Distribution, Population Size, and Habitat Characteristics of the Endangered European Ground Squirrel (Spermophilus citellus, Rodentia, Mammalia) in Its Southernmost Range

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Abstract: The European ground squirrel (Spermophilus citellus) is an endangered species, endemic to Central and Southeastern Europe, inhabiting burrow colonies in grassland and agricultural ecosystems. In recent years, agricultural land-use changes and increased urbanization have largely contributed to a severe population decline across its range, particularly in its southernmost edge. Assessing the population and habitat status of this species is essential for prioritizing appropriate conservation actions. The present study aims to track population size changes and identify habitat characteristics of the species in Greece via a literature search, questionnaires, and fieldwork for assessing trends in population size as well as spatial K-means analysis for estimating its relation to specific habitat attributes. We found that both distribution size (grid number) and colony numbers of the species decreased in the last decades (by 62.4% and 74.6%, respectively). The remaining colonies are isolated and characterized by low density (mean = 7.4 ± 8.6 ind/ha) and low number of animals (mean = 13 ± 16 individuals). Most of the colonies are situated in lowlands and did not relate to specific habitat attributes. Habitat aspect and system productivity (NDVI) were the main factors contributing mostly to the clustering of the existing colonies. These results demonstrate that the species is confined to small, isolated anthropogenic habitats. Specific conservation actions such as population reinforcement, habitat improvement, and specific common agricultural policy measures could effectively improve agroecological zones that are suitable for the maintenance and protection of existing and potential habitats for populations of the species.

Keywords: Greece; souslik; conservation; Mediterranean

1. Introduction

European ground squirrels (Spermophilus citellus Linnaeus, 1766; hereafter referred to as EGS) are hibernating squirrels endemic to Central and Southeastern Europe which live in colonies in grassland and agricultural ecosystems. Along with other ground squirrel species, EGS are considered a keystone species of these ecosystems. They constitute prey for top endangered predators [1], increase the diversity and structural complexity of grasslands [2], limit specific plant dispersal (especially that of invasive plants [3]), affect soil structure and a variety of soil processes by constructing elaborate burrows [4], and may host other species such as reptiles, birds, and arthropods in their abandoned burrows [5].

Even though the species is listed in Appendix II of the Bern Convention and Annexes II and IV of the EU Habitats and Species Directive (92/43), recently the IUCN red list has classified EGS as endangered (EN) with a decreasing population trend [6]. Habitat loss, land-use changes, a lack of grassland management, inappropriate arable land management, and associated habitat fragmentation are the major drivers behind this population decline [3,7]. Consequently, the fragmentation and deterioration of available habitats can
cause dysconnectivity and endogamy, which are unfavorable to maintaining local genetic diversity [8,9].

Therefore, identifying the habitats where the species lives is crucial for determining its survival. Generally, EGS favor short and dry non-forest steppe grasslands with various soil types and sufficient drainage [3]. These habitat characteristics are found in natural or semi-natural and artificial grasslands where mowing or grazing occurs. Currently, important refuge areas of EGS colonies in Europe are sport areas, airports, playgrounds, and recreational areas [10]. The species avoids industrial farmland and intensive cultivated land, although it also occurs in vineyards, orchards and gardens, and alfalfa fields (sometimes with high densities), suggesting a high dependence on human activities [10–14]. However, anthropogenic land use seems to affect population dynamics, life-history, and dispersal, and may increase stress levels [12,13,15,16]. Moreover, as food availability and quality are crucial for population fitness, a lack of nutritious and abundant food sources could also reduce the survival of populations [17].

As habitat features are important for understanding the population dynamics of EGS, this study aims to investigate the interrelations between spatial distribution, habitat use, and population size of EGS in Greece. In Greece, EGS are distributed in three separate sub-populations in the northern part of the country: western Macedonia, central Macedonia, and Thrace [18–20]. Due to unfavorable agricultural practices and large-scale urbanization, these populations are heavily fragmented even at local level, creating isolated metapopulations [14]. In Greece, the conservation status of both populations and habitat is unfavorable-inadequate (U1), despite the fact that the national legislation has incorporated EU conservation policies. The Greek populations belong to the southern phylogenetic lineage of the species (which is considered to have higher haplotype diversity) along with populations in Bulgaria, North Macedonia, and European Turkey [21]. Additionally, Greek EGS populations are important since they are found at the southernmost border of the range of the species and have adapted to the Mediterranean climate [14]. These populations are exposed to increased climate-related anthropogenic pressures (including climate change). Understanding trends in the overall population status and habitat characteristics of this species is important for identifying priorities for appropriate conservation actions in order to elaborate a national conservation action plan [14]. In this context, the present study aims to identify the habitat characteristics and track current population size changes of EGS in Greece. This is a vital step towards elucidating the status of the species and its habitats in the country and will contribute to a sustainable management of the populations.

2. Materials and Methods

2.1. Spatial Distribution and Population Size

For the purposes of the present study, a three-fold approach was followed: (a) a literature search, (b) questionnaires, and (c) fieldwork. All of the available data from journal articles, books, and technical reports between 1932 and 2015 concerning the distribution of EGS in Greece were collected. All of the information on dates, locations, and context of EGS’s presence were documented, resulting in 149 records. In addition, two types of questionnaires regarding information on the presence/absence of the species were created in 2019–2020: (a) information from published photographs by wildlife photographers on social media, and (b) information from interviews of people working in the field (e.g., National Park officers, field researchers, farmers, livestock breeders, hunters, etc.). At the end of this procedure, 56 persons were contacted, resulting in 81 records. Based on the data from the literature search and the questionnaires, 11 areas and 128 different precise localities were mapped (Figure 1). To estimate distribution size, we considered the occupied 10 × 10 km grid cells.
Of all these localities in Northern Greece, 119 were visited and inspected in situ in the spring of 2019 and 2020. In all localities with active EGS colonies, we tracked all active burrow entrances by a GPS-device. Recording the number and location of active burrow entrances in a colony is a common technique for EGS surveys to calculate population density [22,23]. Counting active burrow entrances has been shown to be predictive of the relative changes in local ground squirrel population density with respect to both time and space [24–26], despite the indirectness of the method and its variable predictive power [27]. An active burrow entrance was identified by signs of recent use such as clear entrance, fresh soil mounds, feces, feeding signs, and evident runways. Spatial analysis of these data was performed using ArcGIS® 10.7.1 (Esri China (Hong Kong) Ltd., Kowloon, Hong Kong, www.esri.com, accessed on 3 June 2021).

In order to quantify the relationship between burrow entrances and active individuals by locality, we observed individuals directly from multiple viewpoints using binoculars, scanning for 5 min every half-hour during a full day (6:30–20:30) [28,29]. The total number of individuals was the sum of the different animals temporally and spatially distributed within the colony throughout the day. The observations were carried out the same day or the day after the burrow entrance counts in order to obtain comparable values. We excluded the localities where the morphology of the landscape or/and the height of vegetation caused low visibility. A dataset of burrow entrance-individual counts was created. Specifically, we calculated the Individual-per-Burrow Entrance ratio for 17 populations in Northern Greece between 2019 and 2020, this being 0.14 ± 0.09 (Table 1). We assumed that the same relationship holds for all populations in Northern Greece and used this ratio to extrapolate population size (N) from burrow entrance counts for each locality. Lastly, we calculated population density (ind/ha) by dividing the population size (N) by the area of the locality (area covered within the limits of the most peripheral burrow entrances at each locality). We classified the population density of all colonies into four categories according to [30]: (A) 100–15 ind/ha; (B) 14–2 ind/ha; (C) <2 ind/ha; and (D) insignificant, only single individuals and/or burrows.
Table 1. Individuals-per-burrow entrance ratio for 17 populations in Northern Greece (see Figure S1 for the location of the localities in Supplementary Material).

| Locality                          | Counted Burrows | Observed Individuals | Individual-Per-Burrow Entrance Ratio |
|-----------------------------------|-----------------|----------------------|--------------------------------------|
| 2019                              |                 |                      |                                      |
| Alexandroupoli                    | 60              | 8                    | 0.13                                 |
| Analipsi                          | 219             | 15                   | 0.07                                 |
| AUTH School of Agriculture        | 108             | 14                   | 0.13                                 |
| Chortiatis                        | 15              | 1                    | 0.07                                 |
| Dion                              | 107             | 24                   | 0.22                                 |
| Drakontio                         | 18              | 3                    | 0.17                                 |
| Feres West                        | 52              | 6                    | 0.12                                 |
| Galatista                         | 27              | 12                   | 0.44                                 |
| International Hellenic University | 138             | 11                   | 0.08                                 |
| Ptolemaida                        | 32              | 3                    | 0.09                                 |
| Seli                              | 27              | 4                    | 0.15                                 |
| Mean                              |                 |                      | 0.14                                 |

2.2. Spatial Analysis of Site-Attributes

Several environmental, spatial, and climatic variables were used to describe the colony habitats. For the purposes of this study, we considered altitude, aspect, slope, solar incidence, and the normalized difference vegetation index (NDVI) as the main environmental variables; colony area, distance from freshwater bodies, distance from residential/industrial areas, and distance from roads as the main spatial variables; and mean winter and summer precipitation, mean winter and summer relative humidity at 2 m, mean winter and summer temperature of earth surface, maximum winter and summer temperature at 2 m height, minimum winter and summer temperature at 2 m height, and mean winter and summer temperature at 2 m height as the main climatic variables. The peripheral burrow entrances of each colony were used to create the minimum convex polygon of the occupied area. We used these areas as the layer to extract the mean values of the calculated environmental and spatial variables. The spatial analysis included data from 26 localities/colonies. Five out of the thirty-one localities with no data or less than two individuals were excluded. Normalization of variables was implemented through the BBmisc [31] package in R Package version 4.1.0 [32]. Feature importance with k-means clustering analysis was used to classify and visualize the 26 sampling sites. This approach uses Euclidean distance as a measure of dissimilarity and simplifies the variables into linear combinations, increasing the interpretability of clustering results. In addition, the algorithm finds the variables which drive the cluster assignment and scores them according to their relevance. We used R platform through the FeatureImpCluster [33] and flexclust [34] packages to perform the analysis [32]. For those categorical variables that considered land use, localities were classified according of Corine Land Cover Level 1 (www.land.copernicus.eu, accessed on 20 May 2021). All of the climatic data were extracted from NASA POWER’s website (https://power.larc.nasa.gov/, accessed on 18 July 2021), which provide valuable weather data sets when field stations are unavailable [35]. The variables correspond the mean values in each of the localities over the last 10 years (2009–2019) for winter (October–March) and summer (April–September).
3. Results

3.1. Spatial Distribution and Population Size

The data from the literature and the questionnaires revealed that EGS are confined to Northern Greece, representing a total 125 $10 \times 10$ km squares and 119 historical localities (Figure 1). More precisely, most EGS colonies were located in Central Macedonia (63.3% of occupied grid cells) and less than 40% were located in Thrace and Western Macedonia (19.4% and 17.3%, respectively). A little less than one third of the records date before 2000 (30.5%), whereas the majority spans the period between 2010 and 2017 (53.4%).

Our recent field surveys (2019–2020) revealed a distribution size decrease of 62.4% of presence in $10 \times 10$ km grid cells, and the species was found in only 31 of the original 119 historical localities, indicating a drastic decrease of 74.6% in colony numbers. Almost seventy percent of the current EGS localities are found in Central Macedonia (21/31), while 19.3% are in Western Macedonia (6/31), and only 12.9% are in Thrace (4/31) (Table 2). The estimation of the total number of individuals per locality ranged from 1 to 60, with a mean of $13 \pm 16.4$ individuals (median = 7, $n = 29$). A minimum estimate of total population size amounts to 378 individuals (Table 2). Most localities (62.1%, 18/29) contained less than 10 individuals each. Mean population density was $7.4 \pm 8.6$ ind/ha (median = 5.8, range = 0.47–37.46, $n = 26$). More than half of the colonies (51.7%) was classified to the population density category B (14–2 ind/ha) and almost one third to population density category C (<2 ind/ha, 27.6%). The highest (A: 100–15 ind/ha) and the lowest (D: Insignificant) population density categories were equally represented (10.3% each).

Table 2. The 31 sites of Spermophilus citellus colonies surveyed in the current study (2019–2020). Burrow entrance number is the total burrow entrances found in each locality. Population size (N) and population density (ind/ha) of each locality is shown.

| A/A | Locality * | Burrow Entrances | N | Occupied Area (ha) | Density (ind/ha) |
|-----|------------|------------------|---|--------------------|-----------------|
| 1   | Agios Vasileios | 95               | 13 | 0.57               | 23.33           |
| 2   | Analipsi     | 219              | 31 | 6.61               | 4.64            |
| 3   | Anatoliko (Thessaloniki) | 397 | 56 | 29.7               | 1.87            |
| 4   | Chortiatis   | 15               | 2  | 0.65               | 3.23            |
| 5   | Dion         | 107              | 15 | 2.5                | 5.99            |
| 6   | Drakontio    | 18               | 3  | 0.52               | 4.85            |
| 7   | Galatista    | 84               | 12 | 1.09               | 10.79           |
| 8   | IHU          | 138              | 19 | 2.56               | 7.55            |
| 9   | Kalamoto     | 2                | 1  | -                  | -               |
| 10  | Kalochori    | 429              | 60 | 40.76              | 1.47            |
| 11  | Loudias      | 17               | 2  | 5.1                | 0.47            |
| 12  | Nea Mesimvria| 57               | 8  | 1.09               | 7.32            |
| 13  | Nea Raidestos| 2                | 1  | -                  | -               |
| 14  | Noesis       | 10               | 1  | 1.34               | 1.04            |
| 15  | Nymfopetra   | 8                | 1  | 0.69               | 1.62            |
| 16  | Evangelismos | 51               | 7  | 1.13               | 6.32            |
| 17  | Agriculture, AUTh | 108 | 15 | 2.5                | 6.05            |
| 18  | Pella        | 347              | 49 | 6.42               | 7.57            |
| 19  | Thermi       | 198              | 28 | 0.74               | 37.46           |
| 20  | Axios        | -                | -  | -                  | -               |
| 21  | SEDES air base | -              | -  | -                  | -               |
Table 2. Cont.

| A/A | Locality * | Burrow Entrances | N | Occupied Area (ha) | Density (ind/ha) |
|-----|------------|------------------|---|--------------------|-----------------|
|     | West Macedonia |                 |   |                    |                 |
| 22  | Anatoliko South (Ptolemaida) | 9 | 1 | 0.11 | 11.45 |
| 23  | Anatoliko North (Ptolemaida) | 37 | 5 | 9.45 | 0.55 |
| 24  | Koila (Kozani) | 34 | 5 | 0.83 | 5.73 |
| 25  | Ptolemaida | 32 | 4 | 0.18 | 24.89 |
| 26  | Seli | 27 | 4 | 2.48 | 1.52 |
| 27  | Oros Vermio | - | - | - | - |
|     | Thrace |                 |   |                    |                 |
| 28  | Alexandroupoli | 60 | 8 | 3.17 | 2.65 |
| 29  | Feres West | 52 | 7 | 4.33 | 1.68 |
| 30  | Feres East | 50 | 7 | 1.21 | 5.79 |
| 31  | Kavisos | 79 | 11 | 1.5 | 7.37 |
|     | TOTAL | 2682 | 378 |        |                 |

* please refer to Figure S1 for the location of the localities.

3.2. Spatial Analysis of Site-Attributes

EGS colonies in Greece were mostly found in agricultural (cereal crops, alfalfa fields, olive groves, 48.4%) and artificial (38.7%) areas, while the lowest number of colonies were found in natural, seminatural and wetland habitats. Moreover, 82.8% of total EGS populations (as per individuals) was in agricultural and artificial areas. A noticeable exception was Kalochori, the largest colony in the present study, which was characterized by a wetland habitat (salt marshes) and represented 16.2% of total EGS individuals.

The k-means analysis of the 26 current EGS localities resulted in four clusters (Figure 2). The means of the considered variables for each cluster are provided in Table S1 (in Supplementary Material). Cluster 1 (12% of localities, n = 3) were found in high slope (mean 4.7°) and altitude (mean 766 m), away from residential/industrial areas (mean 6912 m). Cluster 2 (69% of localities, n = 18) grouped most of the localities of lowlands Central Macedonia and Thrace without a strong relation to any variable. Cluster 3 (4% of localities, n = 1) was characterized by large area (407,611 m²) and high distance from roads (mean 708 m). Cluster 4 (15% of localities, n = 4) grouped most localities of Western Macedonia, far from freshwater bodies (>10,000 m) and with relatively high altitude (642 m) and lower climatic variables (Figure 2). Moreover, the feature importance of k-means analysis revealed that mean habitat aspect (south-east to south-western values) and, secondly, system productivity (NDVI) were the most relevant variables (Table 3). Minimum distance to a residential/industrial area, slope, and area were less important. Concerning the climatic data, only mean winter and summer precipitation had a small contribution to the clustering (Table 3).
Minimum distance from residential/industrial area–MNDRIA (m) 0.07 (0.04, 0.16)

Figure 2. The feature importance plot of four colony clusters and the contribution of the variables of Spermophilus citellus habitats situated in Northern Greece (n = 26). Red circles indicate zero level of influence. The feature bars on the left of the red circles are affecting negatively the clusters, while the feature bars on the right positively [refer to Table 3 for parameter abbreviations].

Table 3. Misclassification rate of k-mean analysis of importance with the main habitat parameters that relate the 26 colonies of Spermophilus citellus in Northern Greece.

| Habitat Parameters                                | Median (Min, Max) |
|---------------------------------------------------|-------------------|
| Altitude–ALT (m)                                  | 0.04 (0, 0.13)    |
| Slope–SLO (°)                                     | 0.07 (0, 0.12)    |
| Aspect–ASP (°)                                    | 0.29 (0.25, 0.34) |
| NDVI                                              | 0.126 (0.75, 0.16) |
| Area–ARE (m²)                                     | 0.07 (0.07, 0.07) |
| Solar incidence–SI (Wm⁻²)                         | 0 (0, 0)          |
| Mean winter precipitation–MWP (mm/day)            | 0.01 (0, 0.01)    |
| Mean summer precipitation–MSP (mm/day)            | 0.01 (0, 0.01)    |
| Mean winter relative humidity at 2 m height–MWRH2M (%) | 0 (0, 0)        |
| Mean summer relative humidity at 2 m height–MSRH2M (%) | 0 (0, 0)        |
| Mean winter surface temperature–MWST (°C)         | 0 (0, 0)          |
| Mean summer surface temperature–MSST (°C)         | 0 (0, 0)          |
| Maximum winter temperature at 2 m height–MXWT2M (°C) | 0 (0, 0)        |
| Maximum summer temperature at 2 m height–MXST2M (°C) | 0 (0, 0)        |
| Minimum winter temperature at 2 m height–MNWT2M (°C) | 0 (0, 0)        |
| Minimum summer temperature at 2 m height–MNST2M (°C) | 0 (0, 0)        |
| Mean winter temperature at 2 m height–MWT2M (°C)  | 0 (0, 0)          |
| Mean summer temperature at 2 m height–MST2M (°C)  | 0 (0, 0)          |
| Road distance–RD (m)                              | 0.04 (0.04, 0.07) |
| Distance from freshwater bodies–DFB (m)           | 0.06 (0.04, 0.07) |
| Minimum distance from residential/industrial area–MNDRIA (m) | 0.07 (0.04, 0.16) |

4. Discussion

In the last few decades, EGS have experienced a continuous decline in distribution and population numbers throughout its entire range [6,36]. This study represents the first attempt to estimate the overall status of the species in Greece, particularly in its southernmost range. Our data indicate a significant decline of the EGS population with respect to both its historical range (62.4%) and number of known colonies (74.6%). Most of
the literature and questionnaire records (53.4%) referred to the last decade 2010–2017. It is very likely that during this period the smallest of the populations had difficulty recovering their viable population size and that over half of the colonies collapsed. The severity of this situation was also revealed during our field surveys, when some colonies in Central Macedonia (e.g., Axios, Drakontio, Nea Raidestos, Noesis) disappeared between 2019 and 2020.

During the study period (2019–2020), we recorded 31 colonies in northern Greece. Most of these colonies were located in Central Macedonia, with smaller numbers in Western Macedonia and Thrace (Figure 1). Most of the recorded colonies appeared to be small, with 62.1% of them containing <10 individuals (indicating an extended threat of population collapse). Density distribution in Greece, with medium (15–2 ind/ha) and low (<2 ind/ha) density categories dominating (51.7% and 27.6%, respectively), was similar to that found in Bulgaria [30]. The calculated mean density for Greece (7.4 ind/ha) appeared to be pronouncedly lower than that of other resident countries, such as Eastern Romania (27.33 ind/ha; [37]), the Czech Republic (15.1 ind/ha; [10]), and Austria (range 9–110 ind/ha; [11,12]). Nevertheless, it appeared to follow the pattern of extremely low densities of small and fragmented areas, such as the populations of the Jakupica mountains in North Macedonia (0.8–5.5 ind/ha; [38]). Additionally, the low density of EGS populations in Greece might further reflect the peripheral metapopulational nature of the species’ southernmost distribution boundaries [10]. Such small numbers, especially when combined with increased fragmentation (as revealed by the small mean distance from roads in our analyses; Table S1), might have a negative impact on the survival of the species. Small and fragmented EGS populations could end up suffering from inbreeding depression leading to decreased biological fitness and, eventually, extinction [9]. Nevertheless, in other ground squirrel species (e.g., *Callospermophilus lateralis*), the immigration effect can promote a demographic recovery and counter the genetic effects of bottleneck, especially in regards to the loss of allelic richness [39]. Thus, immigration may be one of key rescue events to prevent a population from extinction and to recover from very low densities [40]. Unfortunately, natural immigration is extremely difficult in most Greek colonies due to the species’ intense fragmentation and isolation. A potential solution would be human-mediated reinforcement, but this would require a national legal framework.

In Northern Greece, most colonies were located near human settlements (and, thus, human activities), as reflected in the low values of the minimum distance from residential/industrial areas (Table S1). About 45.10% of the estimated population was mainly found in agricultural areas such as non-irrigated arable land, occupying grass stripes along roads and fallows of crops [3]. The confinement of these colonies in such habitats most likely resulted in quite high densities (e.g., 37.46–10.79 ind/ha in olive groves; 23.33 ind/ha in gardens), and slightly lower densities in pastures (11.45–0.47 ind/ha) (see also [10,12,14]). On the other hand, 37.7% of the estimated population was found in highly anthropogenic areas such as discontinuous urban, industrial, and commercial areas, leisure facilities, airports, and potential construction sites. The colonies of these areas also exhibit variably high densities (24.89–1.04 ind/ha in urban areas; 7.57–1.62 ind/ha in leisure facilities; 2.65 ind/ha in airport; and 3.23 ind/ha in construction site). The occurrence of the species in these human modified environments most likely suggests the high dependence of the species on human activities (e.g., mowing, grazing), which help maintain short and renewed vegetation and a steppe-like environment, necessary for the survival of the species [7,10,11,13,14,41]. Vegetation height is considered to be the most critical factor for the species [42,43]. EGS avoid dense tallgrass vegetation as visual cues play an important role for communication and vigilance [44,45]. The evolution of grassland ecosystems in Eurasia during the Pleistocene with the presence of large wild ungulates, and later with that of domestic grazers and human modifications, interacted positively with ground squirrel expansion [46–48]. Conversely, the replacement of grasslands by arable land and the reduction of livestock in the first half of the 20th century caused a pronounced decrease of burrow abundance and distribution [49,50].
Our site-attributes analysis showed that the majority of EGS colonies (69%) in Greece did not present any specific environmental or spatial characteristic (Cluster 2, Figure 2). This cluster consisted of anthropogenic habitats and both this cluster and Cluster 3 are situated in the south-aspect lowlands of Central Macedonia and Thrace. Additionally, almost all of the colonies of Western Macedonia were grouped together, having distinctive topographic and climatic conditions (Cluster 4, Figure 2). In Greece, most EGS populations are adapted to higher temperatures (total annual mean 14.7 °C), lower precipitation (total annual mean 582 mm), and moderate humidity (total annual mean 65.2%) compared to populations of higher latitudes [3,51,52]. However, the low winter mean surface temperature in Western Macedonia (4.8 °C), compared to that of the lowlands of Central Macedonia and Thrace (8.6 °C), may affect the torpor and the life cycle of these populations [53]. Nevertheless, high summer temperatures seem to be tolerated by EGS, as they avoid extreme conditions by spending more time into their burrows [54].

Habitat aspect (mainly south-east to south-west orientation) contributed mostly to the clustering of the localities (Table 3 and Table S1). Southern and eastern habitat orientation is associated with greater solar radiation and upcoming evaporation, thus resulting in warmer and dryer soils [55]. Previous research has demonstrated that aspect and slope of EGS habitats, along with climatic conditions (e.g., precipitation), are among the most important environmental factors for establishing viable EGS colonies [52]. These topographic variables are directly related to specific microclimatic conditions, and particularly to vegetation cover that appear to favor site selection by EGS [52]. Among those topographic variables, altitude (see Table 3) seems to be an exception as it seems to not have a strong influence [52]. In Europe, EGS distribution covers a wide range of altitudes, from −0.5 m in Kalochori (present study) up to 2592 m in the Rila Mountains in Bulgaria [3]. Nevertheless, most colonies are found at relatively low altitudes in Greece (Table S1; mean = 228 m; present study), Eastern Romania (below 300 m; [52]), Czech Republic (317 m; [10]), and Bulgaria (below 500 m; [30]). Low altitudes favor year-round grazing by livestock and therefore create suitable habitats for EGS [56,57].

The normalized difference vegetation index (NDVI) was the second most influential variable based on our analyses. The NDVI is associated with climatic and topographic conditions and habitat quality [58–61]. In dry grasslands, NDVI values predict the management tolerance and nutrient content of the habitats, but not vegetation species richness [61]. For example, habitats with high frequencies of cutting or management intensity, e.g., crops, pastures in Central Macedonia, and airports (such as in Cluster 2) have a lower mean NDVI than leisure fields, pastures in Western Macedonia, and natural habitats (such as in Clusters 1, 3 and 4). This relation indicates that the type of land use plays an important role for the ecological functions of the ecosystems, which is more marked in the Mediterranean climate [52]. Moreover, an increase in vegetation productivity most likely affects ground squirrels via changes in vegetation height and, consequently, foraging activity [63,64]. The combination of an arid Mediterranean climate and intense habitat management resulting in sparse vegetation (low NDVI) could influence the home range of individuals, which try to surpass the food limitations by foraging in larger areas in poor environments [14,65,66]. Taking into account the cost of foraging and predation, foraging intensity of ground squirrels is primarily governed by proximity to burrow entrances and open sight lines [67]. This could probably explain the higher individual-per-burrow entrance ratio (1:7) of populations in Greece (Table 1), compared to that encountered in other European countries, where one individual is related to 1–5 burrow entrances [1,68], or 1–10 burrow entrances [28]. Certainly, the number of used burrow entrances depends on the demographic and environmental factors of habitats such as micro-topography and consistent soil and land use [13,29,69], calling for further investigations.

The fact that most EGS colonies in Greece are found in anthropogenic areas poses serious obstacles for the efficient and sustainable management of populations [3]. As many of these anthropogenic areas represent rural areas, the EU Common Agricultural Policy (CAP) could eventually contribute to the sustainable conservation of the species. However, the
continuous population decline appears to indicate that this policy has not been efficiently applied [70]. The integration of measures already promoted by the CAP, such as subsidies for extensive livestock grazing and organic farming (Pillar II), or adjustment of pesticide use (Pillar I & II), and the inclusion of EGS as bio-indicators in high nature value farming systems could help in maintaining suitable grasslands, improving habitat quality, and decreasing intoxication from pesticides, eventually ameliorating the conservation status of EGS habitats and populations. Moreover, following the Austrian example, a marketing campaign for ground squirrel favoring olives and olive oil could further contribute to the protection and expansion of EGS populations in permanent agricultural areas.

5. Conclusions

In summary, our results demonstrate that this species of squirrel is confined to fragmented and isolated anthropogenic habitat patches in Greece. The low number of individuals and colony density may have a negative impact on the survival of the species in the near future due to the lack of population recovery. The great reduction in species distribution area and the number of colonies in the last decade indicates a continuing decrease of the EGS population. The species is currently found in agricultural, urban, and industrial areas and is confined to habitats with low system productivity. The south-east to south-western habitat aspect of the colonies is associated with solar radiation and microclimatic conditions (e.g., temperature, humidity, and precipitation at a colony-scale). Therefore, specific conservation actions such as population reinforcement, habitat improvement (appropriate management of grazing and mowing), and specific CAP measures (vide supra) could effectively improve agro-ecological zones that are suitable for the maintenance and protection of potential and existing EGS habitats and populations [71].

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/su13158411/s1. Figure S1: Location of European ground squirrel active colonies in northern Greece; Table S1: Average values of the four clusters from the k-means analysis based on numerical characteristics of each locality.

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