



# Combining local monitoring data and scientific models to prioritize conservation for European ground squirrel and safeguard grassland habitats

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## Abstract

**Context** Promoting grassland habitat networks within agricultural landscapes is essential for supporting biodiversity. However, the characteristics of these networks are often poorly documented, making it difficult to prioritize conservation strategies and effectively protect grassland-dependent species.

**Objectives** We set to identify conservation priorities for (semi)natural grasslands by assessing habitat network characteristics based on a combination of monitoring data and scientific model output for European Ground Squirrel (EGS), a keystone grassland specialist, in agricultural settings of northern Serbia.

**Methods** We used the spatially explicit model, LARCH, to determine the current habitat networks and available monitoring data on presence/absence and habitat suitability together with Circuitscape to better understand the characteristics of those networks. The combination of modeling results and monitoring data was used to prioritize conservation measures for each network to support a stable and viable EGS metapopulation.

**Results** We identified 15 habitat networks. Our analysis showed that two of these need no interventions, but most of them need a mix of improving habitat quality and connections within and between the networks to support local populations and the metapopulation overall.

**Conclusions** Results revealed areas in which spatial adaptation measures (e.g., grassland restoration and

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corridor development) should be deployed to accommodate the long-term survival of EGS. It might be considered to stop conservation efforts in some abandoned networks as the network characteristics are too poor, and resources should be used to improve habitat networks that are still occupied. Our findings may guide the conservation of (semi)natural grasslands and future sustainable land-use planning in intensively farmed landscapes.

**Keywords** European ground squirrel · Grasslands · Connectivity · Habitat monitoring data · Presence/absence data · Conservation · Habitat networks

## Introduction

Increased food production in agricultural areas (especially during the second half of the twentieth century) often results in habitat degradation, fragmentation and loss, requiring conservation actions to protect species inhabiting the remaining (semi)natural habitats, e.g., grasslands (Kehoe et al. 2015; Ortiz et al. 2021). Often, these conservation actions focus on using the remnant fragments and isolated sites as a foundation for developing regional green networks within which measures and actions may be deployed, albeit with limited resources (Green et al. 2018). Since small and isolated populations are more vulnerable to random events, increasing population size by enlarging habitat patches, improving their quality, connecting them with corridors, and creating new habitats through restoration can enhance the habitat network's resilience and support metapopulation dynamics, essential for adapting to global changes (Isaac et al. 2018). A network of well-connected sites facilitates species' access to food, water, and mates, and promotes the colonization of new habitats. It also supports the exchange of individuals between populations (Hilty et al. 2020; Unnithan Kumar and Cushman 2022). In the long term, a stable habitat network also offers species the chance to shift their ranges as an attempt to adapt to climate change (Heller and Zavaleta 2009; Hannah 2011; Littlefield et al. 2019; López-Sánchez et al. 2024). It is evident that habitat patch quality, size, and density, as well as the matrix in between the habitat patches, must be considered when designing conservation strategies for endangered species (Hanski and Ovaskainen 2000; Fahrig

2003; Opdam et al. 2003; Fahrig et al. 2011; Didham et al. 2012; Rybicki and Hanski 2013; Synes et al. 2020). However, limited resources should be used for the most effective conservation measures. Therefore, not only information on the size of patches or the network's connectivity, but also the habitat suitability and the actual presence of protected species are important characteristics of habitat networks for prioritizing conservation measures. Only network-level habitat connectivity rarely guides plans of conservation actions and measures (Jalkanen et al. 2020).

Scattered within a heavily used agricultural landscape of central and south-eastern Europe, lives the endangered European ground squirrel (*Spermophilus citellus* L. 1766, EGS). Due to agricultural intensification, land abandonment, urbanization, and increasing road networks many (semi)natural grasslands have disappeared. Once abundant and diminishing across its range today, the EGS has shifted from a pest to a globally endangered species. As a result, it currently holds the status of strictly protected in the Serbian legislature (Službeni glasnik Republike Srbije 5/2010, 47/2011), is listed in Annex II of the Habitats Directive and Annex IV of the Species Directive, and Appendix II of the Bern Convention, and has been categorized as endangered (EN) on the IUCN red list of species (Council Directive 92/43/EEC; Council of Europe 1979; Hegyeli 2020). The iconic grassland inhabitant requires precise management actions. As it is a keystone species of (semi) natural grasslands, its disappearance from these areas negatively impacts broader grassland communities (Lindtner et al. 2018, 2020). EGS is a small herbivore mammal (Rodentia: Sciuridae) with a functional role in improving soil structure, nutrient cycling, and maintaining plant community composition (Lindtner et al. 2020). Its presence influences the abundance of other animal populations as it is an essential link between different trophic levels; and since individuals can alter habitats and regulate resources, EGS is considered a terrestrial ecosystem engineer (Lindtner et al. 2018, 2019, 2020). Therefore, we consider it a reliable indicator and model organism for conserving (semi)natural grassland ecosystems.

Understanding habitat- and landscape-level connectivity is essential in addressing the decline of natural grasslands (Marini et al. 2019). The EGS now persists in fragmented (semi)natural grassland patches within northern Serbia's predominantly agricultural

landscape. Connectivity in such landscapes is influenced by habitat suitability, landscape heterogeneity, and the agricultural matrix, which can either facilitate or impede species movement (Fahrig et al. 2011; Vasudev et al. 2015; Keeley et al. 2021; Suraci et al. 2023). For habitat specialists, like the EGS, maintaining connectivity is critical for long-term survival, as it enables movement between habitat patches and sustains population dynamics (Opdam et al. 2003; Rudnick et al., 2012). Since evidence indicates that EGS use grasslands and partially modified grasslands as corridors for both short- and long-range movements (Zaharia et al. 2016; Kenyeres et al. 2018; Nikolić et al. 2019; Rammou et al. 2021), when considering landscape connectivity, attention must be paid both to smaller habitat patches, acting as stepping stones's and larger patches, which usually attract less mobile species (Herrera et al. 2017). Connectivity is usually described as either actual, when inferred directly from species movement or potential, that uses secondary information to describe movement (Fletcher et al. 2016). In this study, we assess potential connectivity by analyzing habitat networks and landscape permeability, as direct movement data for EGS are unavailable. This approach is particularly valuable when considering single species, especially keystones (Beier et al. 2008; Keeley et al. 2021; Marjakangas et al. 2023). By integrating habitat connectivity concepts with proactive conservation strategies, spatial planning can enhance grassland network sustainability. However, incorporating monitoring data with metapopulation models in a geospatial framework remains an unexplored opportunity to further improve conservation outcomes for the EGS and similar species. Proactively addressing landscape connectivity could ensure that conservation initiatives in SEE are science-driven and effective in safeguarding biodiversity (Nikolić et al. 2019).

Natural grasslands are vital for ecosystem services and biodiversity, particularly in agricultural settings (Bardgett et al. 2021). Species such as EGS (a key grassland-dependent species) serve as umbrella species, maintaining ecological balance, but they face connectivity challenges since they depend on continuous or well-connected grassland patches for survival. Connectivity is essential, yet conservation strategies often fall short due to a lack of monitoring data integration with tools designed for fragmented landscapes. While various tools have been developed to

address issues, such as species distribution (Hao et al. 2019; Lissovsky and Dudov 2021), corridor identification (Velázquez et al. 2022; Ortega et al. 2023; Poor et al. 2024), or habitat suitability (Wintle et al. 2019; Moilanen et al. 2022), their outcomes are rarely validated. Large-scale monitoring datasets remain underutilized in these studies, limiting their practical application. To bridge this gap, our approach integrates multiple network modeling with monitoring data on habitat suitability and species presence/absence. This provides a robust understanding of habitat quality and connectivity, informed by real-world data. Similar approaches have been implemented on a large scale to align conservation planning with international frameworks like Natura 2000 and the Emerald Network, but mostly in Western countries that dominate the field (Velázquez et al. 2022; Cobb et al. 2024). By focusing on southeastern Europe, our study improves the effort of using geospatial tools for conservation planning and translating monitoring data into practical conservation solutions (Prokić 2008; Puzović 2009; Vujić et al. 2016; Dobričić et al. 2018; Vasiljević et al. 2018; Nikolić et al. 2019; Požar and Cirella 2020; Bajić et al. 2022; Papazekou et al. 2022; Cvetković et al. 2023).

We used the following four elements to determine the habitat network characteristics of EGS in northern Serbia: presence/absence data, monitoring data on habitat suitability, LARCH model output, and connectivity model output, aligning with translating monitoring data into practical conservation solutions. Combining species-specific monitoring information, population viability assessments (LARCH) with landscape-level connectivity analysis (Circuitscape) offers a robust and innovative approach. It improves upon existing methods by ensuring both ecological viability and connectivity, addressing challenges in fragmented landscapes caused by land use change or climate-driven shifts, aiming to optimize landscape solutions for an overview of all connectivity links and potential corridors for endangered grassland species. The study's findings and recommendations could help inform conservation efforts and management strategies to support the viability of EGS populations and enhance the overall conservation of natural grassland habitats in northern Serbia. Thus, the investigation aimed to (1) establish the locations of connected grassland habitat clusters (habitat networks) and sustainability of these networks, (2) assess potential

connectivity within and between the networks and identify areas of “interventions” which might serve as corridors after restoration work and (3) use the presence/absence and monitoring data to determine the differences among these networks and prioritize conservation measures. Using different kinds of information helps in different phases of conservation (Salafsky et al. 2019) and combining local monitoring data with scientific tools can be helpful in choosing between conservation measures together with local stakeholders (Pouwels et al. 2011).

## Materials and methods

To achieve the set objectives, we applied a framework (Fig. 1) that combined local knowledge of EGS habitat preferences and dispersal capacity (Ćosić et al. 2013; Nikolić et al. 2019), two scientific models, and monitoring data (Nikolić et al. 2019). The models were used to assess the potential viability of the populations within the habitat networks and the connectivity within and between these networks. The monitoring data was further used to distinguish between networks and populations that are still occupied or locally abandoned and prioritize conservation measures such as improving quality or connectivity within or between the networks.

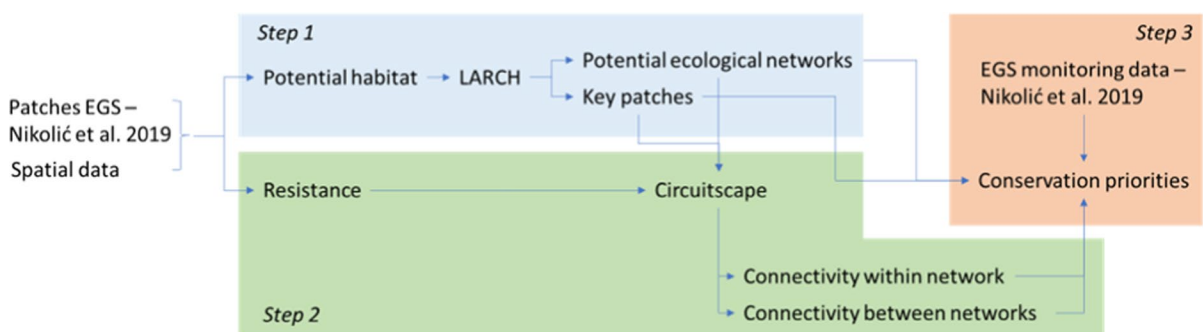
### Study area

The study was conducted in Vojvodina, an autonomous province in the northernmost part of Serbia with a total area of around 2 million ha. Only about 6% of the area is under some form of protection (Puzović

et al. 2015) and vast areas are designated for intensive agricultural production – altogether 81.3% of the area – 74.5% as arable land and 6.8% as meadows and pastures (Službeni list AP Vojvodine 10/2016). EGS occupies 2.3% of the study area and its distribution has rapidly declined in the last few decades (Nikolić et al. 2019). The number of occupied and abandoned patches (Fig. 2) varies across different spatial scales, reflecting the species’ response to the declining landscape heterogeneity (Fahrig et al. 2011).

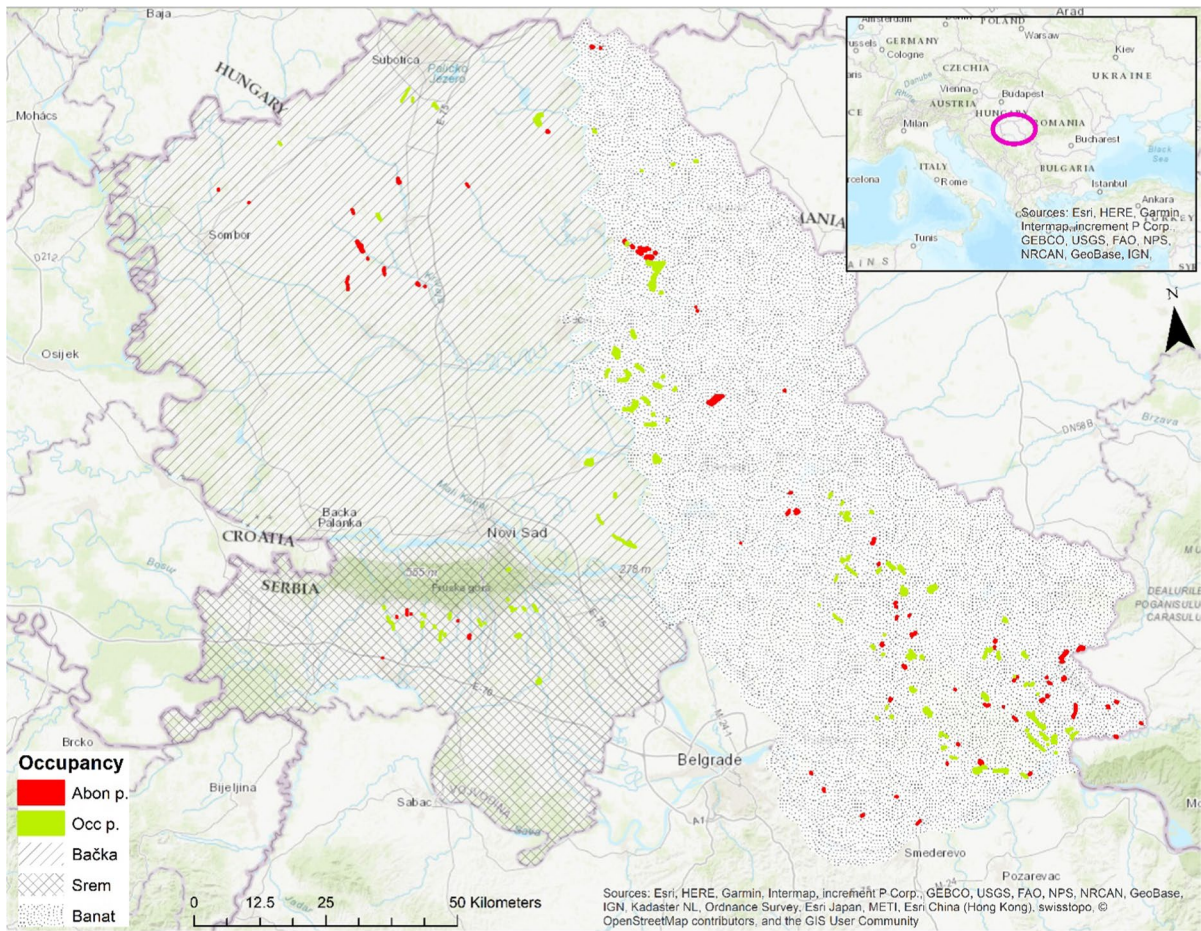
## Overview of modelling framework

We used a three-step framework to identify the conservation priorities in grassland habitat distribution for EGS (Fig. 2). In the first step, we identified the ecological networks for EGS by using monitoring data of EGS local populations and their habitat patches (see details below in the Section Ecological network of EGS habitats). The habitat map with information on patch quality and size, was input for LARCH (Opdam et al. 2003; Verboom and Pouwels 2004) to identify the habitat networks based on the habitat patch carrying capacity and spatial configuration of patches. Patches within a 5 km dispersal distance were considered as one ecological network and the population viability was assessed for all identified habitat networks. As the LARCH model indicates potential habitat networks based on species’ dispersal capacity ‘as the crow flies’, it might overestimate the connectivity between patches for ground-dwelling species such as EGS. To control this limitation, the presence/absence data were used to avoid having a network of unoccupied patches



**Fig. 1** Flowchart of the three steps used to identify and prioritize conservation measures for EGS





**Fig. 2** Habitat occupancy of the patches defined by Nikolić et al. (2019) (abon p—abandoned patches; occ p—occupied patches). In the upper right: the geographic position of Serbia

and Vojvodina (in the purple circle). \*Bačka, Banat and Srem are the three subregions of Vojvodina

labeled viable in the LARCH model output. For this reason, to evaluate the potential connectivity, we used Circuitscape (McRae et al. 2008, 2009) in the second step. We developed resistance maps for EGS to identify areas with weak connectivity within the ecological networks. We also determined the potential connectivity between the networks to identify locations of potential corridors between ecological networks. For this step, we chose to use the model Circuitscape that is specifically developed to assess connectivity in heterogeneous landscapes using resistance maps (McRae et al. 2008) and provides good outcomes compared to more complex individual based dispersal models like PathWalker (Unnikumar and Cushman 2022). By integrating

the outputs of these two models, species-specific habitat suitability information can be combined with functional connectivity, ensuring that spatial conservation strategies consider both habitat configuration and potential movement dynamics. This provided information on which network lacks connectivity and where areas are located that could connect different networks. Then, in step three, we combined the information from the potential ecological network model and connectivity models with monitoring data to distinguish between different categories of ecological networks and prioritize conservation measures for EGS in northern Serbia. Lastly, we evaluated our viability model with presence/absence and monitoring data from an independent data set from 2019.

## Ecological network of European ground squirrel habitats

For the present study, the map of 195 identified potential habitat patches provided by Nikolić et al. (2019) was adopted along with researchers' field data and experience. Thus, the summary of the methodology established by Nikolić et al. (2019) in which various organizations, along with the authors, provided data on species presence, is as follows: "In 2014 we visited only sites (in total 209) where European ground squirrels had been observed at least once, as well as habitats where the species was previously present but confirmed absent over a five-year period (2009–2013). Collaborating with local conservation organizations, we confirmed the presence or absence of EGS colonies in 2014 by surveying 209 previously recorded sites. We visited and mapped burrow distributions and vegetation characteristics using GPS to determine habitat patch areas and population extents. A 0.25 ha buffer, representing average individual home ranges, was applied around each habitat patch, with adjustments made for overlaps with unsuitable land use types [see details in Nikolić et al. (2019)]. A digital habitat occupancy map was created at a spatial resolution of 100 m x 100 m in QGIS. We also collected qualitative data on on-site management practices such as grazing, mowing, and habitat type (e.g., steppe, saline or marginal) in each habitat patch. We superimposed the habitat occupancy map on the Corine Land Cover Classes (Level 3) to describe landscape characteristics surrounding each habitat patch. We generated two additional categories—Occ p. (occupied patch) and Abon p. (abandoned patch). The same methodology was applied in the fieldwork campaign in 2019 and the data from 2019 were used to validate model outputs.

We used the land use type surrounding Occ p. and Abon p. to determine mapped patch habitat suitability and four additional criteria as correction factors (see details in Supplementary file section S1.1). The total score for habitat quality in the patch was based on all five criteria (Table S1). Even though the selected broad land cover products simplify grassland category suitability for species such as EGS, they provide an essential first-step tool for understanding general habitat patterns. On the other hand, in combination with the monitoring data set, we managed to assess occupied area suitability by considering patch habitat

type, core area, number of patches in a surrounding area, etc. (see also Nikolić et al. 2019, 2020). Moreover, genetic analyses for EGS have shown that even smaller areas can support more extensive and stable populations in these habitats (Ćosić et al. 2013), indicating that combining model output with local knowledge improves the robustness of the results. The full list of scores and locations of the mapped habitat patches is available in Table S2. For the final step of setting conservation priorities, data on occupation/abandonment and the average habitat quality of patches within habitat networks were used from the monitoring data.

The habitat map with information on patch quality and size was input for LARCH to assess the potential habitat patch carrying capacity and determine the habitat networks of EGS. For this study, a dispersion capacity of 5 km for EGS was adopted from Nikolić et al. (2019). Based on genetic data, i.e. the lack of genetic bottlenecks, we conclude EGSs can disperse even further (Ćosić et al. 2013; Nikolić et al. 2019). However, since dispersal distance in LARCH is defined as one that includes 90% of all dispersal events (Opdam et al. 2003), these less common long dispersal events have been neglected. LARCH estimates the potential number of reproductive units (RUs) in every patch based on the habitat quality and size of the patches (Verboom and Pouwels 2004). For small mammals, a patch of one ha with the highest quality index is expected to potentially accommodate at least 5 RUs. The obtained results of the potential patch carrying capacity can be used to identify key patches (KPs). A key patch is a patch large enough to contain a population with an extinction chance of less than 5% in 100 years, given an immigration rate of 1 individual per generation (Verboom et al. 2001). These patches act as sources within ecological networks and are often occupied when the species is present in that specific ecological network (Verboom et al. 2001). The threshold for short-lived mammals of 100 RUs was used in this study to identify key habitat patches (Verboom et al. 2001; Verboom and Pouwels 2004). As individuals live in small colonies with a female-biased sex ratio that are more sensitive to local extinction due to disturbances compared to species that reproduce as pair, we used 500 RUs as a threshold for a viable network for EGS instead of the standard of 200 RUs that is used for small rodents like voles (Verboom and Pouwels 2004).

The previous practice has shown that potential habitat carrying capacity is a sensitive model parameter (Verboom et al. 2001; Verboom and Pouwels 2004; Regolin et al. 2021). For this reason, we conducted additional field research to evaluate the potential habitat carrying capacity values yielded by the LARCH model. For the final step of setting conservation priorities, the viability of habitat networks and the number of key patches in the habitat networks was used from the LARCH model.

#### Assessing connectivity within and between ecological networks

We used different methods to assess the connectivity within and between ecological networks. We differentiated between the connectivity assessments to (1) identify patches within the networks that could be situated beyond the range of key patches, which are, therefore, difficult to occupy and (2) to pinpoint potential corridors between ecological networks. There is a lack of precise data on how EGS interacts with the agricultural matrix and on crop type distribution. Due to these uncertainties, we used an indirect approach. The agricultural matrix was modeled using “within habitat network surfaces” from patterns in Nikolić et al. (2019) and “between habitat network surfaces” using Corine land use categories (e.g., arable land, complex cultivation patterns).

For the connectivity within ecological networks, we assessed the connectivity of key patches to other patches in the ecological network as key patches act as sources and an ecological network is more stable when patches are well connected to key patches (Fortin et al. 2021). We followed the variation in landscape patterns and their impact on EGS habitat cohesion at previously tested scales found by Nikolić et al. (2019). We assume that the movement of individuals within the network is constrained by the quality of the habitat and its surroundings. The characteristic of the habitat is defined in Table S1 and for the quality of the surroundings, we used information from Nikolić et al. (2019, 2020). To assess the connectivity between ecological networks, we assessed the connectivity between all patches, as potential gene flow between networks is determined by all patches in the landscape. We assumed that dispersal of individuals is mainly determined by the type of land use, elevation and water courses between networks and not by

detailed information within the networks (Mateo-Sánchez et al. 2015).

We chose to use Circuitscape (v 4.0; McRae et al. 2009) to identify the area of the highest landscape permeability (between networks) and the potential movement trajectories of individuals within the habitat networks (within networks). It uses circuit theory and resistance (or conductance) surfaces to predict node connectivity. We employed a pairwise mode with an eight-neighbor connectivity scheme to evaluate between network connectivity, modeling effective resistance and current flow between predefined focal nodes. For within-network connectivity, we used the advanced mode with active independent sources and grounds, where each focal node was iteratively treated as an independent source, while all others acted as grounds (see details below). This dual approach enabled us to comprehensively assess connectivity both between and within networks, capturing the complexity of movement pathways across the heterogeneous landscape (McRae et al. 2009; Phillips et al. 2021). The high current intensity between the nodes identifies areas and paths potentially crucial for patterns of animal movement (McRae et al. 2008, 2009). Thus, we developed species-specific baseline maps of landscape permeability and habitat connectivity for EGS in the lowland area of Vojvodina. We employed the resistance-by-distance method between mapped EGS patches (source–network nodes) to develop between and within network connectivity models. All 195 patches from the dataset Nikolić et al. (2019) were used as input for assessing connectivity between networks and key patches generated by the LARCH model for assessing connectivity within networks.

We generated a “current density” surface within the study area to assess between networks connectivity with the developed conductance raster and mapped habitat patches (see details in Supplementary file Sect. S2.1). Circuitscape estimates connectivity across every possible movement trajectory among every pair of locations (mapped patches) in the so-called pairwise mode. To generate potential movement maps of individuals within habitat networks, we used the conductance surface, key populations as source nodes, and all other mapped patches as ground nodes—the locations individuals dispersed into (see details in Supplementary file Sect. S2.2). This way, the “current” surface is estimated based on a 1:1 iteration between source and ground nodes, where we set



source nodes to have a current value of 1 and ground nodes to have a current value of 0.

We analyzed connectivity using CircuitScape outputs, identifying which nodes belong to each network. Average Within-Network Connectivity was quantified by calculating the mean connectivity among the cells within each network, ignoring zero or NA values. Maximal Between-Network Connectivity for each network was determined by finding the maximum connectivity value to nodes in external networks, representing the strongest potential linkage (corridor) between networks. All statistical analyses were performed in R (version 4.0.2, R Foundation for Statistical Computing, Vienna, Austria). The connectivity output of Circuitscape was classified in three classes, low, moderate and high, based on the lowest and highest values in the maps and our field expertise. For the final step of setting conservation priorities, the three classes of average connectivity within habitat networks and of max connectivity between habitat networks were used. A low connectivity within habitat networks was used to determine habitat networks that need extra patches or improvements in quality and a high connectivity between habitat networks was used to indicate the potential of corridors between different habitat networks.

We performed validation assessment using independent, unpublished data from a 2019 monitoring campaign. To test model validity, we compared predicted network population viability (e.g., strong (viable) versus not-viable networks) against observed local patch occupancy conditions in 2019. We assume that within predicted (strong) viable and well-connected population networks the number of occupied patches will increase, and that in not-viable and not-connected networks the number of occupied populations will decrease, and number of new occupied populations will be 0. This approach allowed us to evaluate the accuracy of our model's predictions in capturing real-world occupancy patterns.

#### Prioritizing conservation measures for each network

To prioritize conservation measures, we integrated multiple data sources: occupation/abandonment data, monitoring data on habitat suitability, LARCH model output and Circuitscape model output. The combined information from the LARCH analyses and the Circuitscape analyses with monitoring data was used to

choose which main conservation measures (Hodgson et al. 2011) or a combination of measures might be needed to improve the viability of population networks of EGS in northern Serbia. We distinguished between networks that need no extra conservation measures as all network characteristics are sufficient, networks that are unoccupied and networks where the networks characteristics are partly sufficient and need extra conservation measures to ensure a stable and viable EGS metapopulation in northern Serbia:

“preserve current status of network”, when the average habitat quality is above 0.5, the network is occupied, viable and the connectivity within the network is at least moderate,

“improve quality”, when the average habitat quality is below 0.5,

“improve connectivity within network”, when connectivity within network of at least 5 patches is low and at least 50% of patches are occupied,

“restore more patches within network”, when the connectivity within the network is low,

“connect to other (viable) networks”, when the network is not viable and need a lot of extra suitable habitat to be viable on its own,

“no further conservation efforts”, when the network is not occupied and not viable.

For currently unoccupied networks it could be considered not to invest in further conservation efforts and use resources for improving still occupied networks that are not viable. However, EGS is used as an indicator for prioritizing conservation measures of all (semi) natural grasslands in the study area. For networks that are currently unoccupied by EGS but still are of good quality and contain other endangered species, extra conservation measures might be needed to protect these areas too. Therefore, we provided conservation measures for these networks, as well.

## Results

### Viability of habitat networks of EGS

All habitat patches cover a combined area of 2586 ha in Vojvodina. Within the Banat region, 12.8% of the patches are of excellent or good quality, while only 1% of the patches in Bačka and Srem are in this



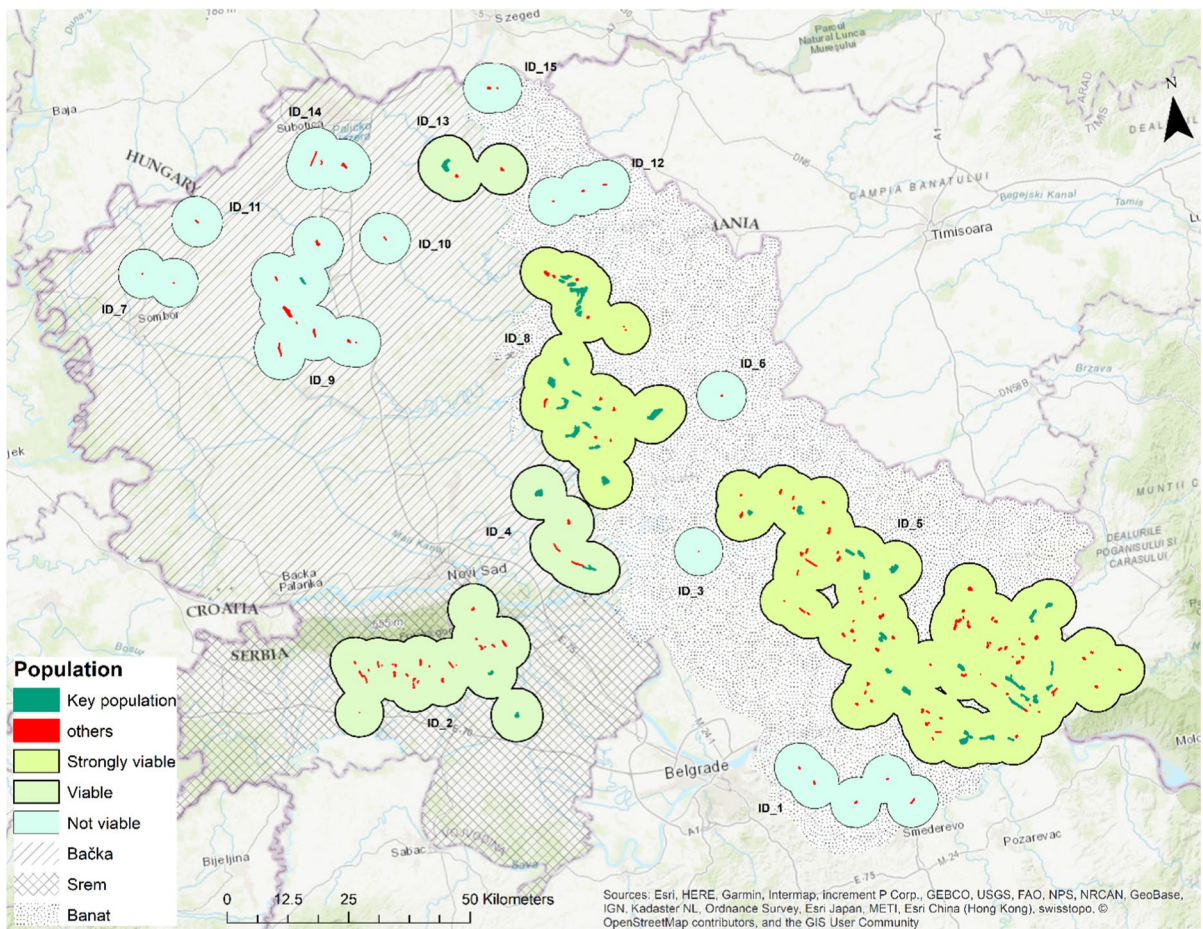
category (Supplementary file Sect. S1.2; Table S2, Fig. S1). LARCH defined 15 potential habitat networks. Six of these networks have habitat patches big enough to sustain populations with more than 100 reproductive individuals (i.e., key populations; Fig. 3a). The number of key patches within those six networks vary (Table 1). Five networks, with ID\_2, 4, 5, 8, and 13, are considered potentially viable (Table 1). One network, with ID\_9, is not viable although it contains a key patch. The total network is expected to be too small for sufficient exchange between patches and sustain a viable ESG population.

#### Connectivity within and between ecological networks

The ecological networks with the highest viability are the best-connected ones (Fig. 4b; Table 1). Of all

the networks with more than ten patches, network 8 shows the highest connectivity (0.76 for within average connectivity and 7.59 for max between connectivity Fig. 4a, b, see Table S5 in Appendix). Network 5 is also well connected for most of the patches with a moderate average within patch connectivity (0.38) and high maximal between network connectivity (6.63). Of all the viable networks, network 2 shows the lowest maximal between network connectivity (5.34) and many patches are not well connected with the more stable key patches (with average within habitat network connectivity of 0.15). Network 13 shows a high max between (7.21) and high average within (0.58) network connectivity (see details of connectivity results in Appendix Tables S5 and 2).

Validation analysis for the habitat network viability showed that in 2019, there were ~8.6% new occupied



**Fig. 3** The location of key patches and the viability of the 15 habitat networks

**Table 1** LARCH modeling results for the fifteen habitat networks

Network ID	Name	# Patches	# Key patches	Average quality	Sum RU	Viability
1	Small South Banat	5	0	0.45	84	No
2	Fruška gora	27	2	0.74	1012	Yes
3	Farkaždin	1	0	0.00	0	No
4	Lok	5	2	0.65	607	Yes
5	Greater South Banat	96	22	0.72	9187	Yes (strongly)
6	Begejci	1	0	0.75	14	No
7	Gakovo	3	0	0.33	2	No
8	Central Banat	32	19	0.73	6885	Yes (strongly)
9	Tomislavci	12	1	0.33	364	No
10	Bačko Dušanovo	1	0	0.50	4	No
11	Aleksa Šantić	1	0	1.00	23	No
12	Aradac	3	0	0.50	35	No
13	Trešnjevac	3	1	0.83	805	Yes
14	Bikovo	3	0	0.67	98	No
15	Srpski Krstur	2	0	0.38	41	No

Names are based on the location within the regions of the potential populations within the habitat networks (see also Fig. 4a, b)

patches within strong (viable) networks; and ~7% (in strong-viable, ID\_5 and ID\_8) and ~2% (in viable, ID\_2) of new abandoned habitat patches, respectively. As expected, the highest rate of new abandoned patches ~9.4% and 0 new occupied patches were detected within non-viable networks.

#### Prioritization of conservation measures

Comparing the LARCH results and the monitoring data showed that potentially viable population networks and key patches provide a good base for protecting EGS. The only patch occupied in network 9 was, in fact, the key patch. When the current network only has a few patches and these are all abandoned, they may be considered as a lost cause. Alternatively, they may be given a low priority as large efforts are probably needed; networks with ID 1, 3, 6, 7, 10, and 15 (Table 2). When resources are scarce, priority should be given to currently occupied patches at risk if they are not viable or have low connectivity. Based on the analyses, we conclude that two networks (5 and 8) need no further conservation measures. However, connecting them with the surrounding non-viable networks will improve overall networks sustainability. The analyses showed that the third viable network (2) lacks connectivity. It can be restored by improving the permeability within the network or by

restoring more patches (Table 2). This will improve the gene flow in these networks' total population of EGS. The analyses also show that in the northern part of Vojvodina, several small networks contain occupied key patches that are not viable; networks with IDs 9, and 13 and occupied networks without key patches; networks with IDs 11, 12 and 14. These networks are at risk of becoming abandoned as they are isolated or with low habitat quality (IDs 7, 9, 10, 11, 14 and 15). Connecting these networks with other ones or with network with ID 8 will improve the stability of the total EGS population in the northern part of Vojvodina. The results show that 93% of all key patches and 54% of others are occupied. Also, 66% of all patches are occupied in viable networks, and in non-viable networks, only 38%.

#### Discussion

The species-specific network approach (although criticized) is well-suited to highly modified agricultural landscapes where biodiversity is concentrated in remaining semi-natural areas (Jalkanen et al. 2020). In this context, we identified specific conservation strategies to improve connectivity and habitat quality within our study area. Key populations (KPs) identified by our analysis require improved connectivity

with local populations by enhancing surrounding grassland habitat links, such as those within sustainable network ID\_2. Effective management of sustainable network links is crucial, particularly for networks like ID\_2, whose viability depends more on environmental factors than stochastic demographic processes (Ćosić 2015), highlighting the importance of spatial factors in preserving this part of the studied landscape. Similarly, connecting KPs to abandoned patches by increasing habitat area and quality through active management (e.g., mowing and grazing) could restore and maintain habitat quality, thereby ensuring network stability. Isolated networks like ID\_9 might benefit from translocation efforts, provided adequate preparatory measures are taken (Koshev et al. 2019 references therein; LIFE Sysel project). For medium-capacity networks such as ID\_4, steppingstone grassland corridors could enhance population viability (Howell et al. 2018; Mims et al. 2023; Mohammadpour et al. 2023; Kim et al. 2024). Additionally, improving habitat density within the sustainable network in its impermeable parts (e.g., KP and other habitats in network ID\_5) would positively impact adjacent unsustainable ones such as network ID\_1. These proposed measures will boost population resilience to extreme weather events, as larger, stable populations are more likely to survive (Coetsee 2017; Frankham et al. 2017; Ashrafzadeh et al. 2020). Connectivity between networks, even with limited gene flow, supports population health and prevents genetic bottlenecks, as evidenced in the study by Ćosić et al. (2013) on EGS in Vojvodina. However, land-use changes can push EGS out of newly unsuitable areas, as documented by Nikolić et al. (2019), who observed a shift of EGS populations southeastward, where they now thrive in greater numbers.

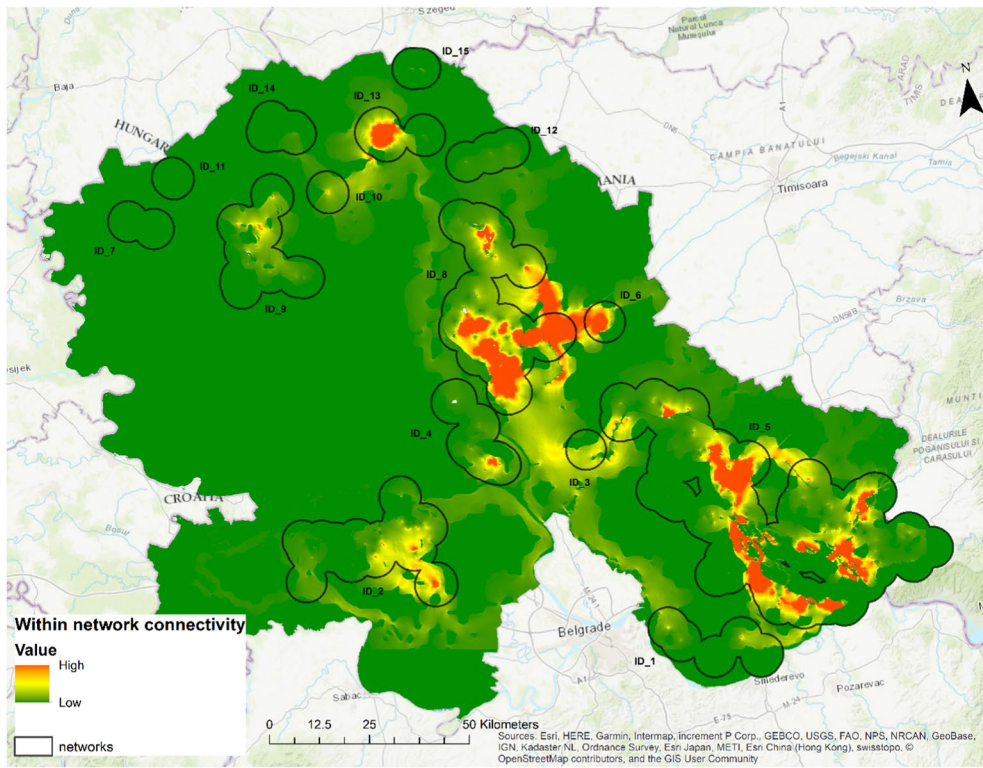
The current levels of EGS patch quality across Vojvodina directly mirror the regional level agricultural practices of the last 70 years. Intensive land use and monoculture production in the northern part (Bačka), hinder current local-scale conservation efforts. The region's agricultural practice direction is based on soil productivity and water availability. Since the northern part (Bačka) is characterized by the most fertile soils, most of the area is dedicated to crop production. On the other hand, central and southern part (Banat) has been used for cattle grazing due to vast areas of inland salt marshes and salty areas. This distribution of agricultural practices

induced a 70% range constriction and a south-east range shift of the EGS population in Vojvodina in the last 50 years (Nikolić et al. 2019). However, in this study, we propose strategic spatial landscape planning to create synergies between habitat preservation and food production. Research has repeatedly shown that maintaining or increasing natural habitats in agricultural areas positively impacts production in various ways. First, the presence of natural habitats supports biodiversity, especially beneficial insects such as pollinators and predators of crop pests (Garibaldi et al. 2013; Holland et al. 2017). Natural habitats can contribute to better soil structure, prevent erosion, and maintain nutrient cycling, improving the quality of soil for agriculture (Holland et al. 2017). Therefore, it is evident that more diverse landscapes provide ecological services that improve resilience (Bennett et al. 2021). Additionally, we suggest the introduction of need-driven buffer zones, also proposed by Nikolić et al. (2019). This integrated approach balances ecological conservation with agricultural productivity, fostering a more sustainable landscape management strategy.

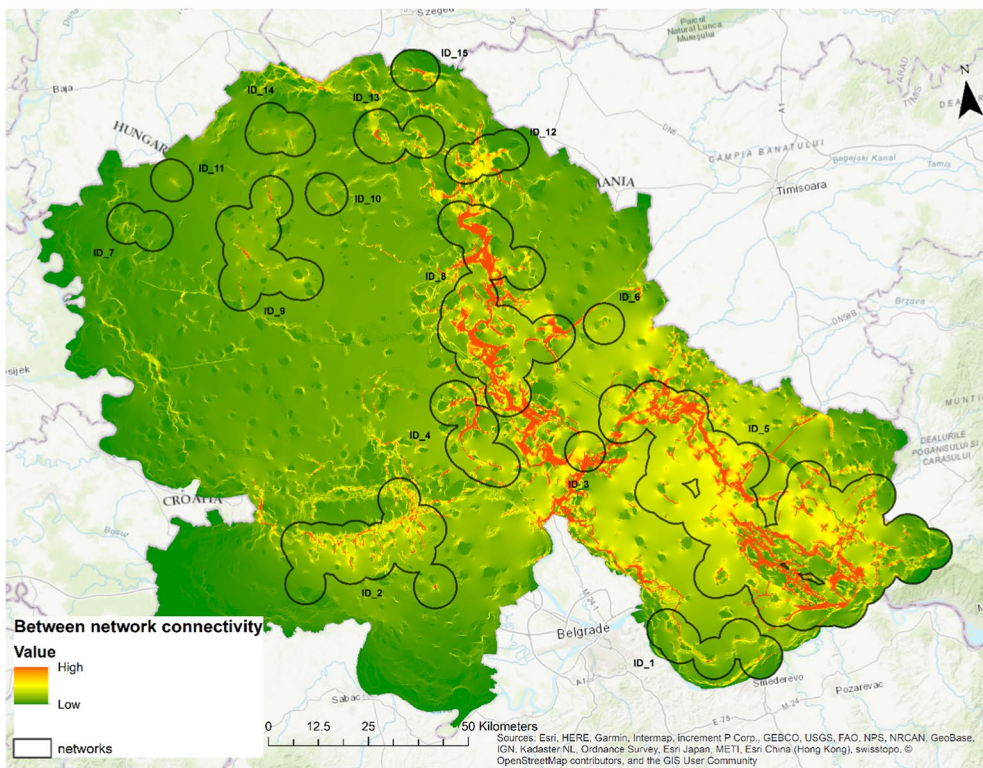
Many of the remaining (semi) natural areas in our study region of Vojvodina (some of which are EGS habitats and have been a part of this study) have been declared part of the Regional Ecological network (Službeni Glasnik Republike Srbije 102/2010). The network, designed as the backbone of the future Natura 2000 network in Serbia, gathers corridors and areas of biodiversity value that are not formally protected to preserve the continuity of green infrastructure within the agricultural landscape. Although the intended purpose of these areas must remain unchanged (e.g., converting pasture into arable land is illegal), the author's field experience suggests that this is often not the case. Encroachment is a persistent issue, frequently occurring without penalties or adequate enforcement. Furthermore, since agri-environmental measures (AEM), as they exist in the EU, are not present in Serbia, farmers and other stakeholders need different incentives to adopt biodiversity-friendly practices.

On the other hand, a regional study was conducted that evaluated options for future AEMs in Serbia by: (1) simulating farmers' adoption based on different contract options (duration, administrative effort, payment per hectare), and (2) assessing the environmental impact of implementing five common European





a



b



◀**Fig. 4** The within (a) and between (b) networks connectivity

AEMs (Tarčak et al. 2023). The study showed the willingness of the local community to adopt different AEMs, among others, such as arable land conversion to flower strips and grassland. No country-level strategy exists for this, but several small-scale projects have been implemented that included, e.g., an educational component for local stakeholder groups such as associations of cattle owners (Arok 2014; Nikolić 2019). Revitalization of grasslands has been performed on a smaller scale by protected area managing bodies, but we lack a planned, data-informed and coordinated action. Since studies show that the EGS reacts well to habitat improvement (Kenyeres et al. 2018; Petluš et al., 2021), we see the results of the present study as the first step in formulating such an action. Therefore, the findings of this study can help designate new Special Areas of Conservation (SACs) for inclusion in the Ecological Network, as 43.9% of EGS habitats in Vojvodina currently lack any form of protection. (Nikolić et al. 2019). Ensuring a stable and well-connected metapopulation of EGS colonies in Vojvodina would provide a basis for recolonizing abandoned areas in the broader Pannonian landscape to the North and the East. This assumption is because this area has been recognized as the refugium for the species (Říčanová et al. 2013), with populations that, despite being highly fragmented, still exhibit greater genetic diversity than those in Central Europe (Ćosić et al. 2013).

Circuitscape simplifies the way EGS uses the landscape during dispersal. Our findings are insufficient for determining how common EGS movements are, as the assessment of habitat connectivity within the heterogeneous matrix depends not only on individual traits but also on the available empirical data on the movement of individuals (Zeller et al. 2012, 2014). Therefore, the main limitation of the present study stems from the need for more information on movement patterns of EGS within and between habitat networks. Future research should focus on telemetry studies that would provide actual connectivity data (Fletcher et al. 2016) and landscape genetics analysis. Both would refine our connectivity parameters, improving the current knowledge of the movement of EGS individuals through the landscape matrix and the response of individuals and populations to changes in

land use. Furthermore, obtaining improved habitat maps (e.g., EUNIS level IV) would offer more precise permeability values of the landscape and improve upon the CLC information that, as mentioned already, might oversimplify the actual state, especially in heavily fragmented landscapes, such as Vojvodina. For example, this knowledge might be helpful in prioritizing the conservation measures needed in the northern part of the region where networks need to be connected to protect currently occupied networks, like networks ID\_9 and 11–14.

Combining the results from LARCH and Circuitscape with the monitoring data from Nikolić et al. (2019) provided a good overview of habitat network characteristics that can be used to provide potential conservation measures for each network. Combining this information systematically and transparently will increase the support for the models used in decision making processes with stakeholders (Addison et al. 2013). The combination of local data with scientific models is also helpful to find a balance along the clarity-complexity axis (Pouwels 2019). In decision making processes with stakeholders, finding this balance is important (Sarkki et al. 2013) as scientist often tend to use complex, and in their eyes more credible, models, while stakeholders need to understand why conservation efforts are needed. The challenge is to link the habitat network characteristics to the interests stakeholders represent (Opdam et al. 2018; Cebrián-Piqueras et al. 2020).

In conclusion, this study emphasizes the need for strategic conservation measures to enhance grassland habitat connectivity in Vojvodina, particularly for EGS, but also for grassland-dependent species. We propose actions such as increasing habitat connectivity by establishing stepping-stone corridors and restoring degraded grasslands, as well as improving habitat quality through active management practices such as mowing and grazing, at locations highlighted by the results of our analyses. Thus, spatial plans should include an increase in habitat surface area, habitat density, and habitat quality (Verboom and Pouwels 2004; Bierwagen 2007; Kalarus and Nowicki 2015; Van Teeffelen et al. 2015; Albert et al. 2017; Benedek and Sîrbu 2018; Benedek et al. 2021; Barão et al. 2022). Ultimately, balancing biodiversity conservation with agricultural productivity fosters sustainable landscape management. This study is a foundation for stakeholder discussions and strategic

**Table 2** Overview of networks and preferred conservation measures based on the LARCH and Circuitscape results, and monitoring data

Netw. ID	Name	Average quality	Patches	% Occupied	Key patch	Viability	Connectivity within networks	Connectivity between networks	Cons. measures*	Conservation measures (Hodgson et al. 2011)
1	Small South Banat	0.45	5	0	No	No	Low	Low	1 and 4	No further conservation efforts; or improve quality and connect to 5
2	Fruška gora	0.74	27	78	Yes	Yes	Moderate	Low	2 and 3	Improve connectivity within the network and restore more patches within the network
3	Farkaždin	0.00	1	0	No	No	–	High	1 and 4	no further Conservation efforts; or improve quality and connect to 5
4	Lok	0.65	5	100	Yes	Yes	Low	High	2 and 3	Improve connectivity within the network and restore more patches within the network
5	Greater South Banat	0.72	96	61	Yes	Yes (strongly)	Moderate	High	0	Preserve current status of the network
6	Begejci	0.75	1	0	No	No	–	Moderate	2 and 4	No further conservation efforts; or restore more patches and connect to 8
7	Gakovo	0.33	3	0	No	No	Low	Low	1 and 4	No further conservation efforts; or improve quality and connect to one large network with ID's 9–14
8	Central Banat	0.73	32	69	Yes	Yes (strongly)	High	High	0	preserve Current status of the network
9	Tomislavci	0.33	12	8	Yes	No	Low	Low	1, 2 and 4	Improve quality, restore more patches and make one large network with ID's 9–14

**Table 2** (continued)

Netw. ID	Name	Average quality	Patches	% Occupied	Key patch	Viability	Connectivity within networks	Connectivity between networks	Cons. measures*	Conservation measures (Hodgson et al. 2011)
10	Bačko Dušanovo	0.50	1	0	No	No	–	Low	1 and 4	no further conservation efforts; or improve quality and make one large network with ID's 9–14
11	Aleksa Šantić	1.00	1	100	No	No	–	Low	2 and 4	Make one large network with ID's 9–14
12	Aradac	0.50	3	100	No	No	Low	High	1 and 4	Improve quality and make one large network with ID's 9–14 and/or connect to 8
13	Trešnjevac	0.83	3	67	Yes	Yes	Moderate	High	4	Make one large network with ID's 9–14
14	Bikovo	0.67	3	100	No	No	Low	Low	4	Make one large network with ID's 9–14
15	Srpski Krstur	0.38	2	0	No	No	Low	Moderate	1 and 4	No further conservation efforts; or improve quality, connect to one large network with ID's 9–14

Connectivity within networks is assessed as high when large parts of the network have a high connectivity, moderate when some parts of the network have a high connectivity, low when none of the network has a high connectivity (Fig. 4a and Table S5) and it is not assessed when the network consist of one habitat patch. Connectivity between networks is assessed as high when a potential corridor, regardless the distance, to another network is all high, it is assessed moderate when a potential corridor is partly high and low when it shows no clear potential corridor (Fig. 4b and Table S5)

\*0 current measures are sufficient, 1 improve quality of patches, 2 restore more patches within network, 3 improve connectivity within network and 4 connect to other networks (with ID's)

planning to promote ecosystem resilience, support species adaptation, and mitigate climate change effects.

In the future, combining species-specific research and field validation with modelling, will enable decision makers to:

- translate monitoring data into actionable insights;
- establish a baseline for effective strategic planning, large-scale management, and connectivity;
- propose baseline for planning active measures in buffering climate change through informed land optimization;

researchers to:

- identify priority areas and understand general patterns;

all stakeholders to:

- foster a multifunctional landscape for people and nature, as only ecosystems with preserved integrity can promote species adaptation, mitigate adverse effects of climate change, and support ecological integrity and human needs in a climate-change environment.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the

corresponding author on reasonable request. No datasets were generated or analysed during the current study.

#### Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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