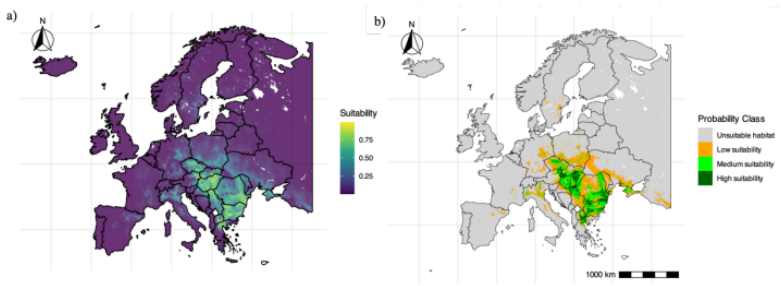


Figure 4. (a) Continuous habitat suitability map for the European ground squirrel under current conditions. (b) Reclassified map showing the spatial distribution of unsuitable, low, moderate, and high suitability habitats

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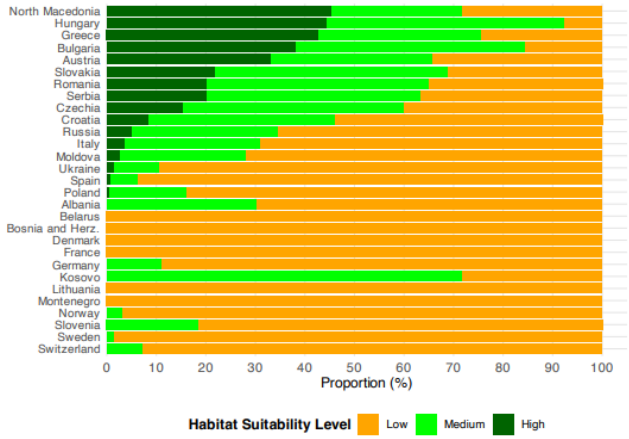


Figure 5. Percentage contribution of European countries to four habitat suitability classes derived from Maxent species distribution modelling. Values represent the proportion of areas of each habitat suitability level within European countries (i.e. area of each suitability level of each country/total suitability area of Europe. Low: 0.2–0.5; Moderate: 0.5–0.7; High: >0.7. The histogram illustrates the relative importance of different countries for maintaining habitats of varying quality, with taller bars indicating countries that contain larger shares of Europe's total habitat area for each suitability class. Results inform conservation prioritization by identifying countries that disproportionately contribute to high-quality habitat availability for the target species

4.3. Future changes of suitable habitat

Future climate scenario projections show a big reduction in suitable habitats for the European ground squirrel. But how serious this is and how things will develop depends a lot on the social and economic path we choose. Compared with the current distribution, the total area of suitable habitats (suitability >0.2) is expected to drop by 4% to 9% by the middle of the century (2050) (Tab. 2). By the end of the century (2090), the total loss will go up to 12% to 24%. The worst and fastest habitat loss happens under the high-emission SSP5-8.5 scenario. On the other hand, the sustainable SSP1-2.6 scenario shows that habitats may become stable by 2090 (As shown in the Figure 7). They might even recover a little. This shows how important active climate mitigation is to reduce biodiversity loss.

Analyzing future habitat structure shows a more worrying trend than just the overall area loss: high-quality habitats are being badly damaged and split into small parts. Under SSP5-8.5, the total suitable area is projected to fall by about 9% by 2050. But the core highly suitable habitats (suitability >0.7) could lose up to 72%—that is a devastating loss. Moderately and lowly suitable habitats will have very different fates in different scenarios. Under SSP5-8.5, these habitats will also decrease. This means the whole living environment is getting worse. In contrast, under SSP1-2.6, moderately and highly suitable habitats may increase by 2090. This suggests that climate mitigation can help the species set up populations in new areas with suitable climate. The wide decline in habitat quality means the number of squirrels the habitats can support will drop much faster than the simple reduction in area.

Projections also show a big geographical shift in the European ground squirrel's suitable living range. There is a clear trend of moving to areas with higher latitudes (As shown in the Figure 6). This shift has two main parts: a lot of habitat loss in the southern part of their current range (like in the southern Balkans) and new, small, scattered suitable habitats appearing beyond their current northern range (like in northern Poland and the Baltic states). This pattern of "losing habitat in the

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south and possibly expanding in the north" is a typical sign of a species moving to cooler areas to find the suitable temperature conditions they need.

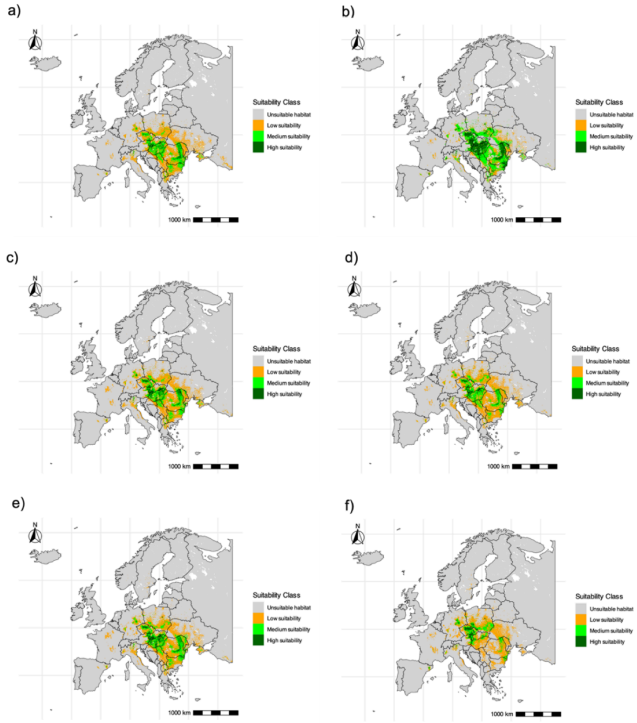


Figure 6. Predicted future distribution of the European ground squirrel (reclassified maps): a) SSP1 2050, b) SSP1 2090, c) SSP2 2050, d) SSP2 2090, e) SSP5 2050, f) SSP5 2090

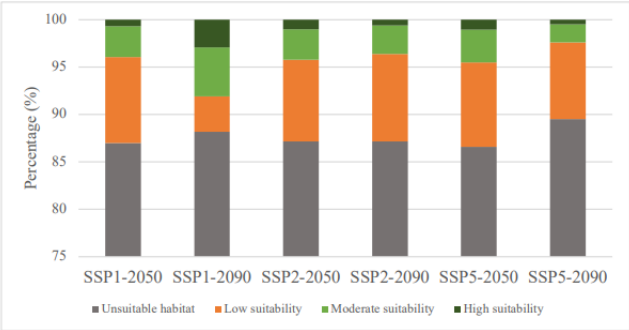


Figure 7. Distribution area proportions of the European ground squirrel under each climate scenario in 2050 and 2090

Table 2. Proportion change between future and current distribution of the European ground squirrel (proportion of future distribution (%) – proportion of current distribution area (%)) under different climate scenarios in 2050 and 2090

Suitability Class	SSP1-2050	SSP1-2090	SSP2-2050	SSP2-2090	SSP5-2050	SSP5-2090
Unsuitable habitat	0.85	2	0.98	1	0.44	3.33
Low suitability	0.96	-4.34	0.52	1.14	0.79	0
Moderate suitability	-0.73	1.22	-0.74	-0.95	-0.5	-2.05
High suitability	-1.08	1.12	-0.76	-1.18	-0.72	1.28

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5. Discussion

5.1. Robustness and uncertainty of model projections

The MaxEnt model built in this study showed very good ability to make accurate predictions. Its mean test AUC is 0.876 ± 0.001. This high model performance provides a reliable foundation. It helps us understand the key environmental drivers that have been identified and their response curves. This means the variables with the highest contributions are really important for the European ground squirrel's habitat choice. They are not just problems caused by the modeling method. So the conclusions about current distribution patterns and future changes from this model are reliable.

Though the model works well, our predictions have several important sources of uncertainty. Firstly, there is bias in the collection of species occurrence data. This is a major limitation. GBIF data are likely biased towards areas that are easy to reach. This may lead us to underestimate the species' real distribution in remote or hard-to-access places. And this could result in overestimating future habitat loss in those regions [20]. Secondly, even though we chose variables carefully, our model did not include some factors. These factors are related to ecology but hard to measure. For example, competition between different species, diseases, and small-scale microhabitat conditions [17]. Not including these factors might make our predictions too optimistic in very local areas [21]. Finally, the MaxEnt model is a method based on correlations. It cannot establish clear cause-and-effect relationships between variables and species distribution [22].

Our predictions naturally include the uncertainties of future climate scenarios. We did not do a quantitative analysis of how uncertainties break down. But an analysis of our findings suggests that the biggest uncertainty comes from the choice of socio-economic pathways (SSPs). It is not from differences between climate models (GCMs). The "qualitative difference" in habitat changes between SSP1-2.6 and SSP5-8.5 is huge. One is stabilization and the other is collapse. This difference is much larger than the "quantitative variation" among GCM predictions under a single pathway. This finding turns uncertainty from a technical issue into an important scientific and policy insight. The long-term survival of the European ground squirrel depends less on how precise climate models are. It depends more on how ambitious and effective global greenhouse gas mitigation efforts are [17]. So conservation planning must be proactive and flexible. We should avoid the mistake of waiting for a single "most accurate" prediction [23]. Instead, strategies should be designed for a range of possible futures. At the same time, they should include ways to avoid risks under worst-case scenarios. And they should make use of opportunities under the most favorable ones [24].

5.2. Drivers and conservation priorities of the current distribution

Our results show that the European ground squirrel's current distribution is not caused by just one factor. It comes from a combined filtering effect of both human-related influence and specific climate limits. The great importance of human population density shows the species' close connection to landscapes changed by humans. This is especially true for traditional agricultural systems with low intensity. These systems keep the open grassland habitats that the species needs [17,25,26]. But this reliance is a double-edged sword. It brings both chances and risks when it comes to the development of more intensive farming or giving up using land [27]. At the same time, climate factors strongly limit where the species can live. It prefers areas with a smaller annual temperature range (BIO7) and higher isothermality (BIO3)(As shown in the Figure 8). This suggests that its body cannot stand extreme temperature changes (As shown in the Figure 7). Low

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precipitation in the coldest quarter (BIO19) also plays a big role. It further highlights that wet conditions in winter are a key limiting factor. Winter wetness may lead to burrow flooding and low body temperature for the species [6,17]. So, the current hotspots of the species' distribution can be explained as areas that meet three key conditions at the same time. These conditions are: open habitats maintained by human activities, stable temperature, and dry weather in winter [28].

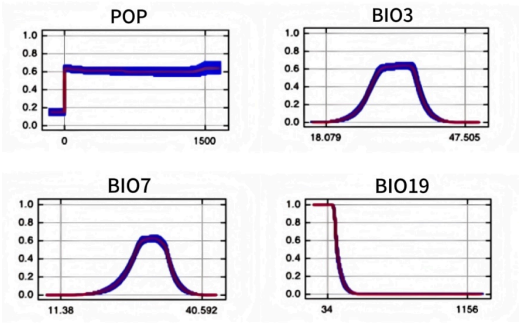


Figure 8. Response curves of key variables in the current distribution model

The fact that distribution hotspots are concentrated in the Pannonian Basin and surrounding areas directly shows how these drivers work together (As shown in the Figure 6). This region has a unique biogeographical situation that combines all the key conditions for the species' survival. Its continental climate offers relatively stable temperature conditions, which is shown by higher BIO3 values and moderate BIO7 values. It has a long history of traditional agriculture, especially animal farming, which has created and kept large areas of open short-grass steppes. Also, its soils that drain well (like loess) and relatively dry winters reduce the dangers caused by precipitation in the cold season [17,29,30]. On the other hand, regions such as the Alps may be limited by harsh winters and a lack of open habitats below the treeline. Parts of Western Europe are probably unsuitable too, because of highly intensive agriculture or overly wet winters [4,31]. This distribution pattern proves that the European ground squirrel is a species that is well-adapted to "semi-natural" grassland habitats. These habitats are maintained by traditional agriculture in areas with a continental climate.

Our analysis clearly points out that Romania, Hungary, and Bulgaria are the top priority areas for conservation. But to better understand the drivers behind this, we need a flexible understanding of these priority areas. The very existence of these hotspots depends on traditional land use methods, and these methods are changing quickly [10,15,17,32]. So the map of current conservation priorities should also be seen as a map of inherent vulnerability. Any change in land use that leads to giving up traditional farming (which causes the spread of shrubs) or making farming more intensive (using pesticides and mechanical harvesting) can quickly damage the habitat conditions that support these populations [15,17,29]. This means that conservation actions cannot only focus on setting up protected areas. They must also actively take part in habitat management [33]. This includes working with local communities to keep or copy traditional agricultural practices that preserve the open, short-grass vegetation structure [34,35]. For the large populations living outside the current protected area network, promoting agricultural policies that are friendly to ground squirrels becomes extremely important.

5.3. Habitat trajectories and vulnerability under future climate change

Analyses of future scenarios show serious structural damage to the European ground squirrel's suitable habitats. This trend is caused by changing key climate-related stress factors. More extreme

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summer heat (BIO5) and more winter precipitation (BIO19) have become main threats. They test the species' ability to stand high temperatures and its survival during hibernation, respectively. And they lead to big reductions in suitable habitats under the high-emission SSP5-8.5 scenario. What is more important than just the loss of area is the serious decline in habitat quality. The expected loss of core highly suitable habitats (suitability >0.7) can reach up to 70%. This loss is much greater than the drop in the total suitable area. This means that future populations may have to live in environments that are only barely suitable. And this will basically harm their ability to reproduce successfully and survive for a long time.

This change in habitats is also followed by big geographical shifts, which make the species much more vulnerable. The model predicts that the species' living range will shrink and move towards areas with higher latitudes or altitudes. This process is full of uncertainty and brings two main risks. For one thing, the southern and low-elevation edges of the current range will become high-vulnerability hotspots. In these places, populations face "climate cul-de-sacs" and a higher risk of extinction. For another, the usefulness of newly identified potential climate refugia (such as those in northern Central Europe) depends on their "accessibility" and "habitability". That is, can the species reach these distant areas with its limited ability to move? And are non-climatic conditions (like soil suitable for digging burrows) good enough? So, future conservation work must focus on finding these potential refugia and connecting them effectively. At the same time, it should actively manage existing hotspots to build a strong and resilient conservation network.

5.4. Implications for conservation practice and management

Our predictions point out a clear need for conservation: the suitable habitats for the European ground squirrel are expected to get much smaller and undergo spatial changes in the next few decades. The analyses show three linked main challenges: (1) Current distribution hotspots (like the Pannonian Basin) are facing threats from both climate change and land-use change at the same time; (2) The species needs to move to possible climate refugia in areas with higher latitudes or altitudes to keep their populations alive and healthy; (3) More and more habitat fragmentation seriously stops this necessary range shift. So, any effective conservation strategy must be a combined plan that brings together on-site protection, better connectivity, and flexible management to deal with these many-sided and changing threats [12,36].

To deal with these challenges, we suggest a conservation strategy that is clear in spatial terms and has three levels. First, strengthening on-site protection of current distribution hotspots is of great importance. In core areas such as Romania and Hungary, we should focus efforts on making the protected area network larger and encouraging agricultural practices that are friendly to ground squirrels (for example, keeping low-intensity grazing) [14,37,38]. These actions directly respond to the finding that "human population density" is a key driver. They aim to keep the semi-natural grassland habitats that the species relies on [34,39,40]. Second, finding and restoring ecological corridors that connect current hotspots to future suitable areas is very important for adapting to climate change [15,41,42]. This includes projects to restore habitats along important landscape features, which helps the species disperse naturally [43]. Finally, taking active steps to assess and manage habitats in the found future climate refugia (like in northern Central Europe) is necessary. It ensures these areas can provide livable conditions when the climate becomes suitable, making it possible for populations to establish there in the future.

In the end, the successful use of this conservation plan depends on putting its main principles into wider policy tools. This includes combining habitat conservation goals into the agri-environment schemes of the EU's Common Agricultural Policy (CAP). This is to encourage land management

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that is friendly to wildlife. It also includes adding connectivity planning into regional green infrastructure strategies [44,45]. Besides, achieving success needs to promote cooperation across different disciplines among ecologists, climate scientists, and socio-economists. They need to work together to design solutions for complex challenges such as habitat restoration and engaging with stakeholders [46]. If we regard the conservation of the European ground squirrel as a sign of broader ecosystem health and climate adaptation goals, we can gather more political support and social resources. This will ensure that this species can survive for a long time in a changing world.

6. Conclusion

This study clearly describes in a systematic way the distribution patterns of suitable habitats for the European ground squirrel. It also explains how the species responds to future climate change by combining environmental data from many different sources and species distribution models (which are effective tools for predicting where species live). The results show that the current distribution of the species is influenced by both habitats kept by human activities (such as traditional agricultural landscapes) and specific climate conditions. These climate conditions include stable temperatures and dry winters. Whether the species can survive in the future mainly depends on global emission pathways. Under the high-emission scenario (SSP5-8.5), the study predicts a big reduction in suitable habitats and a drop in their quality. This case makes it clear that there is great methodological importance in combining anthropogenic and climatic factors. This is especially true when we want to accurately assess the vulnerability of species that have adapted to landscapes modified by humans in the Anthropocene. So, conservation strategies must develop into a framework that has clear spatial targets and uses adaptive management. This includes strengthening the protection of current habitat hotspots, building connectivity corridors to link different habitats, finding future climate refugia where the species can survive, and putting these actions into broader agricultural and climate policies. Doing so can combine biodiversity conservation with sustainable development in a effective way. Future research should connect distribution models with population dynamics. It should also include high-resolution remote sensing data and gene flow data. These steps will help us move from just predicting habitat shifts to making precise forecasts about whether the species' populations can persist.

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