

Small grassland fragments and connectivity support high arthropod functional diversity in highly modified landscapes

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Abstract

1. Grassland ecosystems undergo dramatic habitat loss and fragmentation worldwide due to agricultural expansion and intensification. Among different taxonomic groups, grassland arthropods are particularly sensitive to this process and, therefore, are exposed to considerable risk.
2. Although many studies focus on land use impacts on arthropod diversity, these mostly consider taxonomic diversity and neglect trait-mediated functional responses. However, studying functional diversity often provides more accurate insights into ecosystem processes.
3. Here, we assessed the effect of fragment size and connectivity on the functional composition (community-weighted mean trait values) and diversity (Rao's quadratic entropy) of two diverse and abundant arthropod groups: spiders and true bugs. We assigned functional traits for more than 300 species collected from 30 sandy steppe (forest-steppes) and 30 loess steppe fragments (kurgans) in the southern part of the Hungarian Great Plain.
4. Functional responses to fragmentation were observed for spiders in forest-steppes and for true bugs in kurgans. We found higher functional diversity in better-connected fragments for spiders and in small fragments for both groups. We collected small, humidity-preferring and web-building spiders in small fragments, and there were more ballooning spiders with moist habitat preferences in well-connected fragments. Furthermore, increasing grassland connectivity resulted in a significantly higher proportion of polyphagous and humidity-preferring individuals in the true bug communities.
5. Our results highlight the importance of small grassland fragments in maintaining high arthropod functional diversity. Even small fragments in a well-connected grassland network can promote ecosystem functioning and associated services within human-dominated landscapes.

KEYWORDS

arable land, community weighted mean, fragmentation, landscape, pine plantation, RaoQ, spiders, steppe, traits, true bugs

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INTRODUCTION

Due to agricultural expansion and land use intensification, grasslands have become one of the most threatened ecosystems worldwide. This process leads to homogenous landscapes with small, fragmented and isolated remnant habitats (Batáry et al., 2020; Deák, Tóthmérész, et al., 2016; Habel et al., 2013). As a consequence, communities associated with grasslands are adversely affected resulting in their altered species richness (Gallé et al., 2022; Rösch et al., 2013), functional composition (Birkhofer et al., 2015; Török et al., 2022) and ecosystem functioning (Kuli-Révész et al., 2021; Martinson & Fagan, 2014).

Arthropods often react sensitively to habitat loss, fragmentation and other environmental changes (Debinski & Holt, 2000; Habel et al., 2019) as they have relatively short generation times (Longcore, 2003) and represent the largest and most species-rich group (Santos et al., 2021). In addition, they have a broad spectrum of functional groups (e.g., herbivores, predators and pollinators); thus, their persistence, especially in an agricultural landscape, is essential to maintain key ecosystem services (Martinson & Fagan, 2014; Öckinger & Smith, 2007). Among them, spiders (Araneae) are important generalist predators in all terrestrial ecosystems and are a frequently used indicator group because of their sensitivity to habitat and landscape structure (Buchholz, 2010; Gerlach et al., 2013). True bugs (Heteroptera) are also highly diverse and abundant in almost every habitat type and have a wide range of trophic levels, including herbivores, omnivores and predators (Di Giulio et al., 2001; Gerlach et al., 2013). Due to the high proportion of phytophagous species, they often react quickly to environmental changes associated with altered vegetation composition (Friess et al., 2017; Zurbrügg & Frank, 2006).

Although species richness is a widely used and important measure of community response to disturbance, it neglects the functional properties (traits) of individual species (Díaz & Cabido, 2001). Functional traits are measurable morphological, physiological, phenological or behavioural characteristics of individuals that affect species' fitness or are related to ecological variables (Simons et al., 2016). Functional traits of species can directly or indirectly influence ecosystem functioning and result in differences in species' roles in the ecosystem. Consequently, variation in functional diversity and composition can be a strong driver of ecosystem functioning and services (Wood et al., 2015). Therefore, assessing functional diversity rather than the classical taxonomic diversity measures, for example, species richness, can provide better insight into ecosystem processes (Díaz & Cabido, 2001; Gagic et al., 2015).

Habitat loss and isolation alter functional diversity across different taxa as these factors act as environmental filters and reduce the variety of trait-state combinations (Buchholz et al., 2020; Hatfield et al., 2018; Uhl et al., 2021). Body size and dispersal ability are often used as a proxy for changes in land use intensity and habitat disturbance. Other traits such as stratum use, feeding mode, host plant specialisation and moisture preference are important descriptors of trophic structure and reflect species adaptation to environmental conditions (Birkhofer et al., 2015; Gallé & Batáry, 2019; Simons et al., 2016). For instance, small, good dispersing and generalist

arthropods have better capabilities to reach suitable resources in highly modified landscapes at the expense of large-bodied, less mobile and specialist species (Ewers & Didham, 2006; Martinson & Fagan, 2014; Tscharnkte et al., 2002). In addition, the increasing proportion of intensively used elements in the landscape is often associated with altered structure and composition of original vegetation (Kleijn et al., 2009; Ramankutty et al., 2018) and is also likely to reduce the quality of the remaining habitats (Perner & Malt, 2003; Schmidt et al., 2017). This process might filter out arthropods that utilise a certain set of microhabitats (Torma et al., 2019, 2023), including species preferring complex vegetation structures, such as web-building spiders (Diehl et al., 2013; Lyons et al., 2018).

Despite the growing body of literature, there are still large gaps in understanding how arthropod functional diversity responds to habitat fragmentation in highly modified landscapes (Schirmel et al., 2016). In this study, we investigated the effect of fragment size and connectivity on functional diversity and traits of spider and true bug communities in two threatened grassland ecosystems: sandy and loess steppe grassland fragments. We had the following expectations: (1) Increasing connectivity and fragment size contribute to the high functional diversity of arthropods; (2) Well-connected and large fragments support a high proportion of large-bodied, herbaceous plant-dwelling and humidity-preferring spiders and true bugs in their communities; (3) There are more actively hunting spiders, generalist (i.e., polyphagous) true bugs and good dispersing arthropods (i.e., ballooning spiders and macropterous true bugs) in isolated and small grasslands.

MATERIALS AND METHODS

Study area and design

We conducted our study in the southern part of the Hungarian Great Plain. This region is characterised by a continental climate with a mean annual temperature of 10–11°C and annual precipitation of 550–600 mm (Deák, Valkó, et al., 2016; Tölgyesi et al., 2016). The area includes two types of natural grassland habitats: sandy steppe grasslands within forest-steppes in the western part and loess steppes in the south-eastern part (Figure S1). Forest-steppes are structurally complex ecosystems consisting of a mosaic of dry forests and grasslands. The vegetation of these habitats developed on sandy soil and is composed of drought-tolerant species (e.g., *Festuca vaginata*, *Stipa borysthenica* and *Alkanna tictoria*) and some xeric trees and shrubs scattered on the grassland (e.g., *Juniperus communis*, *Crategus monogyna* and *Populus alba*). Forest steppe remnants have great conservation and ecological importance and are among the most threatened vegetation types in Hungary. In the study area, the replacement of native vegetation with intensively managed alien tree plantations (mainly *Pinus sylvestris* and *Pinus nigra* monocultures) is the most threatening factor (Rédei et al., 2020).

Loess steppes are characterised by generally treeless vegetation dominated by perennial xerophilous plant species (e.g., *Agropyron*

cristatum, *Astragalus austriacus* and *Kochia prostrata*) occurring on chernozem soil. Since this soil type is excellent for agriculture, a major part of the steppe biome has been converted into arable land worldwide. As a result, steppe vegetation is restricted to small fragments unsuitable for arable farming, like roadside verges, field margins and kurgans in the study area. Kurgans are relatively small (from a few metres to 100 m in diameter) round or elliptical-shaped mounds built by ancient steppe cultures (mainly during the IV–I millennia BC), generally for burial purposes. These habitat fragments are important in preserving original steppe vegetation and support a high diversity of grassland specialist species (Deák, Tóthmérész, et al., 2016; Deák, Valkó, et al., 2016).

Prior to the field study, we visited more than 60 potential forest-steppe grasslands and 100 kurgans, from which we selected the final study sites based on calculations using geographic information system (GIS). We calculated Hanski's connectivity index (Hanski et al., 2000) and low quality matrix percentage to quantify landscape configuration and composition using the Ecosystem Map of Hungary (Tanács et al., 2021), Google aerial photographs (taken in 2019) and the Quantum GIS 3.6.1 software (Quantum GIS Development Team, 2019). Forest-steppes and kurgans had two different spatial contexts, that is, forest-steppe fragments were embedded in a matrix of relatively small-scale pine forest plantations, and kurgans were situated in large-scale agricultural landscapes (mostly maize, sunflower, alfalfa and winter cereal fields). Therefore, we made the GIS calculations within a radius of 500 m for forest-steppes and 1000 m for kurgans (Gallé et al., 2022; Kuli-Révész et al., 2021). To calculate Hanski's connectivity index, we used the following equation:

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

where α is a parameter describing a species' dispersal ability, and β is a parameter that describes the scaling of immigration. 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 set both α and β parameters to 0.5 since we applied the connectivity index to entire communities (Rösch et al., 2013). Small connectivity index values indicate isolated grassland fragments, whereas high values indicate connected fragments in the landscape. For low quality matrix calculations, we considered all non-habitat patches in the landscape (coniferous and deciduous plantations, clear-cut areas, young afforestation and arable lands) and calculated their pooled percentage cover in a buffer around each grassland fragment. Since there were strong correlations between low quality matrix percentage and connectivity in both grassland ecosystems (forest-steppes: Pearson's $r = -0.64$, $p < 0.001$; kurgans: Pearson's $r = -0.95$, $p < 0.001$, i.e., the proportion of low quality matrix significantly decreased with increasing connectivity), we decided to use only connectivity index for further analyses.

Finally, we selected 30 forest-steppe fragments and 30 kurgans based on their size and connectivity (Figure 1). We used fragment size (15 small vs. 15 large for both fragment types) as a contrast factor with the exclusion of medium-sized fragments (small: 0.16–0.48 ha

for forest-steppes and 0.01–0.10 ha for kurgans; large: 0.93–6.88 ha for forest-steppes and 0.20–0.44 ha for kurgans) and connectivity index as a continuous gradient (range: 24–811 for forest-steppes and 0–2637 for kurgans). Forest-steppe fragments were situated around three villages, and kurgans were situated around four villages.

Collection, identification and functional traits of arthropods

Spiders and true bugs were collected from the herbaceous vegetation with a D-Vac suction sampler (Ryobi OBV18 Blow-Vac with a fine mesh bag inside the suction tube). This method allows rapid arthropod sampling from open and relatively large habitats (Yi et al., 2012). We collected three samples in the centre part and three at the edge of the fragments to consider microhabitat heterogeneity. Collections were done in early June and early July 2019, when the highest arthropod activity was detected in the study sites. Each sample consisted of 25 subsamples, meaning we placed the D-Vac nozzle on the ground 25 times for a few seconds. The collected materials were placed in plastic bags containing 70:30 alcohol/water solution and deposited at the laboratory of the Institute of Ecology and Botany, CER. Arthropods were identified at the species level based on morphological characters (for the literature used for identification, see [Supplementary material](#)). The nomenclature follows Wachmann et al. (2004–2012) and World Spider Catalog (2022).

For the functional diversity analyses, we classified spider and true bug species based on their body size, humidity and stratum preference. Body size was given for each species as a continuous variable and defined as the mean body length in millimetre averaged over males and females. We used three ordinal categories for humidity preference: drought-preferring (code: 1), generalist (code: 2) and humidity-preferring species (code: 3); and binary coding for stratum trait: ground-dwelling (1) and vegetation-dwelling species (2) (Tables S1 and S2). We also classified spider species according to their ballooning behaviour and hunting strategy using the following categories: species not likely to balloon (1), ballooning species present in the genus (2) and species known to balloon (3) for ballooning behaviour; and actively hunting (1) and web-building species (2) for hunting strategy (Table S1). In addition, true bugs were classified based on species' dispersal ability and feeding specialisation. In the case of dispersal ability, we considered wing morphology: always brachypterous (1), predominantly brachypterous (2), equally brachypterous and macropterous (3), predominantly macropterous (4) and always macropterous species (5). For the specialisation trait, we used three categories: species feeding on a single plant genus (1), feeding on a single plant family (2) and feeding on several plant families (3) (Table S2). Since the proportion of non-herbivore true bugs was low in the communities of both grassland types (less than 8% of all species), we excluded them from this categorisation. We compiled traits from different sources (Buchar & Ruzicka, 2002; Gossner et al., 2015; Wachmann et al., 2004–2012; World Spider Catalog, 2022) and complemented data, if needed, based on the opinion of experts performing species identifications.

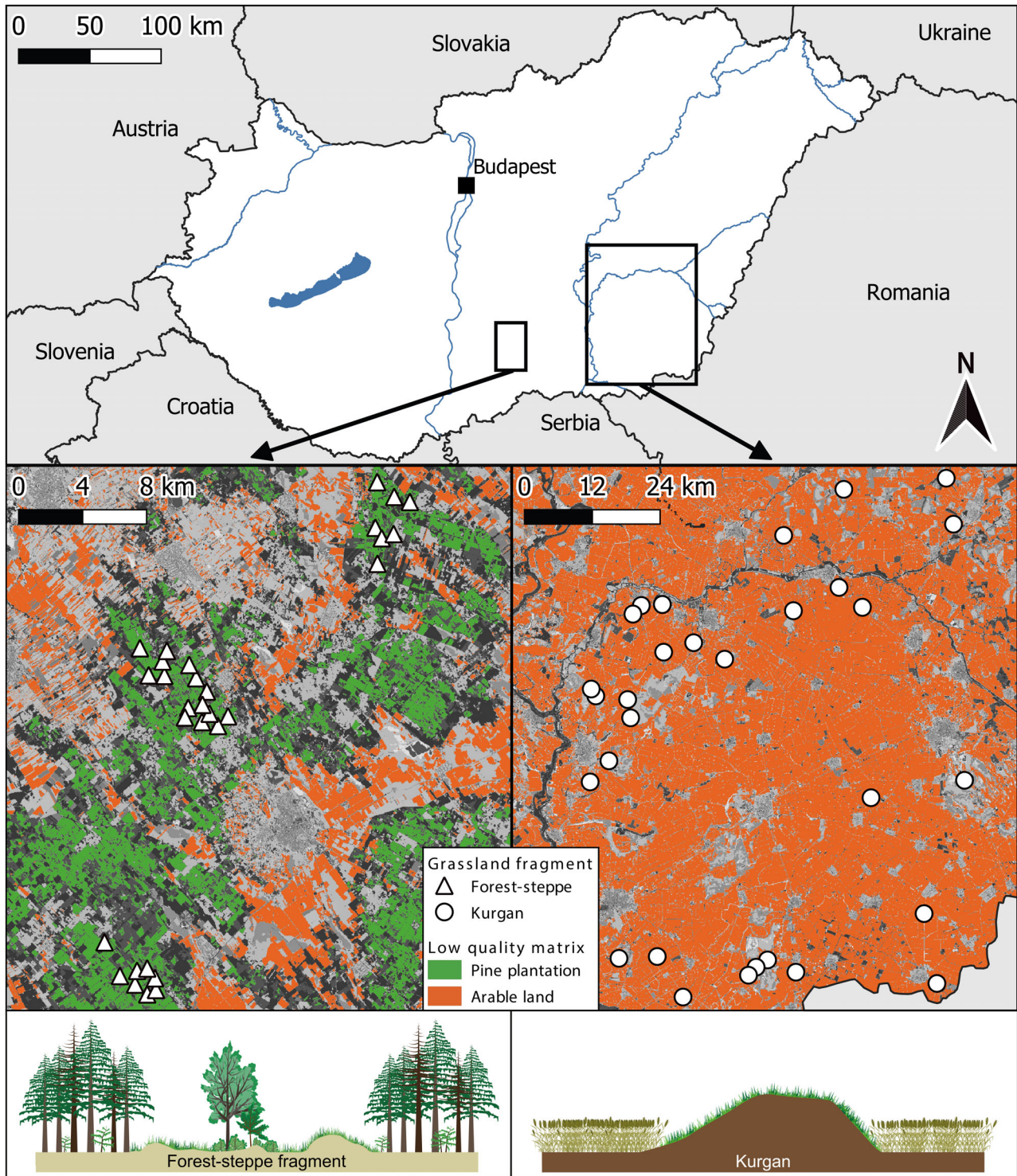


FIGURE 1 Study area in Hungary. Triangles represent the localities of forest-steppe fragments, whereas circles represent kurgan localities. Dominant low quality matrices such as pine plantations and arable lands are marked with green and orange, respectively. Map source: Ecosystem Map of Hungary.

Data analysis

We pooled data across sampling dates and transects (centre and edge) and used the R 3.5.0 statistical environment (R Core Team, 2018) for all analyses. Before the analyses, connectivity

index data were square-root transformed and scaled between 0 and 1 to weight down the high values attributed to well-connected fragments. We performed Student's *t*-tests to check whether our explanatory variables (fragment size and connectivity) were independent of each other. For both grassland types, we

found no relationship between the two variables (forest-steppe: $t = 0.161$, $p = 0.874$; kurgan: $t = -0.885$, $p = 0.384$).

We calculated community weighted means (CWM) for each trait, using the averages of trait values weighted by the relative abundances of each adult spider and true bug species at each grassland fragment with the following equation:

$$\text{CWM} = \sum_{i=1}^S p_i x_i,$$

where p_i is the relative abundance of species i ($i = 1, 2, \dots, S$), and x_i is the trait value for species i . Spider juveniles ($n = 5158$) and true bug larvae ($n = 4024$) that could not be identified at the species level were excluded from the calculations. Since we collected no adult spider individuals in two forest-steppe fragments (two small fragments with connectivity index values of 406 and 616), these data points were excluded from further analyses on spiders. To characterise the functional diversity of our study sites, we used the multivariate RaoQ coefficient as the expected dissimilarity between two randomly selected individuals in the assemblage using the following formula:

$$Q = \sum_{i,j} d_{ij} p_i p_j,$$

where d_{ij} is the dissimilarity between species i and j (Ricotta & Moretti, 2011). A Cailliez correction was applied to prevent negative eigenvalues from being generated from the non-Euclidean matrix. We used the 'FD' package version 1.0–12 to calculate CWM and RaoQ indices (Laliberte & Legendre, 2010). In order to avoid non-normal residual distributions and heteroscedasticity and to improve model fit, some CWM data were square-root transformed or log-transformed, and those with more than two categories scaled between 0 and 1 prior to the analyses. For correlations between selected traits, see Table S3.

We used linear mixed-effect models (LMMs) with normal errors to test whether fragment size and connectivity (explanatory variables) had a significant effect on functional diversity (RaoQ) and CWM of each trait (response variables) separately for the two fragment types using the 'nlme' package version 3.1–143 (Pinheiro et al., 2019). The full model included (1) the fragment size (factorial variable: small and large), (2) the connectivity index (continuous variable), (3) the interaction between fragment size and connectivity as fixed factors and (4) the location (village, as sites were geographically clustered near to them, see Figure 1) as a random factor to account for the spatial non-independence of study sites within each region. We selected the best model with the lowest Akaike Information Criteria values in each model group using the stepAIC function within the 'MASS' package version 7.3–51.4 (Venables & Ripley, 2002). The spatial autocorrelation in the residuals of our models was checked by Moran's I tests with inverse distance weighting using 'spdep' package version 1.1–3 (Bivand & Wong, 2018). There was no evidence of residual spatial autocorrelation in any model (Table S4), and therefore we did not add an auto-covariate to our models. Given that an increasing number of

species can influence the average dissimilarity among species (Botta-Dukát, 2005), we run separate LMMs to test the effect of species richness on the response variables, including the location as a random factor. In these models, forest-steppe spider species richness data were square-root transformed.

RESULTS

In total, we collected 2365 adult spiders representing 136 species; 282 individuals of 55 species in forest-steppes; and 2083 individuals of 109 species in kurgans. The most abundant species were *Euophrys frontalis* (Walckenaer, 1802), *Tibellus macellus* Simon, 1875 and *Talavera aequipes* (O. P.-Cambridge, 1871) in forest-steppes, and *Agyneta rurestris* (C. L. Koch, 1836), *Civizelotes gracilis* (Canestrini, 1868) and *T. aequipes* in kurgans (27% and 30% of total spider abundances, respectively; Table S1). We found significant effects of explanatory variables on functional diversity and traits of spiders only in forest-steppes. According to the best models, functional diversity (RaoQ) and the proportion of humidity-preferring spiders were significantly higher in the communities of small and well-connected grassland fragments (Table 1; Figure 2a–d). The body size and hunting strategy of spiders were significantly influenced by fragment size, as there were more small-bodied and web-building individuals in small grassland fragments (Table 1; Figure 2e,g). Moreover, the number of ballooning spiders increased significantly with better forest-steppe connectivity in the landscape (Table 1; Figure 2f). In addition, an increasing number of species resulted in higher functional diversity of spiders (Table S6; Figure S2a).

We collected 8138 adult true bug specimens representing 202 species (of which 89% were phytophagous); 935 individuals of 84 species in forest-steppes; and 7203 individuals of 157 species in kurgans. Among them, *Acalypta gracilis* (Fieber, 1844), *Europiella albipennis* (Fallen, 1829) and *Pionosomus opacellus* Horváth, 1895 were collected in the largest numbers in forest-steppes; whereas *Halticus apterus* (Linnaeus, 1758), *Lasiacantha capucina* (Germar, 1837) and *Metopoplax origani* (Kolenati, 1845) were the most abundant species in kurgans (54% of total true bug abundances in both fragment types; Table S2). In the case of true bugs, significant effects of fragmentation were found only for kurgans. Similar to the results on spiders, their functional diversity was higher in small fragments, and there were more true bugs with moisture preferences in well-connected fragments (Table 2; Figure 3a,b). Increasing connectivity also resulted in a significantly higher proportion of polyphagous individuals (i.e., feeding on more plant families) in their communities (Table 2; Figure 3c). The models showed no significant interaction effects between fragment size and connectivity on the response variables (Tables 1 and 2). Species richness affected some response variables for forest-steppe true bug communities, that is, an increasing number of species resulted in their higher functional diversity (Table S6, Figure S2b) and higher proportion of moisture-preferring, monophagous and vegetation-dwelling true bugs in the communities (Table S6; Figure S2c–e).

TABLE 1 Results of the best linear mixed-effect models (LMM, lowest AIC) for the functional diversity (RaoQ) and community weighted mean (CWM) trait values of spider and true bug communities depending on the fragment size and connectivity in forest-steppe grasslands (CWM humidity preference: drought-preferring, generalist, humidity-preferring species; CWM body size: continuous in millimetre; CWM ballooning: no information, ballooning species present in the genus, species known to balloon; CWM hunting strategy: active hunters, web-builders; CWM stratum: ground-dwelling, vegetation-dwelling species).

Model	R ²	Variable	Estimate	SE	t-value	p-value
Spiders						
RaoQ	0.39/0.54	Fragment size	−0.027	0.009	−3.083	0.005
		Connectivity	0.062	0.019	3.329	0.003
CWM humidity preference ^a	0.43/0.43	Fragment size	−0.117	0.033	−3.541	0.002
		Connectivity	0.168	0.069	2.427	0.024
CWM body size ^a	0.22/0.38	Fragment size	0.072	0.024	2.955	0.007
CWM ballooning ^a	0.26/0.26	Connectivity	0.259	0.088	2.931	0.007
CWM hunting strategy	0.24/0.30	Fragment size	−0.123	0.056	−2.211	0.037
		Connectivity	0.217	0.116	1.868	0.075
CWM stratum ^a	0.10/0.35	Connectivity	0.104	0.055	1.911	0.068
True bugs						
CWM stratum	0.06/0.31	Connectivity	−0.217	0.149	−1.453	0.158

Note: For the full LMM models, see Table S5. R²: marginal/conditional values. Variable: positive value for fragment size means a higher number in large versus small fragments. Numbers in bold indicate significant (<0.05) p-values.

^aModel: log-transformed variables.

DISCUSSION

We studied the effect of grassland fragmentation on the functional composition of spider and true bug communities. We found that functional diversity and traits were considerably affected by fragment size and connectivity, but these effects varied between taxonomic groups and depended on the focal ecosystem. The most important finding of this study is that small fragments provided relatively high arthropod functional diversity compared to large ones.

In accordance with our first expectation, we found high spider functional diversity in well-connected forest-steppe fragments. However, this variable was also higher in small than large grassland fragments for both taxonomic groups, which was a somewhat unexpected result. Connected landscapes contribute to better permeability between remaining habitat fragments and enhance the ecosystem functionality of arthropod communities (Barber et al., 2017; Buchholz et al., 2020; Uhl et al., 2021). In the case of kurgans, the lack of this effect suggests that connectivity is less determinant for arthropod functional diversity in landscape elements with less or no woody vegetation (Schirmel et al., 2016). Small habitat fragments do not necessarily contribute to species loss and can provide rather diverse local and regional arthropod fauna (Bailey et al., 2010; Knapp & Řezáč, 2015; Lövei et al., 2006). Furthermore, besides specialists, they almost always harbour more generalists compared to large fragments (as reviewed by Volenec & Dobson, 2020), indicating the role of generalist arthropods in reducing the functional redundancy within communities (Gerisch et al., 2012). Higher functional diversity in small versus large fragments may also indicate a better niche differentiation between species and functionally distinct groups within communities

(Ricotta & Moretti, 2011). In the case of forest-steppes, we found strong positive relationships between species richness and trait diversity of spiders and true bugs. This suggests that species loss of these fragments may contribute to a more homogenous trait composition, unlike in kurgans, where more similar traits occur in the communities in general (Petchey & Gaston, 2006).

In line with our second expectation, we found more moist habitat preferring arthropods with increasing grassland connectivity and more small-bodied spiders in small fragments. At the same time, there was a high proportion of humidity-preferring individuals in spider communities of small forest-steppe fragments, which contradicts this expectation. The former result is less surprising as intensively managed landscape elements generally have lower soil moisture and higher temperature due to the altered vegetation structure (Perner & Malt, 2003; Schmidt et al., 2017). Therefore, connected non-crop habitats might serve as movement corridors for species with moisture preferences within highly modified landscapes. The unexpected shift in forest-steppe spider communities towards moisture-preferring individuals with decreasing fragment size can be explained by the spillover of generalist and woodland species into small patches (Volenec & Dobson, 2020) that are less linked to dry and open habitats compared to many forest-steppe specialists (Gallé et al., 2018). The size of organisms is strongly related to their physiological and ecological characteristics. For instance, small-bodied species have shorter life cycles, faster reproduction rates and use less energy and resources (Simons et al., 2016; Tscharncke et al., 2002), thus, have better colonisation capability of small, disturbed habitats than large species (Birkhofer et al., 2015; Ewers & Didham, 2006). Our result on spiders is in

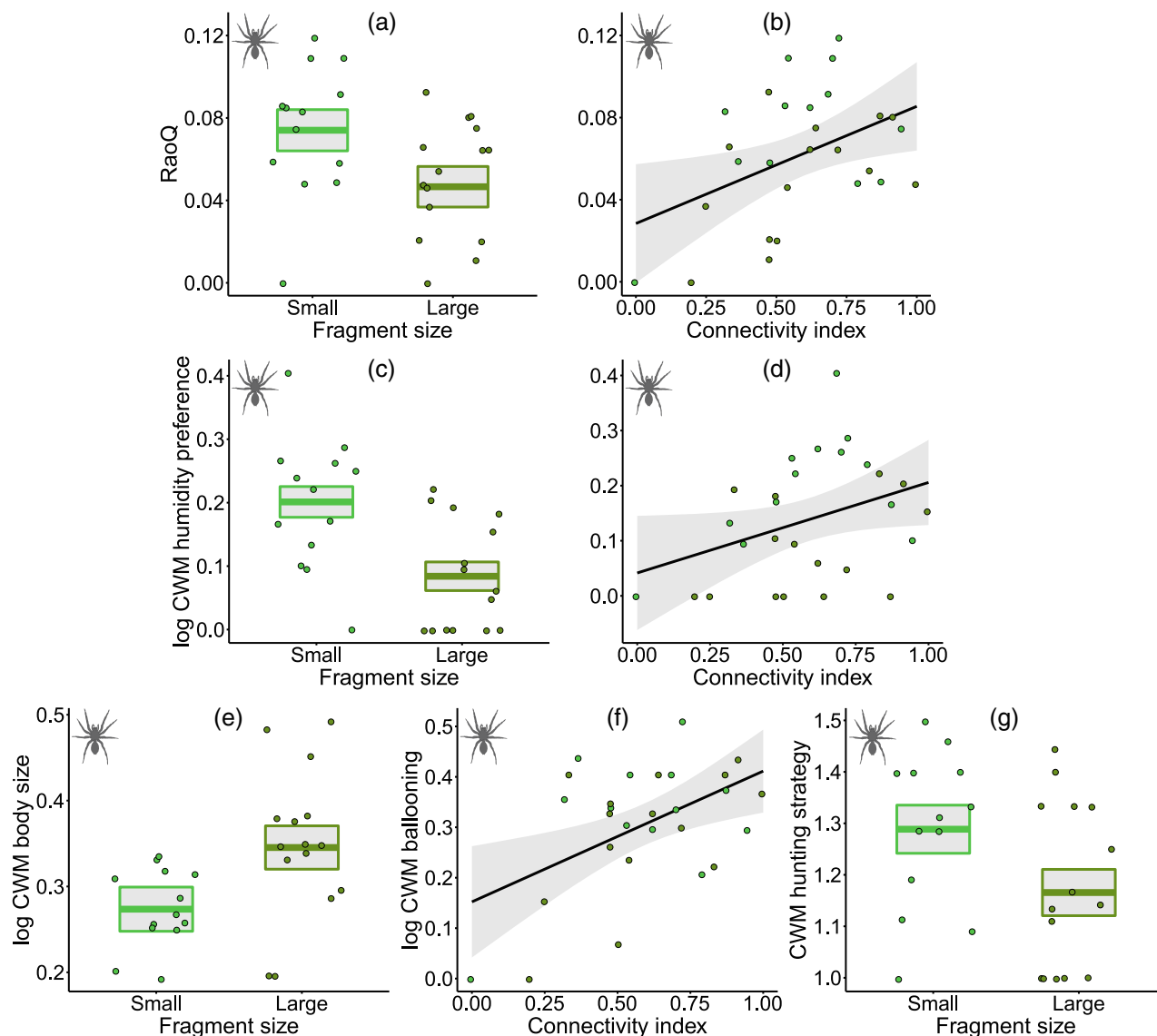


FIGURE 2 Significant effects ($p < 0.05$) of fragment size and connectivity on (a,b) RaoQ and (c–g) community weighted mean (CWM) trait values of spider communities in forest-steppe grasslands: (c–d) CWM humidity preference: drought-preferring, generalist, humidity-preferring species; (e) CWM body size: continuous in millimetre; (f) CWM ballooning: no information, ballooning species present in the genus, species known to balloon; (g) CWM hunting strategy: active hunters, web-builders. Grey bands indicate confidence intervals. On the boxplots, bold lines indicate model estimate values.

accordance with these findings and indicates the sensitivity of large-bodied predatory arthropods to habitat loss.

Against our third expectation, small grassland fragments supported more web-builders, and increasing connectivity resulted in a significantly higher proportion of ballooning spiders and polyphagous true bugs in the communities. Species in small patches are more dependent on the quality of the surrounding matrix than in larger habitats (Volenc & Dobson, 2020), and pine plantations close to forest-steppes have been shown to have a positive impact on web-building spiders (Gallé et al., 2018). Furthermore, there was a relatively strong negative correlation between body size and hunting strategy traits of spiders (Table S3) due to the presence of small web-builders like sheet-web weavers (Linyphiidae) and

cobweb spiders (Theridiidae). These spiders have been found to be more effective colonisers than large ground hunters (Blandenier, 2009; Delgado de la Flor et al., 2020). Ballooning is an efficient passive dispersal strategy of spiders where susceptible species use the wind to colonise new habitat patches. However, this undirected movement is often triggered by unfavourable environmental conditions and carries a high risk as species can accidentally reach low quality or unsuitable habitats (Bell et al., 2005). Given that this kind of dispersal is strongly impeded by pine forest belts around grasslands (e.g., due to reduced wind speed and tall trees; Gallé et al., 2018), well-connected forest-steppe patches might better facilitate the spread of airborne spiders compared to isolated ones (Bonte et al., 2006).

TABLE 2 Results of the best linear mixed-effect models (LMM, lowest AIC) for the functional diversity (RaoQ) and community weighted mean (CWM) trait values of spider and true bug communities depending on the fragment size, connectivity and their interaction in kurgans (CWM humidity preference: drought-preferring, generalist, humidity-preferring species; CWM specialisation: species feeding on a single plant genus, feeding on a single plant family, feeding on several plant families).

Model	R ²	Variable	Estimate	SE	t-value	p-value
Spiders						
RaoQ	0.11/0.11	Connectivity	-0.017	0.009	-1.870	0.073
CWM humidity preference ^a	0.11/0.11	Connectivity	-0.090	0.049	-1.827	0.080
True bugs						
RaoQ	0.19/0.19	Fragment size	-0.013	0.005	-2.507	0.019
CWM humidity preference	0.17/0.38	Fragment size	-0.105	0.063	-1.675	0.108
		Connectivity	0.218	0.090	2.431	0.023
		Connectivity × size	0.166	0.119	1.398	0.175
CWM specialisation	0.15/0.33	Fragment size	-0.146	0.129	-1.132	0.269
		Connectivity	0.392	0.184	2.130	0.044
		Connectivity × size	0.459	0.244	1.882	0.073

Note: For the full LMM models, see Table S5. R²: marginal/conditional values. Variable: positive value for fragment size means a higher number in large versus small fragments. Numbers in bold indicate significant (<0.05) p-values.

^aModel: square-root transformed variable.

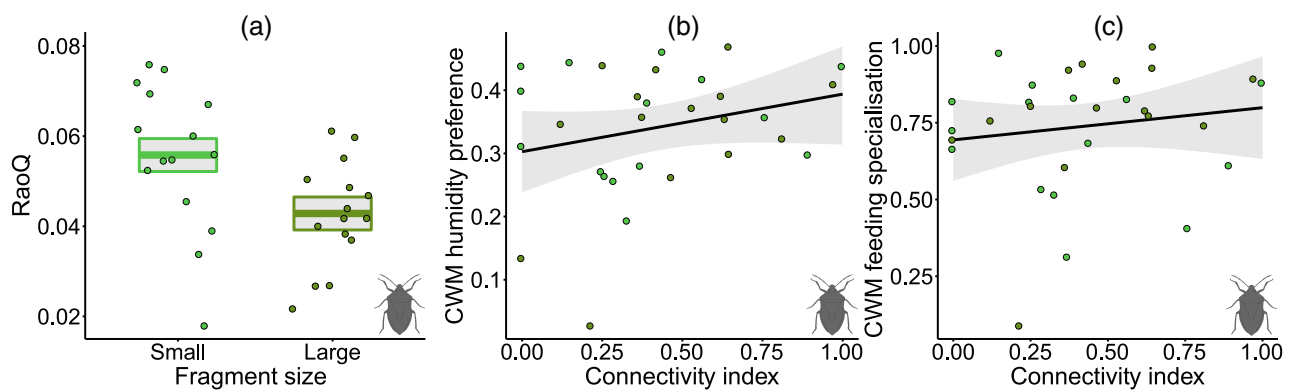


FIGURE 3 Significant effects ($p < 0.05$) of fragment size and connectivity on (a) RaoQ and (b,c) community weighted mean (CWM) trait values of true bug communities in kurgans: (b) CWM humidity preference: drought-preferring, generalist, humidity-preferring species; (c) CWM feeding specialisation: species feeding on a single plant genus, feeding on a single plant family, feeding on several plant families. Grey bands indicate confidence intervals. On the boxplot, bold lines indicate model estimate values.

Fragmented landscapes produce habitat islands for monophagous herbivores. However, they often provide a habitat continuum for less specialised species as they can use secondary or lower quality habitats of the matrix (Ewers & Didham, 2006; Martinson & Fagan, 2014; Tscharrntke et al., 2012). Accordingly, we expected more polyphagous true bugs in isolated fragments but observed a slight increase in their numbers with increasing connectivity of kurgans. This result suggests that connected loess steppe fragments provide more host plants for phytophagous species with broader diet breadth. For instance, a recent study by Gallé et al. (2022) showed an unchanged frequency of specialists but an increased number of generalist plants with better connectivity of small kurgans, indicating the presence of diverse plant communities of some well-connected fragments, offering more potential food for polyphagous herbivores.

Finally, the functional composition of spiders was unaffected by grassland fragmentation in the case of kurgans, and the same was observed for true bugs in forest-steppes. This phenomenon can be explained by several reasons. First, changes in vegetation structural characteristics have been shown to be an important predictor of spider functional composition and diversity (Delgado de la Flor et al., 2020; Lyons et al., 2018; Schirmel et al., 2016). In our study, habitat boundaries between open forest-steppes and dense and shaded pine plantations may form stronger contrast in terms of vegetation structure for spiders than those between two open habitats, kurgans and arable fields. Second, the agrobiont spider species, *A. rurestris* has a great ability to colonise different habitats, especially if it originates from highly disturbed arable lands (Entling et al., 2011). Thus, the observed dominance of *A. rurestris* in kurgans might have

faded the effects of fragmentation on the functional composition of spider communities. Third, winged insects, like many true bug species, are capable of more target-oriented and active movement than spiders (Bonte et al., 2006). Perhaps this rather high mobility can explain why small-scale landscapes of forest-steppes were a less determinant factor in shaping true bug functional composition than larger scale surroundings around kurgans. True bug functional composition was rather explained by species richness in forest-steppes. Since true bug species richness was unaffected by the size and isolation of forest-steppe fragments (Gallé et al., 2022), the associated functional responses might also be explained by some unmeasured local environmental conditions of these habitats.

CONCLUSIONS

In our study, small grassland fragments supported higher arthropod functional diversity than large fragments within intensively managed agricultural and silvicultural landscapes. Compared to taxonomic diversity, functional trait diversity is often more sensitive to environmental changes and most directly related to ecosystem functioning and associated ecosystem services. Consequently, small patches might facilitate essential ecosystem functions provided by arthropods, such as biological control of pests and weeds and food chain maintenance (Gagic et al., 2015; Wood et al., 2015). At the same time, the importance of large fragments cannot be neglected. Besides their well-known positive effect on specialist species and overall richness (Batáry et al., 2021; Volenec & Dobson, 2020), they might support arthropods with specific functional characteristics (e.g., large, xerophilous and actively hunting spiders). Our results suggest that in addition to maintaining extensive grassland areas within an increasingly human-dominated matrix, they should be interconnected by small patches in order to sustain functionally diverse arthropod communities.

AUTHOR CONTRIBUTIONS

Dávid Korányi: Data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Róbert Gallé:** Conceptualization; formal analysis; investigation; methodology; validation; writing – review and editing. **Attila Torma:** Data curation; formal analysis; investigation; validation; writing – review and editing. **Nikolett Gallé-Szpisjak:** Data curation; investigation; validation; visualization; writing – review and editing. **Péter Batáry:** Conceptualization; formal analysis; funding acquisition; methodology; project administration; resources; supervision; validation; visualization; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Photos of the studied grassland ecosystems: sandy steppe-grassland in forest-steppe zone (a) and kurgan as a fragment of loess-steppe vegetation within a maize field (b).

Figure S2. Significant effects ($p < 0.05$) of species richness on (a) RaoQ values of spider communities and (b) RaoQ and (c–e) community weighted mean (CWM) trait values of true bug communities in forest-steppe grasslands: (c) CWM humidity preference: drought-preferring, generalist, humidity-preferring species; (d) CWM feeding specialisation: species feeding on a single plant genus, feeding on a single plant family, feeding on several plant families; (e) CWM stratum: ground-dwelling, vegetation-dwelling species. Gray bands indicate CIs.

Table S1. List of spider species, their trait values, and abundances. Size (in millimeters); stratum: ground-dwelling (1), vegetation-dwelling species (2); humidity: drought-preferring (1), generalist (2), humidity-preferring species (3); ballooning: no information (1), ballooning species present in the genus (2), species known to balloon (3); hunting: active hunters (1), web builders (2).

Table S2. List of true bug species, their trait values, and abundances. Size (in millimeters); stratum: ground-dwelling (1), vegetation-dwelling species (2); humidity: drought-preferring (1), generalist (2), humidity-preferring species (3); dispersal: brachypterous (1), predominantly brachypterous (2), equally brachypterous and macropterous (3), predominantly macropterous (4), macropterous species (5); specialisation: species feeding a single plant genus (1), feeding a single plant family (2), feeding on several plant families (3).

Table S3. Kendall rank correlation coefficients between functional traits of spiders and true bugs.

Table S4. Results of Moran's I tests to check spatial autocorrelation in the models' residuals.

Table S5. Results of the full LMM models for the functional diversity (RaoQ) and community weighted mean (CWM) trait values spiders and true bugs depending on the fragment size, connectivity, and their interaction in forest-steppes and kurgans. Numbers in bold indicate significant (< 0.05) p -values.

Table S6. Results of the full LMM models for the functional diversity (RaoQ) and community weighted mean (CWM) trait values spiders and true bugs depending on the species richness in forest-steppes and kurgans. Numbers in bold indicate significant (< 0.05) p -values.

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