

Landscape-scale connectivity and fragment size determine species composition of grassland fragments



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Abstract

As a consequence of agricultural intensification and habitat fragmentation since the mid-20th century, biological diversity has declined considerably throughout the world, particularly in Europe. We assessed how habitat and landscape-scale heterogeneity, such as variation in fragment size (small vs. large) and landscape configuration (measured as connectivity index), affect plant and arthropod diversity. We focused on arthropods with different feeding behaviour and mobility, spiders (predators, moderate dispersal), true bugs (mainly herbivores and omnivores with moderate dispersal), wild bees (pollinators with good dispersal abilities), and wasps (pollinators, omnivores with good dispersal abilities). We studied 60 dry grassland fragments in the same region (Hungarian Great Plain); 30 fragments were represented by the grassland component of forest-steppe stands, and 30 were situated on burial mounds (kurgans). Forest-steppes are mosaics of dry grasslands with small forests in a matrix of plantation forests. Kurgans are ancient burial mounds with moderately disturbed grasslands surrounded by agricultural fields. The size of fragments ranged between 0.16–6.88 ha (small: 0.16–0.48 ha, large: 0.93–6.88 ha) for forest-steppes and 0.01–0.44 ha (small: 0.01–0.10 ha and large: 0.20–0.44 ha) for kurgans. Fragments also represented an isolation gradient from almost cleared and homogenous landscapes, to landscapes with relatively high compositional heterogeneity. Fragment size, connectivity, and their interaction affected specialist and generalist species abundances of forest-steppes and kurgans. Large fragments had higher species richness of ground-dwelling spiders, and the effect of connectivity was more strongly positive for specialist arthropods and more strongly negative for generalists in large than in small fragments. However, we also found a strong positive impact of connectivity for generalist plants in small kurgans in contrast to larger ones. We conclude that besides the well-known effect of enhancing habitat

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quality, increasing connectivity between fragments by restoring natural and semi-natural habitat patches would help to maintain grassland biodiversity.

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Introduction

Grassland ecosystems worldwide, including Eurasian steppe grasslands and forest-steppes, went through a dramatic habitat loss and fragmentation during the last two centuries (Prishchepov et al., 2021). Land-use changes, such as the abandonment of historical land-use practices like extensive grazing, forest plantation, agricultural expansion, and intensification, deteriorate habitat quality, resulting in a negative effect on biodiversity (Habel et al., 2013, Kamp et al., 2015). Furthermore, it influences functional diversity (Török, Gallé & Batáry, 2022), ecosystem functioning (Kuli-Révész et al., 2021) and food webs (Batáry, Rösch, Dormann & Tschamtké, 2021). Land-use change resulted in a dramatic alteration of landscape structure, vast areas were converted, and only small patches of the original grasslands remained intact or semi-natural. The loss of suitable habitat areas is usually associated with habitat fragmentation; fragmented landscapes hold a few to many habitat patches generally reduced in their size (Fahrig, 2017). Both processes, i.e. habitat loss and fragmentation *per se*, are generally considered to negatively influence biodiversity (Villard & Metzger 2014).

Habitat loss is associated with decreasing amount of suitable habitats, generally leading to many small habitat patches and a few large ones, that is, a reduced heterogeneity of patch size distribution (Ewers & Didham 2006). The community composition of small patches differs from that of the large patches as species have widely varying area, resource, and environmental requirements (Didham, 2010). We applied the simple dichotomous categorization of species to (1) habitat specialists with a high affinity to grasslands and (2) habitat generalists, which also occur in disturbed habitats or other natural habitats, such as arable fields or forests. Classifying species into habitat specialists and generalists supports the understanding of different species distribution patterns.

Specialist species are more strongly affected by fragment size than generalist species with broad habitat tolerance (Öckinger et al., 2012). Therefore, species loss is higher for habitat specialist species than generalists (Miller, Damschen, Harrison & Grace, 2015). The species richness and abundance of generalists may even increase with decreasing fragment size, as these species can utilise the resources of the surrounding matrix efficiently (Fisher & Lindenmayer 2007). Still, small grassland fragments with high habitat quality are refuges for several specialised plant and insect species. They may serve as critical stepping stones for mobile species and

may play an important role in nature conservation (Krämer, Poniowski & Fartmann, 2012; Poniowski, Stuhldreher, Löffler & Fartmann, 2018, Gallé et al., 2022).

Fragmentation and habitat loss not only affect the size of natural patches but also decrease the landscape scale heterogeneity and functional connectivity between the remaining habitat fragments (Poniowski et al. 2016). The matrix, surrounding remnant vegetation, may have a strong influence on species diversity. If the main elements of the matrix strongly contrast with natural habitats, the matrix becomes less permeable for species, as it may impede dispersal across the landscape, because of altered migration behavior and increased mortality (Driscoll, Banks, Barton, Lindenmayer & Smith 2013). This decreases individuals' flow resulting in strongly isolated habitat fragments (Gallé et al., 2022). Therefore, functional connectivity may be linked to matrix quality even more strongly than geographical distance.

In small and isolated grassland fragments, a higher extinction rate due to small populations combined with a lower probability of recolonization may cause a decline in specialist species richness (Rösch, Tschamtké, Scherber & Batary, 2013, Deák et al. 2021a). In contrast, generalist species have a higher probability of occurring in the surrounding landscape than specialists; hence generalist species experience a better functional connectivity of fragments than specialists (Evju, Blumentrath, Skarpaas, Stabbetorp & Sverdrup-Thygeson, 2015).

In this study, we focus on the effects of a patch-scale parameter, the fragment size (large vs. small patches) and a landscape-scale parameter, Hanski's connectivity index (Hanski, Alho & Moilanen 2000) on the species richness and abundance of habitat specialist and generalist plants and arthropods.

We hypothesized that (1) species richness would increase and community composition would change with fragment size and connectivity; (2) this effect would be stronger on specialist species and weaker or even negative on generalists; and (3) connectivity would have a more pronounced positive effect on small fragments than on large fragments.

Materials and methods

Study area and design

We carried out our study in the southern part of the Hungarian Great Plain. This region has a continental climate

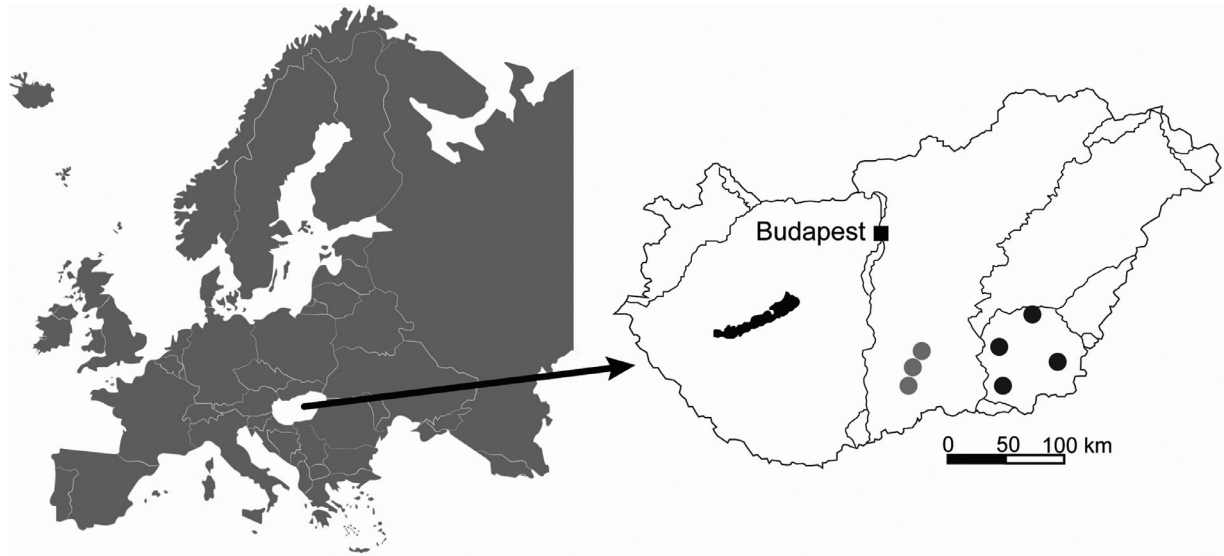


Fig. 1. Study area in the Southern Great Plain region of Hungary. Gray dots represent the localities of forest-steppe fragments, whereas black dots represent kurgans.

with a mean annual temperature of 11°C and a mean annual precipitation of 550–600 mm (Tölgyesi et al., 2015). Two natural and threatened grassland types occur here, the sand steppe grasslands are part of the forest-steppes in the Western part. Furthermore, we studied loess steppes on kurgans in the South-Eastern part of the Hungarian Great Plain.

Forest-steppes are mosaics of grassland and forest fragments covering vast areas in Eurasia. This heterogeneous habitat complex of our study region is developed on sandy soil. Grassland vegetation consists of drought-tolerant plant species (e.g. *Alkanna tictoria*, *Festuca vaginata* and *Stipa borysthénica*) and scarce trees and shrubs (e.g. *Populus alba*, *Crataegus monogyna*, *Juniperus communis*) scattered on the grassland. Relatively small forest-steppe fragments remained in a matrix of forest plantation monocultures composed mainly of *Pinus sylvestris* and *P. nigra*, which are not native in the study area (Rédei et al., 2020). An even-aged structure characterized the plantations, and they were managed with a clear-cut harvest system. In a lower extent, native poplar plantations, intensive pastures, and arable fields were also present in the landscapes.

Loess steppes occur on chernozem soils, excellent for agricultural use. Therefore, more than half of their area was converted to cropland worldwide, and this ratio exceeds 90% in Central Europe. In Hungary, loess steppe vegetation is restricted to very small fragments and areas unsuitable for agriculture, such as field margins, roadside verges, and kurgans (Deák et al., 2016). Kurgans are ancient burial mounds with a diameter between a few meters and 100 meters and a height of 0.5 - 15 m. The estimated number of kurgans is around 500,000 including a few thousand in Hungary (Tóth, Pethé & Hatházi, 2014). They often preserve the original steppe vegetation (dominated by plant species such as *Agropyron cristatum* and *Festuca* species, and several loess

steppe herbaceous species); thus they form especially important refuges for dry grassland species in intensively used agricultural landscapes (Deák et al., 2016). Maize, sunflower, alfalfa, and winter cereals were the region's main crops, with farmhouses and pastures also present in the landscapes.

We conducted our study on 60 natural grassland fragments in two regions of the Hungarian Great Plain (Fig. 1). Forest steppe fragments were situated in a matrix dominated by plantation forests, and kurgans were embedded in an agricultural matrix. We selected 15 small (0.16–0.48 ha for forest-steppe; 0.01–0.10 ha for kurgan) and 15 large (0.93–6.88 ha for forest-steppe; 0.20–0.44 ha for kurgan) grassland fragments for each habitat type for sampling. We calculated Hanski's connectivity index (Hanski et al. 2000) to quantify the landscape configuration for all fragments in the study areas for site selection:

$$Cli = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^\beta$$

Where α is a parameter describing a species' dispersal ability, and β is a parameter that describes the scaling of immigration. We set both parameters to 0.5 since we applied the connectivity index to an entire community (Rösch et al., 2013). A_j is the area of neighbouring grasslands and d_{ij} is the edge-to-edge distance from the focal fragment (i) to the neighbouring fragment (j), we used Quantum GIS 3.6.1 software (Quantum GIS Development Team 2019) and the ecosystem map of Hungary (Tanács et al. 2021). The grain size of the two landscape types differed. The average size of forestry management units of the small-scale plantation forest landscapes surrounding forest-steppes was smaller than the size of arable fields of large-scale agricultural landscapes around kurgans. Therefore, we calculated the connectivity

index within a radius of 500 m for forest-steppe and 1000 m for kurgans (Marcolin, Lakatos, Gallé & Batáry, 2021, Kuli-Révész et al., 2021). Based on fragment size and connectivity data we could select our 60 fragments in a way that size was used as a contrast factor (small and large) with medium sizes missing, whereas we kept the connectivity index as a gradient. Our forest steppe fragments were situated around three villages, and kurgans were situated around four villages.

Sampling methods

Herbaceous plants and shrubs were recorded in twelve 1×1 m quadrats in each sampling site. All species in the plots were identified to species level, and each species' presence/absence data was recorded. Therefore, the frequency of a plant species varied between zero (not present in the focal grassland) to twelve (present in all quadrats). We established six quadrats in the centre of the fragment, and six quadrats were located along the fragment edge, i.e. 1–2 m from the edge to cover the microhabitat heterogeneity of the fragments. We located quadrats approximately 5–6 m from each other to reduce the confounding effect of autocorrelation. We repeated sampling two times in the vegetation periods of 2019 and 2020.

We sampled vegetation-dwelling spiders and true-bugs with a D-Vac suction sampler. The method is effective in collecting arthropods in open habitats, and it allows the sampling of a relatively large area within a short time (Yi, et al, 2012). We collected three samples in the centre and three samples at the edge of the fragments. Each sample consisted of 25 subsamples. So that we placed the D-Vac head on the ground 25 times. We sampled arthropods two times, in early June and in early July 2019. We placed all material caught with suction sampling in 70:30 alcohol/water solution. Spiders and true bugs were sorted and identified in the laboratory.

We sampled ground-dwelling spiders with pitfall traps. We installed eight pitfall traps (plastic cups with a diameter of 8.5 cm) per fragment, four traps in the centre and four traps in the edge. Pitfall traps are the most widely used method for sampling ground-dwelling arthropods in ecological studies (Császár, Torma, Gallé-Szpisjak, Tölgyesi & Gallé, 2018). We also installed a plastic roof above the traps to prevent the dilution of the preservation fluid. We placed a plastic funnel in each trap to eliminate vertebrate by-catches and reduce the chance of arthropods escaping. We filled traps with 50% ethylene-glycol-water solution. Traps were open for 14 days between mid-May and early June 2020 to cover the main activity period of spiders. Traps were filled with 50:50 water/ethylene-glycol solution and a few drops of detergent were added (Császár, Torma, Gallé-Szpisjak, Tölgyesi & Gallé, 2018).

Pollinators (bees and wasps) were sampled using four yellow pan traps placed on sticks of 1 m height. This method is

frequently used to compare pollinator diversity between different study sites (Grundel, Frohnapple, Jean & Pavlovic, 2011). We established the two traps along the edge and two in the centre of the fragment. Traps filled with water and a few drops of odourless detergent to reduce surface tension. Traps were open for two 7-day periods in late May and late June 2019.

We assigned the recorded plant species according to their habitat preference: (1) grassland specialist plants (preference for natural, semi-natural open habitats) and (2) non-grassland plants (generalists and species with a preference for forest habitats; Király 2009). We also classified spiders (Buchar & Ruzicka 2002), true bugs (Wachmann, Melber, & Deckert, 2008), wild-bees (Michez et al., 2019), and wasps (Bees, Wasps & Ants Recording Society, 2021) to grassland specialist species and non-grassland species. We pooled all plant and arthropod data per fragment, resulting in 60 statistical samples (kurgans: $n = 30$ and forest-steppes: $n = 30$). We analysed spider D-Vac suction samples and pitfall trap samples separately.

Data analysis

We analysed the effect of connectivity and fragment size on species richness and abundances with generalised linear mixed-effects models (GLMMs). We used Poisson error term for the total species richness models of plants and arthropods and negative binomial GLMs for the abundances of specialist and generalist species due to overdispersion. We used (1) fragment size (two levels 'large' and 'small', as a habitat-scale factorial parameter) and (2) connectivity index (a continuous landscape configuration parameter) as fixed effects, and 'location' (village) as random factor to account for the spatial non-independence of study sites within each location. We log-transformed and ranged Connectivity index values between 0 and 1 to weight down the high values attributed to well-connected fragments. We assessed overdispersion for species richness models by comparing the residual deviance to the residual degrees of freedom; when we detected overdispersion we recalculated the models with a negative binomial error term. We used Cook's D distance to measure the influence of an observation on the estimation of the coefficients. We regarded observations with $D > 1$ as influential observations and excluded them from further analyses (Zuur, Ieno & Smith, 2007). We used the R statistical software for all computations (R Core Team, 2021).

We examined the species composition of plants and the five focal arthropod groups with the redundancy analysis (RDA) ordination technique using the RDA function in the vegan package (Oksanen et al., 2016). Fragment size, connectivity and the interaction of fragment size and connectivity were included as the main terms in the model. A permutation test, with 5000 permutations, was used to test significance of the terms.

Table 1. Results of GLMM models for forest-steppes. Model estimates \pm SEM and (p values) are given. Significant p values are indicated with bold ($p < 0.05$). Connectivity: size values are the interaction terms of the explanatory variables connectivity and fragment size.

Plants			
	Species richness ²	Specialist abundance ²	Generalist abundance ²
Connectivity	0.237 \pm 0.028 (0.124)	0.159 \pm 0.022 (0.196)	-0.426 \pm 0.068 (0.259)
Fragment size	-0.212 \pm 0.025 (0.122)	-0.172 \pm 0.020 (0.132)	0.166 \pm 0.060 (0.620)
C \times FS	-0.422 \pm 0.077 (0.056)	-0.269 \pm 0.032 (0.134)	0.378 \pm 0.094 (0.467)
Vegetation-dwelling spiders			
	Species richness ²	Specialist abundance ²	Generalist abundance ²
Connectivity	0.147 \pm 0.161 (0.373)	0.939 \pm 0.151 (0.259)	-0.409 \pm 0.069 (0.284)
Fragment size	-0.150 \pm 0.027 (0.316)	-0.375 \pm 0.140 (0.624)	-0.210 \pm 0.062 (0.539)
C \times FS	-0.268 \pm 0.040 (0.256)	-0.561 \pm 0.212 (0.629)	0.423 \pm 0.104 (0.422)
Ground-dwelling spiders			
	Species richness ¹	Specialist abundance ²	Generalist abundance ²
Connectivity	-0.017 \pm 0.040 (0.936)	0.064 \pm 0.070 (0.867)	-0.956 \pm 0.335 (0.062)
Fragment size	0.472 \pm 0.042 (0.043)	0.512 \pm 0.070 (0.165)	1.031 \pm 0.089 (0.038)
C \times FS	0.507 \pm 0.064 (0.152)	0.322 \pm 0.104 (0.574)	1.591 \pm 0.141 (0.040)
Bees			
	Species richness ¹	Specialist abundance ²	Generalist abundance ²
Connectivity	-0.027 \pm 0.063 (0.939)	-0.129 \pm 0.084 (0.780)	-0.111 \pm 0.110 (0.855)
Fragment size	-0.069 \pm 0.057 (0.826)	-0.169 \pm 0.074 (0.679)	-0.486 \pm 0.101 (0.382)
C \times FS	-0.343 \pm 0.090 (0.491)	-0.669 \pm 0.120 (0.318)	-1.060 \pm 0.163 (0.237)
Wasps			
	Species richness ²	Specialist abundance ²	Generalist abundance ²
Connectivity	-0.683 \pm 0.091 (0.172)	-1.430 \pm 0.161 (0.105)	-0.772 \pm 0.086 (0.104)
Fragment size	0.795 \pm 0.085 (0.091)	1.053 \pm 0.142 (0.188)	0.935 \pm 0.083 (0.041)
C \times FS	1.079 \pm 0.134 (0.141)	1.846 \pm 0.227 (0.138)	1.198 \pm 0.128 (0.090)
True-bugs			
	Species richness ²	Specialist abundance ²	Generalist abundance ²
Connectivity	0.225 \pm 0.067 (0.550)	0.383 \pm 0.128 (0.587)	-0.634 \pm 0.037 (0.835)
Fragment size	-0.045 \pm 0.053 (0.878)	-0.241 \pm 0.105 (0.677)	0.246 \pm 0.130 (0.942)
C \times FS	-0.056 \pm 0.094 (0.982)	-0.698 \pm 0.046 (0.893)	0.983 \pm 0.046 (0.801)

¹ models fitted with Poisson error term² model fitted with negative binomial error term

Results

We recorded 181 plant species in the forest-steppes, and 271 plant species in the kurgans. We collected altogether 332 arthropod species in forest-steppes (adult spiders: 55 species with D-vac and 78 species with pitfall traps; bees: 51 species; wasps: 54 species, 84 species). Furthermore, we collected 448 species in kurgans (adult spiders: 110 species with D-Vac and 69 species with pitfall traps; bees: 76 species; wasps: 36 species, true-bugs: 157 species). Connectivity index values of the ranged from 0 to 2637 for kurgan (mean \pm SEM = 689 \pm 748) and 24–811 for forest-steppe (394 \pm 206).

We found that fragment size and connectivity did not have a significant impact on species richness except for ground-dwelling spiders of forest-steppes (Table 1). More

specifically, we collected more ground-dwelling spider species in large than in small forest-steppe fragments (Fig. 2A). Connectivity had a negative impact on generalists spiders abundance in large fragments, however, this effect was positive for small fragments (Fig. 2B). We also collected more generalist wasps in large than in small fragments (Fig. 2C, Table 1.).

Concerning kurgans, we found a stronger positive effect of connectivity on generalist plants in small than in large fragments (Table 2, Fig 3A). Connectivity had a strong positive effect on the abundances of specialist ground-dwelling spiders of large fragments, in contrast to a weak negative effect in small fragments (Fig 3B). We detected a higher abundance of specialist true bugs in large than small fragments (Fig. 3C). Furthermore, we found a negative effect of

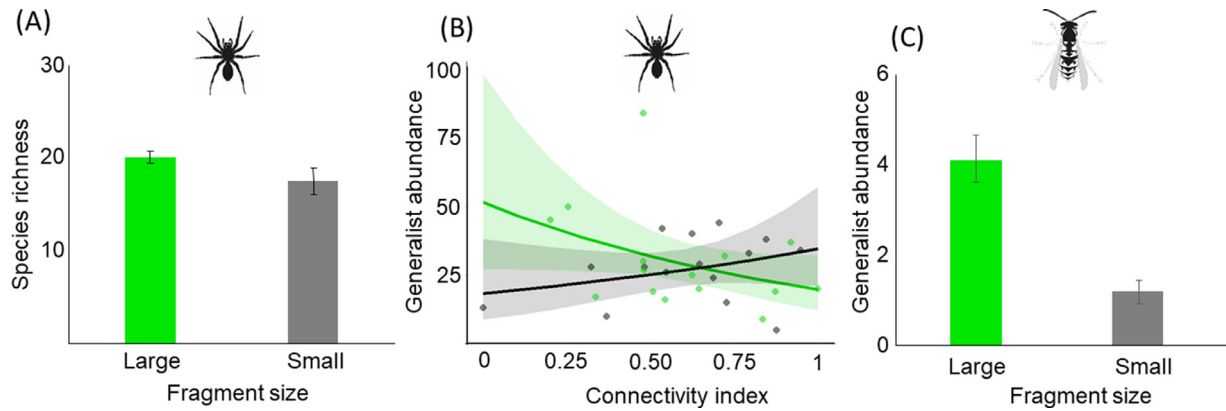


Fig. 2. Landscape-scale connectivity and fragment size effects on the biota of forest-steppe fragments (N = 30). (A) Fragment size affects ground-dwelling spider species richness (mean \pm SEM values are shown); (B) The significant interacting effect of fragment size and connectivity on generalist ground-dwelling spider abundance (estimates \pm 95% CI values are shown); (C) Fragment size affects generalist wasp abundance (mean \pm SEM values are shown). Green symbols represent large fragments; grey symbols are small fragments; shading represents 95% CI intervals

Table 2. Results of GLMM models for kurgans. Model estimates \pm SEM (p values) are given. Significant p values are indicated with bold (p < 0.05).

Plants			
	Species richness ¹	Specialist abundance ²	Generalist abundance ¹
Connectivity	0.139 \pm 0.022 (0.266)	0.233 \pm 0.061 (0.489)	0.100 \pm 0.012 (0.157)
Fragment size	0.021 \pm 0.015 (0.804)	-0.139 \pm 0.041 (0.537)	0.187 \pm 0.009 (<0.001)
Connectivity \times size	0.008 \pm 0.029 (0.965)	-0.236 \pm 0.081 (0.598)	0.239 \pm 0.017(0.011)
Vegetation-dwelling spiders			
	Species richness ¹	Specialist abundance ²	Generalist abundance ²
Connectivity	-0.591 \pm 0.077 (0.167)	-0.501 \pm 0.136 (0.502)	-1.150 \pm 1.276 (0.224)
Fragment size	0.760 \pm 0.878 (0.129)	-1.056 \pm 0.159 (0.224)	1.038 \pm 1.480 (0.482)
Connectivity \times size	0.819 \pm 0.100 (0.138)	1.237 \pm 0.182 (0.216)	1.171 \pm 1.707 (0.492)
Ground-dwelling spiders			
	Species richness ¹	Specialist abundance ²	Generalist abundance ²
Connectivity	0.017 \pm 0.048 (0.948)	-0.714 \pm 0.086 (0.130)	0.151 \pm 0.109 (0.801)
Fragment size	-0.028 \pm 0.034 (0.881)	0.461 \pm 0.062 (0.178)	-0.395 \pm 0.076 (0.346)
Connectivity \times size	0.237 \pm 0.062 (0.490)	1.608 \pm 0.108 (0.006)	-0.181 \pm 0.144 (0.819)
Bees			
	Species richness ²	Specialist abundance ²	Generalist abundance ²
Connectivity	-0.397 \pm 0.048 (0.137)	-0.819 \pm 0.090 (0.098)	0.068 \pm 0.106 (0.907)
Fragment size	0.116 \pm 0.038 (0.580)	1.121 \pm 0.063 (0.729)	0.459 \pm 0.087 (0.337)
Connectivity \times size	0.074 \pm 0.064 (0.833)	-0.487 \pm 0.124 (0.474)	0.453 \pm 0.110 (0.544)
Wasps			
	Species richness ²	Specialist abundance ²	Generalist abundance ²
Connectivity	-0.490 \pm 0.144 (0.537)	-1.149 \pm 0.211 (0.219)	-0.902 \pm 0.215 (0.444)
Fragment size	-0.471 \pm 0.089 (0.334)	0.204 \pm 0.124 (0.765)	0.626 \pm 0.123 (0.356)
Connectivity \times size	-0.324 \pm 0.184 (0.747)	0.480 \pm 0.264 (0.738)	-0.923 \pm 0.239 (0.567)
True-bugs			
	Species richness	Specialist abundance ²	Generalist abundance ²
Connectivity	-0.557 \pm 0.076 (0.181)	-1.348 \pm 0.175 (0.161)	-3.077 \pm 0.162 (>0.001)
Fragment size	0.367 \pm 0.053 (0.212)	1.437 \pm 0.115 (0.022)	1.022 \pm 0.112 (0.095)
Connectivity \times size	0.666 \pm 0.102 (0.233)	1.123 \pm 0.229 (0.371)	2.831 \pm 0.231 (0.025)

¹models fitted with Poisson error term

²model fitted with negative binomial error term

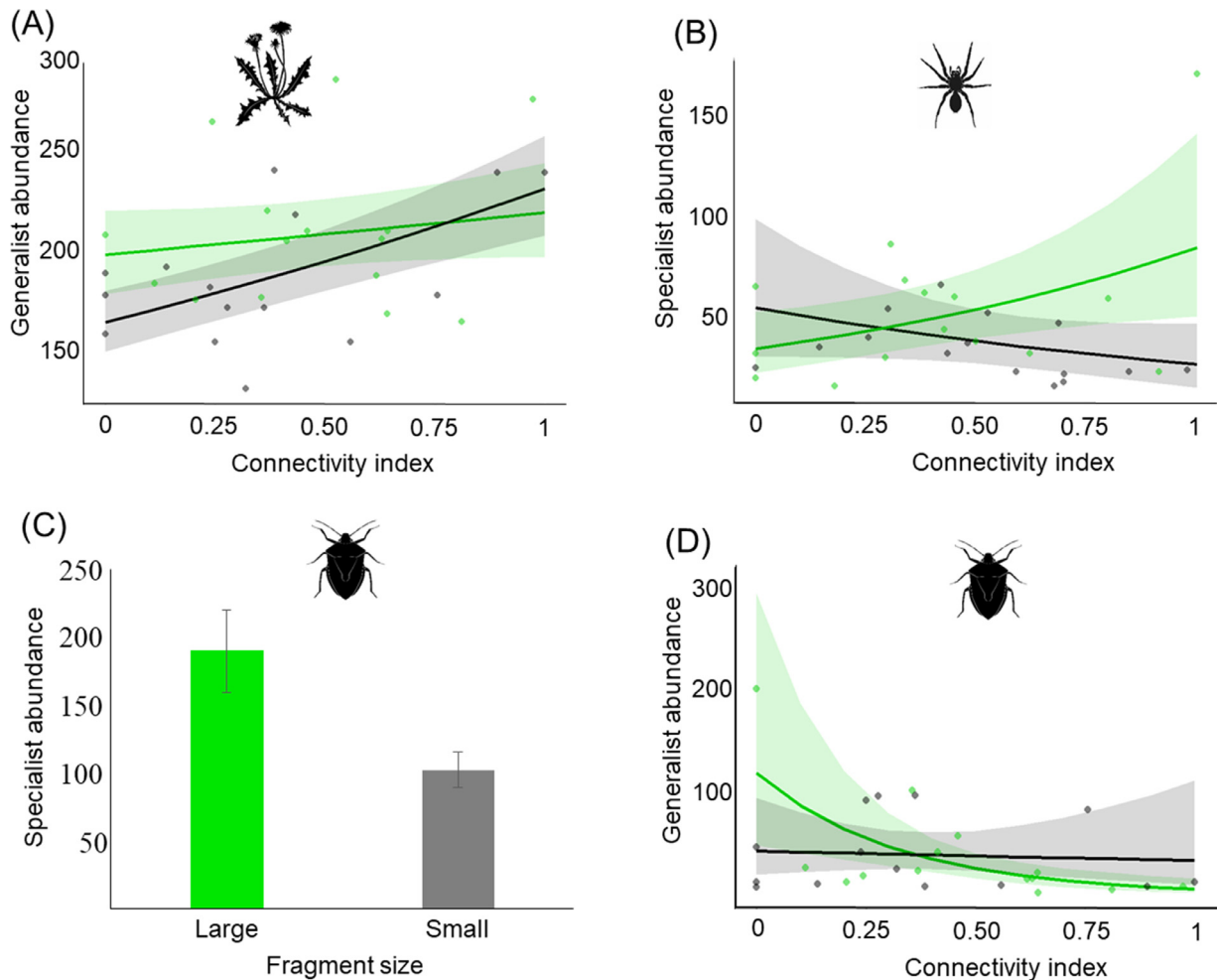


Fig. 3. Landscape-scale connectivity and fragment size effects on the biota of kurgans ($N = 30$). (A) The interacting effect of fragment size and connectivity on generalist plant abundance (estimates \pm 95% CI values are shown); (B) Interacting effect of fragment size and connectivity on specialist ground-dwelling spider abundance (estimates \pm 95% CI values are shown); (C) Fragment size affects specialist true bug abundance (mean \pm SEM values are shown); (D) Interacting effect of fragment size and connectivity on generalist true bug abundance (estimates \pm 95% CI values are shown). Green symbols represent large fragments; grey symbols are small fragments; shading represents 95% CI intervals.

connectivity on the abundance of generalist true bugs in large, but no effect in small fragments (Fig 3D, Table 2.).

Fragment size and the interaction of fragment size and connectivity affected ground-dwelling spider and wasp species composition of kurgans according to the RDA models, however, we found no effect on other taxa (Appendix A).

Discussion

According to island biogeography theory, fragment size is well-known to affect species richness and community composition (MacArthur & Wilson, 1967). We also found a positive effect of fragment size on spider species richness. Similar to our results, Bonte, Baert and Maelfait (2002) also observed a significant effect of fragment size on spider community composition in coastal dunes, structurally similar to

forest-steppe grasslands. Fragment size may determine the population sizes of spider species and may also support spiders indirectly because increasing fragment size increases microhabitat heterogeneity (Bonte, Baert & Maelfait, 2002; Gallé et al., 2010). However, local environmental conditions (such as vegetation structure, shrub cover, grass cover and litter depth) are essential factors, as well. They are presumably better determinants of community structure than fragment size for spider species richness (Torma, Gallé & Bozsó, 2014; Knapp & Řezáč 2015; Horváth, Magura, Tóthmérész, Eichardt, & Szinetár, 2019), indicating a solid habitat filtering for grassland spiders (Samu, Horváth, Neidert, Botos & Szita 2018).

The positive effect of fragment size on the species richness of spiders was the only significant effect on species richness in any of the taxa studied. Therefore, we argue that information on community composition and

abundance patterns may be more relevant for studying the effects of landscape and local-scale heterogeneity than species richness *per se* (Hobbs & Yates 2003, Evju, Blumentrath, Skarpaas, Stabbe, & Sverdrup-Thygeson, 2015). Although species richness is an indisputably important parameter of communities (seemingly not limited by fragmentation here), it does not provide any information on species composition and the changes in species identities (Jeanneret, Schüpbach & Luka, 2003, Torma, Gallé & Bozsó, 2014). However, the species compositions of the whole communities was less affected by our explanatory variables, therefore, we used abundances of generalist and specialist species to gain a more detailed insight into the structural changes in community composition.

Generalist wasps, but not specialists, were positively affected by fragment size. This interaction effect was significant despite the relatively low number of collected individuals. Carnivore wasps inhabit large forest-steppe fragments, such as the generalist social wasps *Polistes nimpha* (Török, Gallé, & Batáry, 2022). These species require large habitat patches for foraging and woody vegetation for nest building. High amounts of scattered *Juniperus* and *Crataegus* bushes were present on the large fragments offering suitable nesting sites for several social wasps.

We found that connectivity had an important role in shaping community composition via its interacting effect with patch size. Connectivity and thereby the dispersal of organisms between habitat fragments depends on the species' characteristics and matrix quality, i.e., the contrast between elements of the matrix and natural habitats. Numerous species may move across habitat edges and enter the matrix if the habitat-matrix contrast is low. A high quality matrix offers more resources and dispersing individuals utilise these resources, allowing a high rate of successful dispersal between habitat fragments (Lindenmayer & Fischer, 2007). Connectivity is also determined by the amount and configuration of habitat fragments in the landscape (Watling, Nowakowski, Donnelly & Orrock, 2011; Freeman et al., 2018). The most extensive elements of the matrix were relatively homogeneous pine forest plantations in the case of forest-steppes (Gallé, Szabó, Császár & Torma, 2018) and arable fields for kurgans (Deák et al. 2021b). Thus, the primary source of landscape-scale heterogeneity was the distribution pattern of natural and semi-natural habitat fragments for both cases, which we measured with Hanski's connectivity index.

The effect of fragment connectivity and size on community composition could be driven by the generalist species, as Rösch, Tschamtko, Scherber and Batáry (2013) and Kornmann et al. (2015) demonstrated for several taxa of calcareous grasslands. Our study revealed that connectivity modified the effect of fragment size on generalist spiders of forest-steppes and generalist plants and true bugs of kurgans. These results emphasize that both landscape and local scale effects on generalists may have a prominent role in

determining the species composition of a fragment. The increasing abundance of generalists may indicate more resources and intense propagule rain from the neighboring habitats. Furthermore, a negative edge effect may influence the species composition of communities on a relatively larger area of small fragments than large fragments. Larger and better connected habitat fragments may offer more resources and a larger core area for predators, such as spiders and many wasp species in our study (Harwood, Sunderland & Symondson, 2001).

We found higher abundances of specialist true bug and spider species in large kurgans than in small ones. This is in line with our hypothesis (2) and supported by a plethora of former studies (e.g. Fisher & Lindenmayer 2007, Hanski, 2011; Fahrig, 2017). The area and number of dry grassland fragments have been declining for the last 150 years due to the expansion of agriculture on fertile soils and forestry on barren soils (Deák et al. 2021a). Large and intact habitats inevitably preserve specialist steppe biota (Deák et al. 2021a, Gallé et al., 2022b). However, many specialist species persisted even in the smallest kurgans and forest-steppe fragments, indicating their natural state and high conservation value. Furthermore, scattered and small fragments not only contribute to the preservation of the landscape-scale species pool by preserving a few specialist species, but they also enhance functional connectivity between large habitats (Saura, Bodin & Fortin, 2014). High connectivity has an important role, as most habitat specialist species are dispersal-limited (Löffler, Poniatowski & Fartmann, 2020). These species may persist only for a specific time before extinction after landscape change, i.e., they are susceptible to extinction debt (Deák et al. 2021b). This emphasizes the urging need to preserve small natural steppe grassland fragments.

Our results on landscape connectivity and fragment size effects were not unequivocal. Therefore, we suggest that the impact of incidental anthropogenic management (mowing, mechanical soil disturbance) on grassland fragments may override the effect of fragment size and landscape configuration for the disturbance-sensitive specialist biota.

Conclusion

In contrast to our hypothesis (H1), we found little evidence that large fragment size and connectivity would support species richness of plants and arthropods suggesting also that small and isolated fragments can act as important refuges for flora and fauna. Although we expected (H2) stronger negative effects of decreasing fragment size or increasing connectivity on the abundance of specialists (this happened in the case of true bugs in kurgans); some generalist groups, such as wasps of forest-steppes, profited from these probably resulting in a homogenisation of communities. Finally, concerning our last hypothesis (H3), connectivity had a more substantial effect in small fragments than in

large fragments for generalist spiders of forest-steppes and generalist plants of kurgans. However, unexpectedly we found the opposite pattern for specialist spiders and generalist true bugs of kurgans.

We found that landscape-scale heterogeneity and fragment size are essential for nature conservation planning. Our main conclusion is that enhancing connectivity between fragments by increasing the amount of natural and semi-natural habitat patches would help to maintain the populations of grassland biota. This goal can be achieved by improving landscape heterogeneity by active restoration of grassland habitats. Transformation of poorly performing forest plantations and arable lands into semi-natural grasslands could considerably increase the area proper for the establishment and maintenance of grassland-related species and also could improve the functional connections among habitat patches. Furthermore, focusing on the generalist species besides specialists would generate helpful knowledge for nature conservation on the compositional change in community structure.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.10.001.

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