



Landscape heterogeneity effects on keystone rodent species: agro-ecological zoning for conservation of open grasslands

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Abstract

Grasslands are one of the most threatened ecosystems in the world. Spatial prioritization of high quality habitat in agricultural landscapes is needed to protect grassland biodiversity. Within this context, we focused on European ground squirrel, a keystone species in steppe and salt steppe ecosystems. Using historical data and habitat field mapping, this study evaluates species distribution and site occupancy along the southern margin of the species range (Serbia) and identifies priority conservation zones in an intensively used landscape. Using gap analysis to evaluate changes in distribution over time and land protection status of the occupied area, we found that the regional species range has been constricted by 70%, and that 43% of mapped areas were outside of conservation networks. We also used a landscape structure model and multivariate analysis to identify the effects of spatial heterogeneity on occupancy. After mapping potential conservation zones with a buffer radius of 4.6 km—the scale with significant effects on occupancy—we identified 19 potential agro-ecological zones that cover the full range of mapped species habitats. The proposed agro-ecological zones differ in percentage of occupancy, which was found to increase with the overall landscape heterogeneity. This study contributes to the ongoing effort to broaden the understanding of the ecology and conservation of the European ground squirrel and the grasslands they rely on. Conservation planning should be designed to protect grasslands occupied by ground squirrels, ensure that the agricultural matrix is permeable, and to sustain or enhance landscape heterogeneity.

Keywords European ground squirrel · Habitat selection · Grasslands · Conservation zone · Agriculture

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Introduction

European ground squirrel (*Spermophilus citellus*, EGS) is a typical species of open grassland, which is recognized as a structural component of steppe ecosystems, species of conservation interest listed in Annex II and IV of the European Habitats Directive (92/43/EEC), on Appendix II of the Bern Convention and as Vulnerable by the IUCN Red List (IAP 1996, 2006; Carpaneto et al. 2011; Coroiu et al. 2008; Janák et al. 2013; SakerGAP 2014; Lindtner et al. 2017). The most severe threat to the species persistence is habitat loss and fragmentation due to agricultural intensification and land use degradation (EU Species action plan, see details in Janák et al. 2013). To impede loss and enable integration across scales there is a need to develop a strategically planned landscape-level agenda and establish agro-ecological zones (Scherr and McNeely 2008; Kremen et al. 2012). For management of open grassland mosaic and preservation of its species we suggest using European ground squirrel, an open grassland specialist and a keystone species, as a tool for identifying and prioritizing measures at a landscape scale. However, evaluations of landscape characteristics associated with European ground squirrel populations have not been conducted, apart from one study at one site in Bulgaria where mean distance, isolation and connectivity between active and inactive colonies were analyzed (Koshev 2008).

The goal of the present study is to identify priority areas for grassland conservation within an agricultural landscape that will sustain long-term European ground squirrel populations. For designation of potential agro-ecological zones in agricultural landscape one should combine the empirically driven effects of landscape fragmentation and the actual status of habitat patch conservation. To quantify the effects of fragmentation, researchers have used patch based metrics and species functional traits to assess structural and functional linkages between populations (i.e. gene flow), habitat connectivity, and how differences in available habitat (local level) and spatial patterns (landscape level) influence population presence or absence (e.g. Hanski 1999; Vos et al. 2001; Tournant et al. 2013; Wang et al. 2014; Mateo-Sanchez et al. 2015; Méréó et al. 2015; Wilson et al. 2016). In agricultural landscapes, which are often characterized by habitat loss and fragmentation, the intensity of land use and landscape complexity are important scale dependent measures of spatial heterogeneity that reflect variability in landscape properties. In these contexts, the proportion of farmland represents intensity, and complexity is reflected by land use diversity, extent of field borders, number and size of patches, amount of natural and semi natural habitat, and dominant land use types (Persson et al. 2010). Therefore, evaluating factors limiting dispersal or foraging activities of grasslands specialists and proposing appropriate conservation measures first necessitates knowledge of grassland fragments distribution and habitat occupancy.

In the present study we use spatial assessment and mapping of endangered species habitat occupancy in a multifunctional landscape, which is a cost intensive and infrequently conducted, to provide information on interactions between life history and spatial traits and also on habitat conservation status. This information is important to identify priority areas, improve green networks (semi-natural and natural areas) and habitat management, distinguish between different levels of fragmentation, and estimate extinction risk (Pan-European Biological and Landscape Diversity Strategy [PEBLDS] 1995, 2003; Pan-European Network Natura 2000; Green Infrastructure Strategy 2012; Baral et al. 2013). Recent studies in agricultural settings by using different spatial techniques examined farmland areas of high conservation value (Lomba et al. 2017), highlighted the areas characterized by biodiversity loss to promote proactive land use planning (Kehoe et al. 2017) or call for its reactive

protection within region specific land use conditions (Kreidenweis et al. 2018). However, it is increasingly recognized that, to mediate agro biodiversity loss and conflict between agriculture and nature, spatial planning and conservation design should also be supported with climate risk assessments (Shackelford et al. 2013; Lawler et al. 2015; Adams et al. 2017).

To achieve the study objective, we mapped habitat occupied and unoccupied (recently abandoned) by European ground squirrel and assessed overlap of mapped habitat with land use maps through gap analysis. We specifically answered the following questions: (i) How does grassland specialist distribution change and how do its spatial patterns overlap with previously identified genetic clusters? (ii) How does habitat (grassland) occupancy change along the increasing/decreasing spatial heterogeneity? (iii) How can agricultural landscape design support grassland and its species conservation? To address these questions, we used FRAGSTAT and multivariate analysis to study whether and how well variation in spatial heterogeneity of the surrounding agricultural landscape reflects European ground squirrel habitat occupancy. Finally, by identifying the landscape scale that captures the most significant effects on occupancy, we delineated agricultural areas of interest for conservation zoning. These proposed conservation zones could help strategically balance biodiversity conservation with increasing food demand.

Methods

Study area

The Vojvodina region of Serbia (North West 46.1894N, 18.0805E and South East 44.6129N, 21.5662E; WGS-84) covers a 21,506 km² area (Fig. 1a, b) and is characterized by a semi-arid climate and intensive agricultural production. Only 6.4% of the region is protected, accounting for 138,000 ha in total (Puzović et al. 2015). This region underwent agricultural and pastoral expansion in the mid-20th and early twenty-first century, before experiencing intensive pastoral abandonment and conversion of open grassland areas into crop fields (Petrović et al. 2012; Puzović et al. 2015). As a result, the open grasslands ecosystem is presently restricted to small fragments surrounded by crop fields with variable use intensity. The majority of arable land is under private ownership, with the rest divided between local and regional administrative bodies.

Sampling design

We sampled the European ground squirrel (*Spermophilus citellus*, EGS) population in the southernmost part of the northern range of the species. This population managed to persist through a range constriction following unsuitable climate conditions, and contains relatively high genetic diversity in relation to Central European populations, with little indication of recent genetic bottlenecks and confirmation of tree genetic clusters (Stewart et al. 2010; Ćosić et al. 2013; Říčanová et al. 2013). The Bird Protection and Study Society of Serbia, the Institute for Nature Conservation of Vojvodina Province and the authors of this paper provided the data on species presence from the joint inventory of previously detected occupied or abandoned grassland areas. To confirm the presence or absence of the colony of the species in 2014, we visited only sites (in total 209) where European ground squirrel had been observed at least once as well as habitats where the species was previously present but confirmed absent over a 5 years period (2009–2013). As part of this effort,

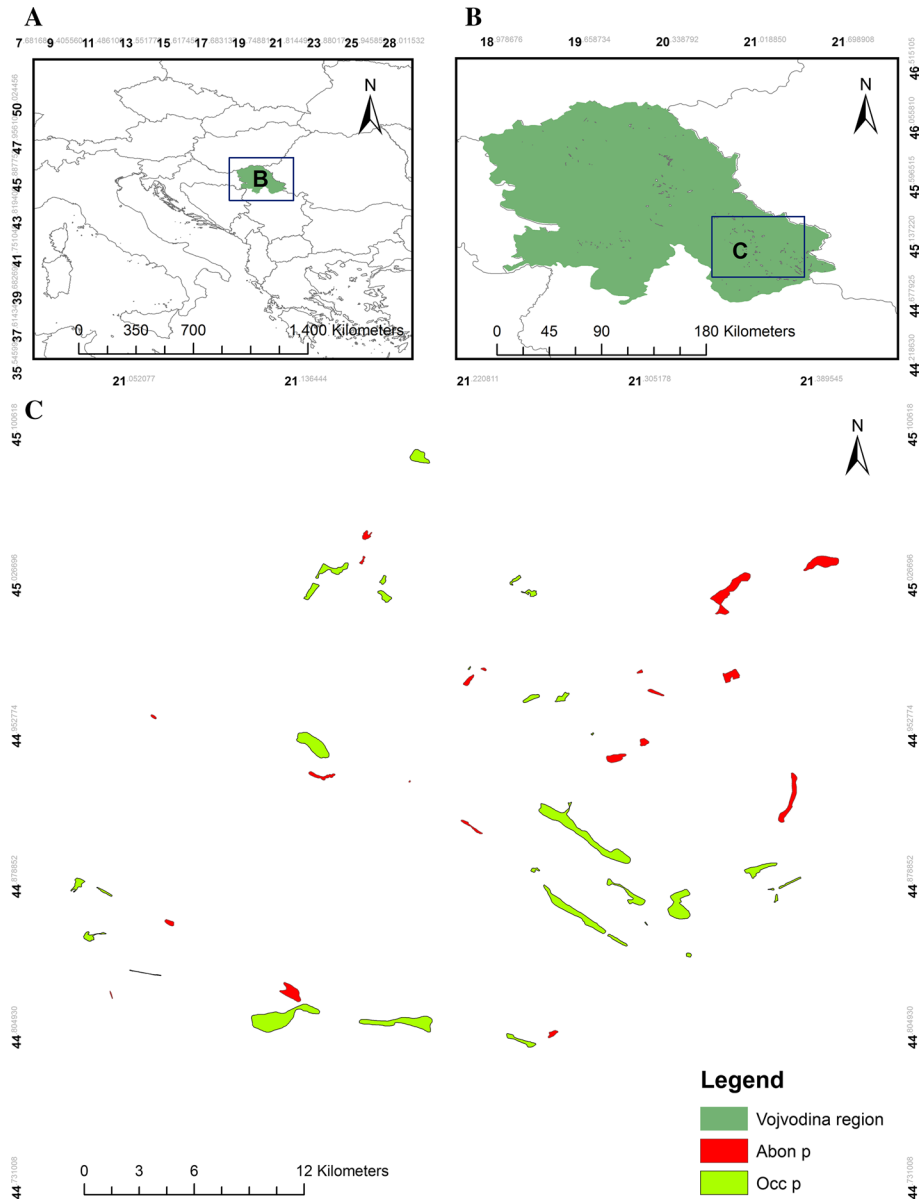


Fig. 1 **a** The location of the study area in the Vojvodina region of Serbia. **b** The distribution of European ground squirrel distribution in the occupied and abandoned habitat patches in the Vojvodina region. **c** The distribution of occupied (green) and abandoned (red) habitat patches in the southern part of the distributional range in Vojvodina. Abon p—abandoned mapped patches, Occ p—occupied mapped patches

burrow distributions (active or used/inactive or collapsed) and local vegetation characteristics were mapped using GPS (Garmin eTrex Venture) for each site to establish habitat patch area and the overall extent of species populations in the region. To map occupied or abandoned habitat patches, we delineated polygons around peripheral burrows and

recorded local vegetation. Next, a 0.25 ha buffer (representing the mean individual home-range size, Ramos-Lara et al. 2014) around each patch was generated in QGIS. In addition, if there was an overlap with a village, water body, first-order road, or any other land use type the species does not inhabit, after buffering, the borders of each patch were corrected. Then, a digital habitat occupancy map was rasterized in QGIS at a spatial resolution of 100 m × 100 m pixel size. For the purpose of analyses, a patch was defined as the area within grassland fragment established after mapping and buffering peripheral burrows. We also collected qualitative data on site management practices [grazing, mowing (grass-cutting) or marginal] on each mapped habitat patch.

Evaluation of regional species range and protection status

Occupancy maps were overlapped with a 10 × 10 km UTM grid in QGIS and compared with the historical extent of the species distribution in the region (prior to 1960). During the 1960s and 1970s populations within the study area experienced a severe decline (Ružić 1979; Petrov 1992). The protection status of mapped occupied and abandoned patches was subsequently assessed by overlapping the occupancy map and the protected area network and areas in the process of being protected (NPA and ProNAP), the ecological network (EN), and the regional plan for protection (PlaNPA) in ArcGis vs. 10.1 (Arc-Map). All the patches that were part of NPA, ProNPA and EN coverage were considered protected whereas those with no conservation status (OutNet) and those that were on the edges of protected coverage networks (EdgeNet) were treated as unprotected. The Institute for Nature Conservation of Vojvodina Province developed the maps of these conservation networks (<http://www.pzzp.rs/rs/sr/zastita-prirode/ekoloska-mreza.html>).

Modelling habitat selection

We calculated differences between occupied and abandoned habitat patches in size, percentage of core area (defined as area > 0.1 km from the edge), percentage of edge in each patch, on-site habitat management, and on-site flooding in R ver. 3.3.2 (R Development Core Team 2016).

To describe landscape characteristics surrounding each habitat patch, we superimposed our digital habitat occupancy map onto Corine Land Cover Classes (Level 3) and generated a land cover layer with two additional categories, Occ p. (mapped occupied patches) and Abon p. (mapped abandoned patches). Next, the area of the largest delineated patch (263.8 ha) was squared to calculate a square diagonal, half of which we used for a circle radius (1147 m) to establish circular sub-regions. The radius of 1147 m, centred on the each mapped patch covers 413 ha was gradually increased to 2294, 4588 and 9176 m, thus creating area of 1650 ha, 6600 ha and 26,400 ha respectively. We adopted the overlapping circles method to ensure full coverage around each mapped habitat patch (O'Regan and Initiative 2008). Moreover, each of these sub-regions was assigned to the occupied (O), abandoned (A) or occupied/abandoned (OA) category (Fig. 2) based on the presence of occupied, abandoned or combined habitat patches within each defined sub-regional scale (from 413 to 26,400 ha).

Sub-regional components were calculated using FRAGSTATS v4 (McGarigal and Marks 1995). After calculating the number of patches (NP), mean patch core area (CORE_MN), and edge density (ED) and the diversity of cover types (SHDI), we summarized data means for the sub-regional configuration and composition and performed

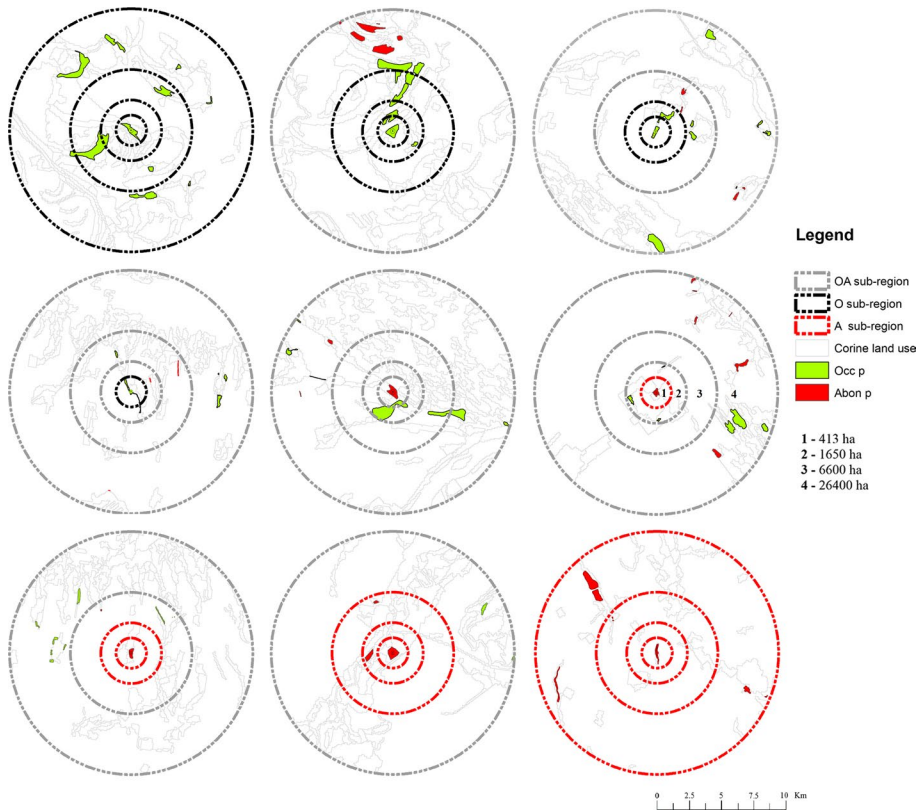


Fig. 2 Overview of nine unique combinations of occupied (O), abandoned (A) and occupied/abandoned (OA) patches within the four sub-region landscape categories denoted by 413 ha, 1650 ha, 6600 ha and 26,400 ha circles. The total number of O, A and OA sub-regions categories differs on each tested scale

ANOVA to test for the presence of significant differences at four previously defined scales (corresponding to 413 ha, 1650 ha, 6600 ha, 26,400 ha; Fig. 2). To understand the intensity, complexity and compositional heterogeneity characterizing the established sub-regions at those scales where significant differences between occupied (O) and abandoned (A) sub-region category (Z and T statistics; Table 1) were noted, we calculated the percentage of land cover types for each sub-region type in R ver. 3.3.2 (R Development Core Team 2016).

We performed a Canonical Discriminant Analysis (CDA) to account for the degree of separation between the O, A and OA sub-regions. The Candisc package (Friendly and Fox 2016) in R ver. 3.3.2 (R Development Core Team 2016) was used. First, we tested whether selected classes differed across the occupied (O), abandoned (A) and occupied/abandoned (OA) sub-regions using a parametric multivariate analysis of variance (MANOVA). Then we used a canonical correlation analysis to better discriminate between sets of selected classes of sub-regional variables and to visualize the discriminant functions by plotting the discriminant scores of the individual categories.

Table 1 Test of the significance of scale and descriptive statistics for variables used to characterize landscape configuration and composition

ANOVA	Sub-regional landscapes of 4.6 km radius (6600 ha coverage)		Sub-regional landscapes of 9.2 km radius (26,400 ha coverage)	
	O, A and OA		O, A and OA	
	F value	<i>p</i> (> F)	F value	<i>p</i> (> F)
NP	10.435	< 0.001	7.9224	< 0.001
ED	2.6396	0.07	2.7974	0.06
CORE_MIN	7.5217	< 0.001	7.9354	< 0.001
SHDI	3.5036	0.03	3.4273	0.03
Summary statistics	O	A	O	A
Parameter	$\mu \pm SD$	$\mu \pm SD$	$\mu \pm SD$	$\mu \pm SD$
NP	38.8 ± 15.8	28 ± 11.3	105.9 ± 39.3	76.4 ± 29.9
ED	16.5 ± 8.1	13.4 ± 5.3	14.5 ± 5.7	11.3 ± 3.8
CORE_MIN	201.3 ± 125.1	264.9 ± 127.2	315.6 ± 258.8	402.8 ± 208.3
SHDI	1.17 ± 0.5	0.9 ± 0.4	1.2 ± 0.4	0.9 ± 0.4
		<i>z</i>		<i>t</i>
		<i>p</i>		<i>p</i>

* O—occupied sub-regional category; A—abandoned sub-regional category; OA—occupied/abandoned sub-regional category; NP—the number of patches; ED—edge density; CORE_MIN—mean patch core area; SHDI—the diversity of cover types

Identification of agro-ecological zones

Based on the results of the habitat selection analysis we used buffers at distances of 9.2 and 4.6 km (corresponding to 26,400 ha coverage and 6600 ha coverage) to identify population structure (Rivers et al. 2010). We consider those two radii relevant under the assumption that environmental conditions will result in the subdivision of the regional geographic distribution to a distinct number of populations (9.2 km) and group mapped localities across region (4.6 km). We then compared the resulting population structure with the previously determined distribution of tree genetic clusters in Vojvodina (Ćosić et al. 2013).

Spatial, environmental and intrinsic constraints pose limitations to species dispersal (Vasudev et al. 2015). Since European ground squirrels have a positive association with small scale habitat selection (Ramos-Lara et al. 2014) we adapted the delineated area at a smaller scale of habitat selection to identify conservation areas (here after Conservation Zones). Finally, we tested for the presence of correlations between the amount and size of arable land and open grassland areas with the number and size of mapped localities with Spearman's pair-wise coefficient within each proposed zone.

Results

Occupancy patterns

The digital occupancy map yielded 196 habitat patches, 117 of which were occupied and 79 abandoned. Occupied habitat patches ranged in size from 0.1 to 184.9 ha (mean = 34.5 ± 45.7 ha), whereas the abandoned ones ranged from 0.03 to 263.8 ha (mean = 17.3 ± 45.5 ha). Habitat mean area was significantly greater for occupied than that measured for the abandoned or total habitat patches (ANOVA; $F = 4.1$; $df = 2$; $p > F 0.012$). Moreover, there was a significant higher core area percentage (Z score = 3.6,

Table 2 Summary (percentage) of European Ground Squirrel occupied and abandoned habitat patches with the conservation status of protected, unprotected, or planned protection

	Protected			Un-Protected		Plan protected
	EN	NPA	ProNPA	EdgeNet	OutNet	PlaNPA
I						
OA p	42.8	9.1	4.08	10.7	33.2	23.4
Occ p	25.5	6.6	4.08	7.1	16.3	13.8
Abon p	17.3	2.5	–	3.6	16.8	9.6
Total mapped occupied and abandoned habitat patches = 196						
II						
Occ p	42.7	11.1	6.8	11.9	27.3	23.1
Total mapped occupied habitat patches = 117						
III						
Abon p	43	6.3	–	8.8	41.7	24
Total mapped abandoned habitat patches = 79						

*OA p—all mapped patches; Occ p—number of occupied mapped patches; Abon p—abandoned patches

Table 3 Summary of selection tests for variables and the significance of canonical dimensions for occupied (O), abandoned (A) and combined (OA) groups of sub-regional landscapes over two selected scales

Analysis of 6600 ha scale							
MANOVA	Df	Test stat	Approx F	Num Df	Den Df	<i>p</i> (>F)	Sig.*
Pillai test	3	1.45	17.0	30	543.00	<2.2e−16	***
Wilks test	3	0.00	143.0	30	526.08	<2.2e−16	***
Analysis of 6600 ha scale							
CDA	CanRsqr	Eigenvalue	Percent	Cumulative	Approx F	<i>p</i> (>F)	Sig.*
	0.28986	0.40818	65.976	65.976	5.4702	3.112e−12	***
	0.17389	0.21050	34.024	100.000	4.2099	5.862e−05	***
Analysis of 26,400 ha scale							
MANOVA	Df	Test stat	Approx F	Num Df	Den Df	<i>p</i> (>F)	Sig.*
Pillai test	3	1.447	17.06	30	549.00	<2.2e−16	***
Wilks test	3	0.006	81.54	30	531.95	<2.2e−16	***
Analysis of 26,400 ha scale							
CDA	CanRsqr	Eigenvalue	Percent	Cumulative	approx F	<i>p</i> (>F)	Sig.*
	0.40650	0.68492	84.588	84.588	6.8175	5.397e−16	***
	0.11094	0.12479	15.412	100.000	2.5235	0.009508	**

*Statistical significance: at *** $p=0$, ** $p<0.001$

$p<0.05$) and a lower percentage of mean edges (Z score = −12, $p<0.001$) in occupied then abandoned habitat patches. Grazing management was common in both types of patches (occupied: 64.9%; abandoned: 54.6%). Total mapped habitat patches accounted for 55.9% of the patches within the NPA, ProNPA and EN. The percent of patches without conservation status (OutNet and EdgeNet) was 43.9% (Table 2). However, five occupied and four abandoned patches will be covered additionally with PlaNet.

We identified significant differences in landscape metrics among the occupied (O), abandoned (A) and occupied/abandoned (OA) sub-regional landscape category at the 4.6 km and 9.2 km buffer distances corresponding to area coverage of 6600 and 26,400 ha, respectively (Table 1). Moreover, while statistically significant differences between O and A sub-regional categories were noted at both scales with respect to NP, ED, and SHDI, such differences in CORE_MN existed at the 6600 ha scale only (Table 1). Open grassland areas and number of patches were key determinants of patch occupancy. In addition, a significant presence of complex cultivation patterns only characterized the O group, whereas pastures were a key variable for both categories at both scales. Abandoned sub-regions include habitat patches with lower mean core area and in general contains higher proportions of arable land. Overall, higher heterogeneity (i.e. mosaic areas comprising of salt-steppe/steppe meadows and small hold crop land where farming practices are moderately intensive) and medium complexity (i.e. agricultural settings with vegetative succession due to lack of management—potential transitional areas) were associated with available habitat patches occupied by European ground squirrel (Table 3, Appendix 1; Fig A1: A, B).

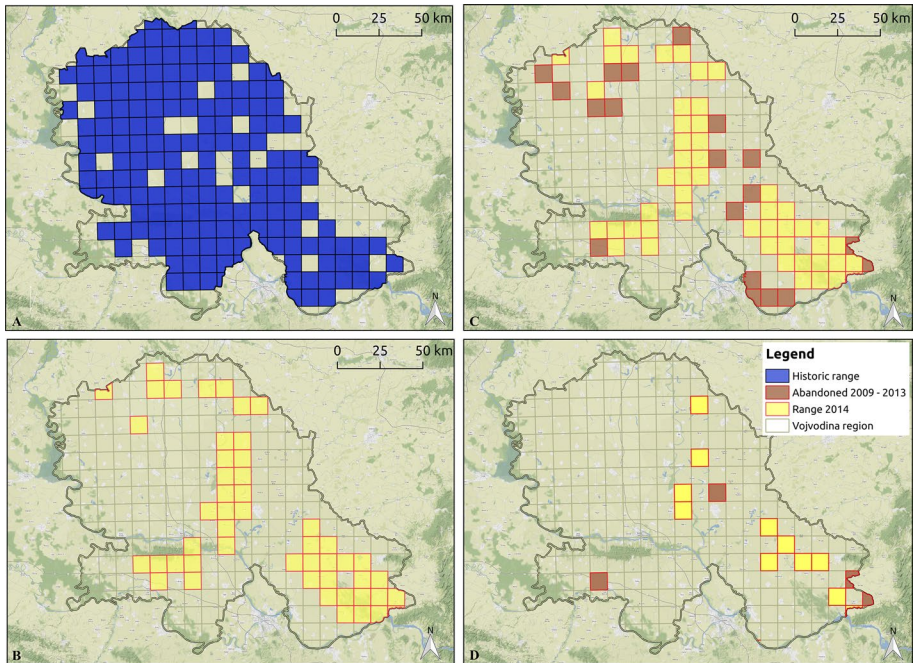


Fig. 3 Historical range and current range of European ground squirrel in Vojvodina region (Serbia) on a 10×10 km grid: **a** The historical extent of the grid cover representing species distribution in the region (< 1960). **b** The extent of the grid cover with the mapped occupied patches in the region for the year 2014. **c** The extent of the grid cover with the mapped occupied and recently abandoned patches for the 2009–2014 period. **d** The extent of the grid cover showing species shift in distribution towards south and east since the 1960s

The extent of European ground squirrel occurrence in our study area constricted more than 70% in relation to the species historical range; with only 50 of the original 171 grid cells are now occupied in the Vojvodina region (Fig. 3).

Spatial zoning

The buffer distance of 4.6 km grouped the mapped localities into 19 distinct zones (Fig. 4b). The area in between each zone differed in its structural and compositional characteristics, number of occupied and abandoned local populations and presence of conservation networks area (Table 4; Fig. 4b, c). The number of mapped occupied localities and the percentage of occupied patches in 19 Conservation Zones were correlated with the mean area size (0.3 and 0.28, $p < 0.05$) and the percentage of open grassland areas (0.42 and 0.38, $p < 0.05$). The number and percentage of all localities are negatively correlated with the percentage of agriculture (-0.42 and -0.29 , $p < 0.05$).

At the 9.2 km buffer distance we identified five populations in Vojvodina (Fig. 4a), two of which overlapped with the previously identified first and second genetic clusters, respectively, while the remaining three (northern) populations overlapped with the third genetic cluster. However, one of these located along the Tisa river stronghold (Fig. 4a Population

3) partially overlapped with the second genetic cluster; confirming the importance of this genetically still unresolved but potential hybridization cluster group, according to our results (Fig. 4a).

Discussion

Occupancy patterns

The analyses performed as a part of the current investigation confirmed that the current range of the European ground squirrel in our study region is 500 km², which indicates a dramatic range constriction. The direction and magnitude of this change is in line with the previously reported agricultural development and intensive land conversion for agricultural use. Although originally European ground squirrel was linked to steppic grasslands, the vast majority of local populations are limited to sub-optimal mowed or grazed areas with limited succession of trees or shrubs, independent of soil type (Matějů et al. 2011; Kryštufek et al. 2012; Janák et al. 2013; Zaharia et al. 2016). Our result demonstrates a shift towards the south and east where the land is less fertile and managed primarily through grazing and mowing but with a higher presence of inland salt wet meadows and salt marshes areas (Fig. 3).

Ćosić et al. (2013) demonstrated European ground squirrel genetic flow patterns were affected by strong and low spatial filtering of topographic barriers and human activities. Our finding is consistent with the result of this study where the identified genetic clusters overlap with spatial distribution patterns of local populations and land use conditions (Fig. 4a). European ground squirrel populations inhabiting this study region are of high interest because of relatively high genetic diversity. Animal mobility across local populations for successful exchange of genes is crucial for sustaining individual and population health. However, European ground squirrel movement strategies could not be established in the present study and remain to be elucidated experimentally. As the populations identified in our study area have conditionally ‘virgin’ distribution since there has been only one translocation to date, they are ideal for such assessment. On the other hand the species foraging and predator avoidance activities within habitat patches have been previously assessed (Hoffmann et al. 2008; Baltag et al. 2015 cited in Zaharia et al. 2016).

Based on the findings yielded by their mark and recapture experiment, Turrini et al. (2008) concluded that local habitat heterogeneity also influenced the home range size and travel distance of juvenile European ground squirrel, both of which were lower in homogeneous alfalfa patches than in steppe grasslands. Preliminary results reported by Kachamakova and Koshev (2018) indicated that the home range size of translocated individuals (15–20 ha) and individuals marked as locals (4.7–5.6 ha) is greater than the mean individual home-range size (on average 0.25 ha; Ramos-Lara et al. 2014). The new insights into European ground squirrel home range formation during individual animal movements to new environments will support open grassland conservation planning and area enlargement in agricultural settings. The changes in landscape heterogeneity have shaped the current distribution patterns of the European ground squirrel and have led to population absence from more intensively used agricultural areas, which is potentially reflected in occupancy patterns as a response to changing land use condition.

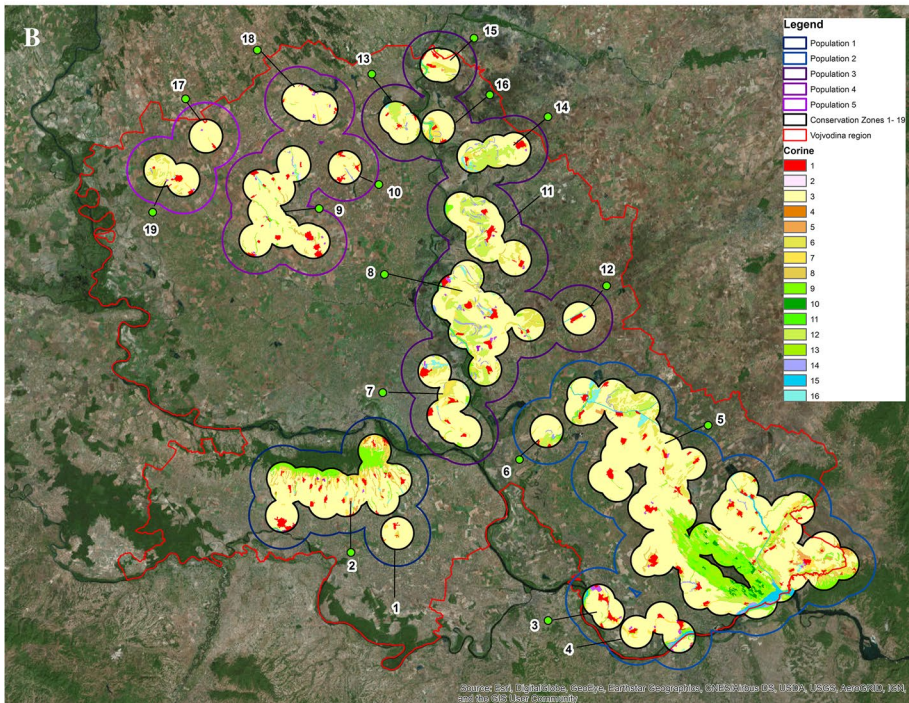
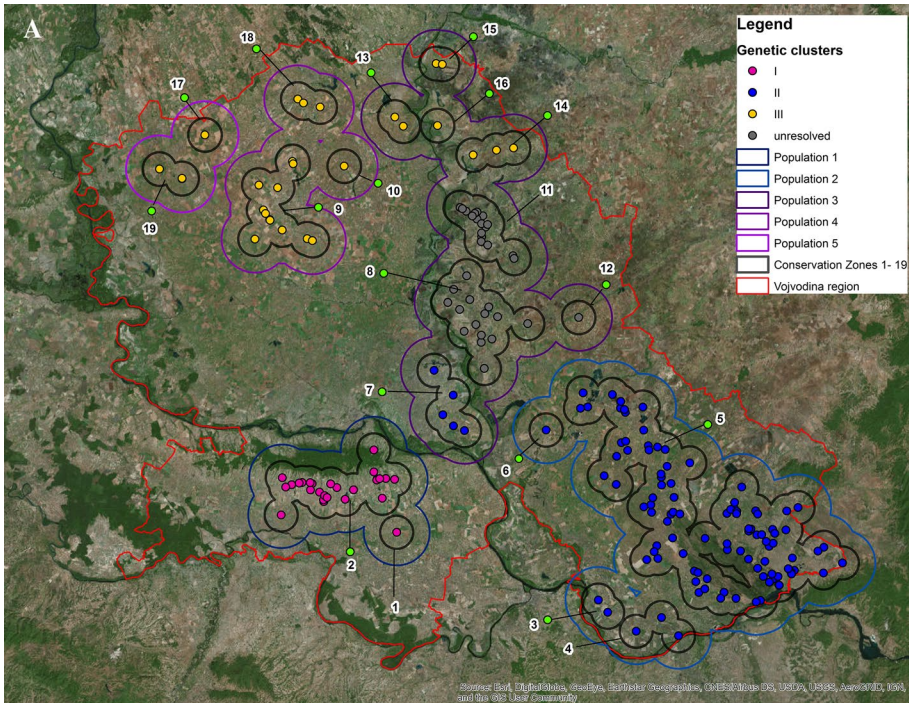
The results yielded by landscape assessment reveals that landscape diversity does not differ between the third (6600 ha) and fourth broader (26,400 ha) scales. The attributes

Fig. 4 **a** Overview of structural distribution of five European ground squirrel (*Spermophilus citellus*) populations, and their locations and tree genetic clusters in Vojvodina. **b** Overview of Corine land use inside 19 designated Conservation Zone area. **c** Map showing the overlap of three Conservation networks and 19 Conservation Zones. 1—Discontinuous urban fabric; 2—Sports and leisure facilities; 3—Non-irrigated arable land; 4—Vineyards; 5—Fruit trees and berry plantations; 6—Pastures; 7—Complex cultivation patterns; 8—Land principally occupied by agriculture, with significant areas covered by natural vegetation; 9—Broad-leaved forest; 10—Coniferous forest; 11—Mixed forest; 12—Natural grasslands; 13—Transitional woodland-shrub; 14—Inland marshes; 15—Water courses; 16—Water bodies; EN—ecological network, NPA—protected area network, ProNPA—area in the process of protection

such as the presence of transitional areas or large tracts of arable land affects European ground squirrel occupancy (Appendix 1, Table 4; Fig. 4b). Mosaic cover (e.g., presence of fallow land in the landscape) can play an important role of a stepping stone corridor as has been reported for other taxa (Neumann et al. 2016; Duflot et al. 2017). This is suitable only to a certain degree as the effects of vegetation succession toward more complex vegetation structure may impede open grassland connectivity. On the other hand, habitat configuration interferes with occupancy because sites with higher patch area and lower edge percentage, and/or closer together provide a better chance for gene exchange, thus promoting species survival in this area. Occupied patches appear to stay grouped in clusters across the regional spatial gradient of available habitats. Land management also influences occupancy of habitat patches (Bylo et al. 2014). In the current study significant presence of pastures amongst both occupied and abandoned landscape categories highlights the fact that the abandonment of pastoral management in patches may induce absence of European ground squirrel population.

The different numbers of occupied and abandoned patches at different spatial scales illustrates the effects of increasing arable coverage, reducing natural grasslands and decreased compositional heterogeneity. All these processes contribute to habitat loss and habitat fragmentation (Fahrig 2003), were more intensive in the abandoned landscapes at both larger scales, 6600 ha and 26,400 ha. However, some ground squirrel species adapt to transitional areas of higher complexity (tall grasslands and shrub-dominated areas with low grazing intensity, vineyards, or annual crops) (Ružić 1979; Hannon et al. 2006; Hoffmann et al. 2008). This adaptability is potentially crucial for dispersal across patches and for maintaining population viability (Wiegand et al. 2005; Niebuhr et al. 2015). In summary, agricultural practices of varying intensity show European Ground Squirrel potential (meta) population structures could be maintained at the scale of approximately 60 km²; given the intensive landscape modification and consequent population decline (Hanski and Gaggiotti 2004). Future research should focus on evaluating functional landscape heterogeneity (see Fahrig et al. 2011) based on the findings yielded by present study. We suggest that future research employs circuit theory approaches in combination with telemetry to reveal and highlight potential movement corridors and individual behaviours of dispersal.

Our study demonstrates the utility of detailed field mapping to identify the habitats and portions of a landscape that species actually use. Alternative approaches based on species distribution modelling (SDMs) may reveal correlations between landscape characteristics and animal distributions, but their predictions of patterns are rather simplistic because species context perception of spatial constraints are not considered (Vasudev et al. 2015). Recent studies that coupled demographic models and SDMs or biotic interaction and SDMs indicate that occupied area is the most important predictor variable; and that the local and large scale interaction refine prediction in estimating species distribution under predicted climate change, respectively (Pearson et al. 2014; Staniczenko et al. 2017). However, these approaches can only be used if data are available and allow such applications,



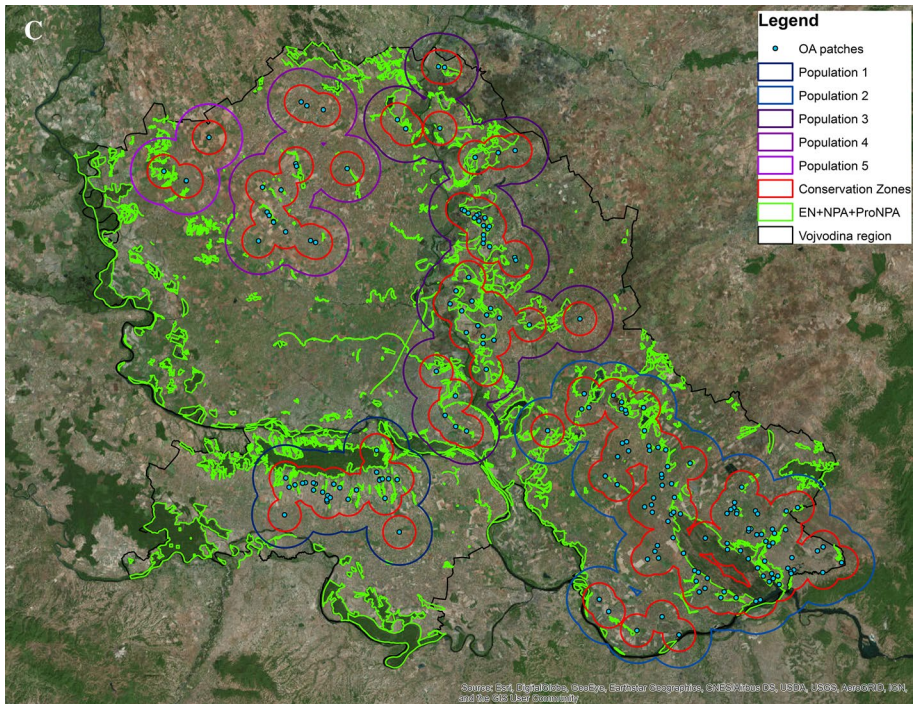


Fig. 4 (continued)

which is presently not the case for European ground squirrel. Finally, as in the present study habitat patch carrying capacity, source and sink dynamics, intra-population dynamics and genetic diversity, and individual animal behavior and fitness were not assessed, this opens up fruitful directions for future research agenda.

Spatial zoning

Our study confirms that grassland conservation within an agricultural setting and grassland dependent species conservation, such as the European ground squirrel, requires strategically planned landscape level agenda (Scherr and McNeely 2008; Janišová et al. 2014). The impact of agriculture on biodiversity will depend both on how protected area networks are developed and managed, and on farm-level habitat management.

To optimize conservation effectiveness of protected area networks, we must identify sets of environmental conditions that will support open grassland biodiversity persistence and compensate for higher use intensity with open grasslands areas larger in number, but smaller (medium) in size. For example, in Fig. 4, within Conservation Zone 9 and 17 open grassland area should be increased, (Table 4), to enlarge the total landscape capacity and maintain gene flow. Additionally, it would also be beneficial to introduce strategies based on a more expensive conventional agriculture within proposed conservation zones, or offer incentives for environmentally friendly agriculture within each defined zone area (see Conservation Zones 1–19 in Fig. 4a). Proposing adequate landscape level adaptation measures

Table 4 Summary of (A) spatial characteristics of all study zones and (B) spatial characteristics of zones grouped by presence of occupied and abandoned patches

A	Zones	Occ p	OA p	nOcc p	nOA p	cZ	mZ	mGA	%GA	mA	%A
Zones I	3	0	2	0.01826	0.02344	51	201.0	45.0	6.6	1796.0	70.1
	4	0	3	0.00891	0.00891	64	286.7	67.9	6.3	1773.1	77.3
	6	0	1	0	4.61E-06	39	166.8	100.9	21.7	915.4	70.4
	10	0	1	0	0.00057	15	433.7	34.8	3.2	2704.0	83.1
	12	0	1	0.00072	0.00072	8	813.1	53.0	1.6	2905.5	89.3
	15	0	2	0	0.00223	47	171.4	90.0	13.4	1183.6	73.5
	19	0	3	0	0.00156	51	235.6	58.6	17.1	4577.0	76.2
	Zones II	1	1	1	0	0.00010	15	433.7	31.3	4.8	5935.0
9		1	12	0.00280	0.00280	97	434.9	27.0	0.6	7478.8	88.6
13		1	2	0.01952	0.02102	33	281.6	130.9	19.7	2281.7	73.6
16		1	1	0.00087	0.00087	44	147.8	128.1	19.7	1022.3	62.9
17		1	1	0.00073	0.00488	6	1084.2	43.0	0.7	6313.0	97.0
14		3	3	0.00865	0.01131	73	217.9	192.0	33.8	601.0	52.9
18		3	3	0.00724	0.00724	21	583.4	56.3	2.8	5689.5	92.9
7		5	5	0	0.00026	83	298.8	94.0	14.0	2319.8	74.8
11		8	17	0.01562	0.02330	118	238.2	129.6	24.9	2281.5	64.9
8		14	15	0.00224	0.00224	305	166.9	124.6	24.2	1335.9	60.4
2		20	26	0.00288	0.00330	339	171.5	55.7	8.4	1309.8	63.1
5		59	97	0	0.00103	1023	221.7	87.3	10.8	1664.0	63.8
B				%A	Ampa	%GA	mGA	cZ			
	Zones I		77.1	2264.9	9	64	39.2				
	Zones II		73.8	3186.1	13.7	91.6	179.7				

*Occ p—number of occupied mapped patches; OA p—all mapped patches; nOcc p—normalized Occ p area; nOA p—normalized OA p area; cZ—number of patches of all classes per Zone area; mZ—Zone mean patch size (in ha); mGA—open grassland area (area of natural grasslands + pastures + complex cultivation patterns, in ha); % GA—percentage area of open grassland area (natural grasslands + pastures + complex cultivation patterns) in a Zone; mA—arable mean patch area (in ha); % A—percentage of arable land in a Zone

will enhance grassland connectivity and facilitate movement of focal species but also improve agro ecosystem adaptive capacity to climate change.

In the case of European ground squirrel populations the EU Species Action Plan (Janák et al. 2013), the most important joint conservation effort of species experts, highlights habitat fragmentation as the dominant threat that needs to be quantified across a species geographical range. The present study provides evidence that fragmentation and habitat loss exert adverse influence on European ground squirrel habitat use at a regional scale. In general, the mapped patches contained a greater number of areas labelled as “protected,” “planned for protection” or “inside established ecological network.” Moreover, a slightly greater percentage of occupied (23.4%) than abandoned (20.4%) patches was outside of the conservation network boundaries (Table 2I). As indicated in Table 2II and III, 39.2% and 50.5% of occupied and abandoned patches were without network coverage, respectively. This finding highlights both the importance of the conservation area networks and the need for their improvement in size and connectivity to achieve conservation objectives for the

European ground squirrel species and open grassland areas (Fig. 4c). The results of the present study, although limited in that we could not address designated functional corridors, show the conservation zone area within which refined conservation network design is needed and which could secure both open grasslands persistence and promote environmentally friendly agriculture.

Using spatial approaches to identify occupied and abandoned habitat patches, together with animal translocations, are likely to be critical for sustaining or re-establishing European ground squirrel populations in agricultural landscapes. Effects of landscape composition and structure on European ground squirrel occupancy of available habitats provide important information for future reintroduction programs inside the previously defined conservation zones within a network of stepping stone habitat patches. In addition, considering spatial properties and connectivity of occupied and abandoned open grassland habitats at a regional level can assist stakeholders in making better informed management decisions to conserve local European ground squirrel populations.

The abandoned features and borders of arable land in agricultural settings are of high conservation value, as they provide valuable ecosystem services, and extend the amount and availability of species habitats (Poschlod and Braun-Reichert 2017). Land diversification and restoration should thus be a priority within proposed conservation zones to lower environmental impact, increase biodiversity, and enhance climate resilience and carbon sequestration (Fig. 4). The agriculture planning and adaptation initiatives vary and involve various policy levels for which pan European landscape management is required (Leventon et al. 2016, 2017). Consequently, a landscape level agenda is needed to improve sustainable productivity, and secure food production and ecosystem resilience considering the differences in agro-ecological zones (e.g. different percentage of grassland and cropland practices see Conservation Zones 8, 11, 14 and 2, 5, respectively in Fig. 4b; Table 4).

Conclusion

The present study provides the first empirical evidence of the negative influence of fragmentation and habitat loss on the occupancy distribution of European ground squirrel, as open grassland keystone species, and habitat on which it relies, at a regional scale. We also emphasize the importance of gaining a better understanding of agro-ecological zone capacity to manage the regional green network, and to propose open grassland conservation strategies within spatial landscape level agenda. We further highlight the need to consider agro-ecological zoning in supporting open grasslands biodiversity in agricultural settings. The importance of extensive and high quality open grassland areas as a key factor in maintaining European ground squirrel populations (ÖPUL-Maßnahme Ziesel 2015) should not be neglected in any species conservation measures or land use planning strategies. Our findings demonstrate that successful conservation of European ground squirrel may assist in more effective protection of open grassland habitats and related wild fauna and flora. Furthermore, the recent study by Wolff et al. (2018) reported agricultural grasslands mosaic will be under increased threat as a result of the predicted land use changes, which demand urgent focus on this ecosystem in both academic research and policy management. Finally, to protect open grasslands area, future dry grassland management actions and research efforts in Europe would benefit from projects such as those conducted as a part of the LIFE (European Commission Environment Life) initiative and dry grassland conservation network (<http://www.edgg.org>) and should consider European ground squirrel

as a target species for integrated landscape planning of agricultural grassland mosaic and open grasslands monitoring.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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