




## ARTICLE

# Landscape structure is a major driver of plant and arthropod diversity in natural European forest fragments

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**Abstract**

Disentangling the effects of different landscape and local attributes on the biota of habitat patches is often challenging. In Central European forest-steppe ecosystems the high number of forest fragments and the relatively homogeneous matrix between them offer the opportunity to disentangle the effects of habitat size and landscape structure (both landscape composition and landscape configuration) on plant and arthropod biodiversity. We selected 40 forest fragments: 20 forest fragments in extensive, dry, sandy forest-steppe region and 20 fragments in a mesic forest-steppe region of Hungary. We classified the detected plant and arthropod species according to their habitat association as forest specialist species or open habitat species. We then tested the effect of fragment size, landscape composition, and landscape configuration on their species richness and abundances. We found that increasing forest fragment size, forest habitat amount, and forest edge length had in general positive effects on forest spider abundance, but negative on open-habitat arthropod abundances and plant species richness, varying a little among the studied taxa. Most interestingly, the effects of fragment size were often moderated by both landscape composition and landscape configuration, as well as habitat association of species. The fragment size effect was more pronounced in landscapes with low forest habitat amount having positive effects on forest spiders and negative effects on open-habitat plants. An effective conservation strategy should take into account not only the presence of forest fragments, but also the size and configuration as well as the connectivity of forest fragments, to maximize diversity benefits of forest patches.

**KEYWORDS**

edge effect, fragment size, habitat amount, habitat fragmentation, landscape composition, landscape configuration

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## INTRODUCTION

As a consequence of agricultural intensification and urbanization since the mid-20th century, biological diversity has declined considerably throughout the world, but particularly in European countries resulting in strongly fragmented landscapes (Foley et al., 2011). The spatial distribution of organisms in such fragmented landscapes is influenced by numerous local (habitat scale)- and landscape-scale factors and presumably also by their complex interactions (Turner et al., 2005). It is, therefore, crucial to identify the drivers of diversity to adequately interpret current and future patterns of biodiversity in the remaining semi-natural habitats.

Two main categories of parameters that describe landscape structure are landscape composition (related to habitat amount in the present study) and landscape configuration (Leitão et al., 2012). Composition involves a set of variables giving information on the amount or portion of different land cover types, such as forests, grasslands, and the agricultural matrix between them with effects constraining specialist species more than generalist ones (Deák et al., 2018; LaScaleia et al., 2018). Configuration describes the spatial arrangement and shape of these land cover types. A higher number of patches with irregular shapes results in a higher configurational heterogeneity (Turner et al., 2005). Configurational heterogeneity may also determine the local-scale diversity (e.g., Wulf & Kolk, 2014). For example, a higher number of patches may influence the movement rate of individuals (functional connectivity) between patches (Pascual-Hortal & Saura, 2006). The mass movement of animals across habitat edges, that is, spillover, often determines species composition and trophic interactions in landscapes with high configurational heterogeneity (Blitzer et al., 2012; Tölgyesi et al., 2018). Due to increased edge densities, these landscapes are likely to support spillover of dispersal-limited populations between patches and this effect is mediated by landscape composition (Martin et al., 2019).

The majority of former landscape ecology studies applied the “habitat patch concept” to assess the effect of landscape change on biodiversity in human-modified landscapes (e.g., Brückmann et al., 2010; Ewers & Didham, 2006). This concept emphasizes the distinct effects of local scale patch size and landscape scale isolation on the species richness of the focal habitat patch (Fahrig, 2013). For example, Zulka et al. (2014) found that the patch size had a stronger independent effect on spiders than isolation; however, their study showed the opposite pattern for plants. In contrast, the “habitat amount hypothesis” states, that the primary predictor of biodiversity change is habitat amount (Fahrig, 2013).

Habitat amount describes the landscape composition with a single variable, the summed amount of suitable habitat areas within an adequate distance from the sample site (local landscape). Habitat amount also includes the area of the focal patch.

Patch size is among the most notable local characteristics of the habitat (Dembicz et al., 2016). It may have a strong effect on the species richness and determine the composition of species assemblages, first highlighted in the classical theory of island biogeography (MacArthur & Wilson, 1967). This concept predicts patterns of species diversity and occupancy in fragmented habitats and has been applied for wide range of terrestrial habitat fragments (Lindenmayer & Fischer, 2013).

Disentangling the effects of habitat size, landscape composition and configuration on biodiversity is among the main challenges of landscape-scale conservation biology (Fahrig, 2013; Lindenmayer & Fischer, 2013). In human-modified landscapes the degree of habitat loss and quantitative configuration metrics are usually correlated as habitat fragmentation is induced by habitat loss (Didham et al., 2012; Martin et al., 2016).

A focus on total species richness ignores the fact that some species are more susceptible to fragmentation than others because they differ in their ecological traits and habitat requirement (Matthews et al., 2014). Species can be partitioned to specialists and generalist, the former depend more on resources located in the patches and generally have higher conservation value than the latter (Lövei et al., 2006). Decreasing patch size has a negative effect on specialist species, and it can also result in an influx of generalist species (Matthews et al., 2014). This influx can be further amplified if the shape of the fragment is irregular, i.e., it has a low area to edge ratio (Magura et al., 2001). Furthermore, habitat amount may have a significant effect on the specialist biota of small patches but not on that of the large patches (Rösch et al., 2013). Small fragments are prone to a higher rate of stochastic extinctions due to low abundances, as it is predicted by the neutral theory (Hubbell, 2001). Neutral species would react to extinction pressures in the same fatal way, yet the extinction of a few species has little effect on the integrity of the community (Alonso et al., 2006). Species traits, however, may modify this effect (Hanski et al., 2000). The probability of recolonization is lowered with decreasing habitat amount and this may cause a decline of specialist species (Batáry et al., 2021). The interaction between habitat amount and patch size implies that small fragments in landscapes with low habitat amount maintain lower biodiversity of specialist species than predicted from independent effects of the two parameters (Didham et al., 2012; Ewers et al., 2007).

The majority of habitat fragmentation studies focus on human-induced fragmentation processes (Lindenmayer & Fischer, 2013). In contrast, here we focused on relatively intact, extensive natural areas with no significant human disturbance. Our aim was to give a comprehensive analysis of plant and arthropod diversity of naturally fragmented forest-grassland mosaics, where both the focal forest fragments and the grassland matrix are naturally developed (Erdős, Ambarlı, et al., 2018). In forest-steppe ecosystems the high number of forest fragments and the relatively homogenous matrix between them offered the opportunity to separate the effects of different landscape characteristics.

Our study focused on the relatively understudied ground-dwelling arthropod fauna (namely spiders and carabid beetles) and the herbaceous vegetation of forest fragments. Spiders and carnivorous carabids are among the main invertebrate predators in terrestrial ecosystems; they are key divers of arthropod assemblages in both grasslands and forests. Furthermore, they are sensitive indicators of habitat and landscape change. Dry forest-steppes have a specialized carabid fauna with relatively low species richness and abundances (Thiele, 2012). We also studied the herbaceous vegetation, as the primary producer plants are a fundamental component of food webs and they provide the structure of habitats for ground-dwelling arthropods.

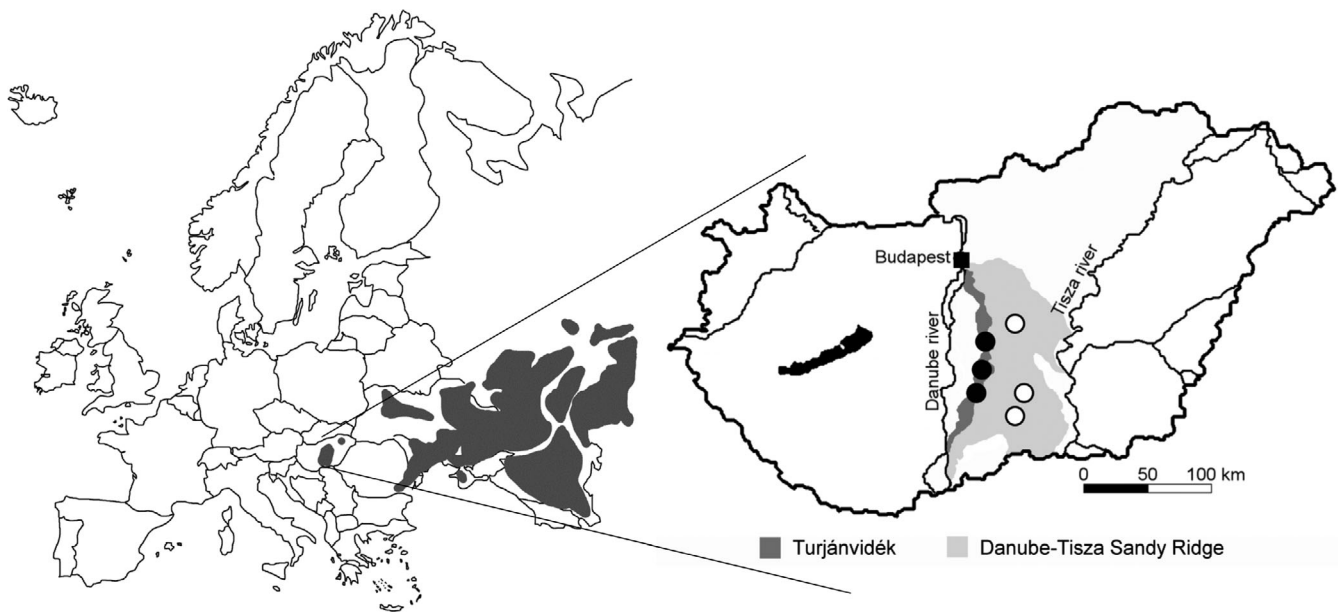
We studied the effect of the following local and landscape parameters: (1) focal fragment size (local variable); (2) forest habitat amount, that is, the proportion of forests

in the landscape (landscape composition); (3) cumulative edge length of the fragments in the landscape, that is, a parameter describing landscape configuration, and all two-way interactions of the above terms. We set up a landscape-scale study design to disentangle the above noncorrelating landscape parameters on two, mostly predatory arthropod taxa and the herbaceous vegetation. Numerous studies focused on the landscape scale effect on small habitat islands (e.g., Evju et al., 2015); however, our study is the first to investigate landscape configuration and composition on forest-steppe plants and arthropods. We tested the following hypotheses: (1) the abundance and richness of forest specialist species increases, whereas the abundance of open-habitat species (i.e., nonforest species) decreases with increasing fragment size, forest habitat amount and simplicity of landscape configuration (i.e., lower cumulative forest edge length); (2) forest habitat amount has a stronger effect on the biota of small fragments than on large fragments; and (3) landscape configuration has a stronger effect if the forest habitat amount is low or if the focal fragment is small.

## MATERIALS AND METHODS

### Study region

We carried out this study in the lowlands of central Hungary (Figure 1), where the majority of the westernmost remaining natural forest-steppe areas are concentrated in



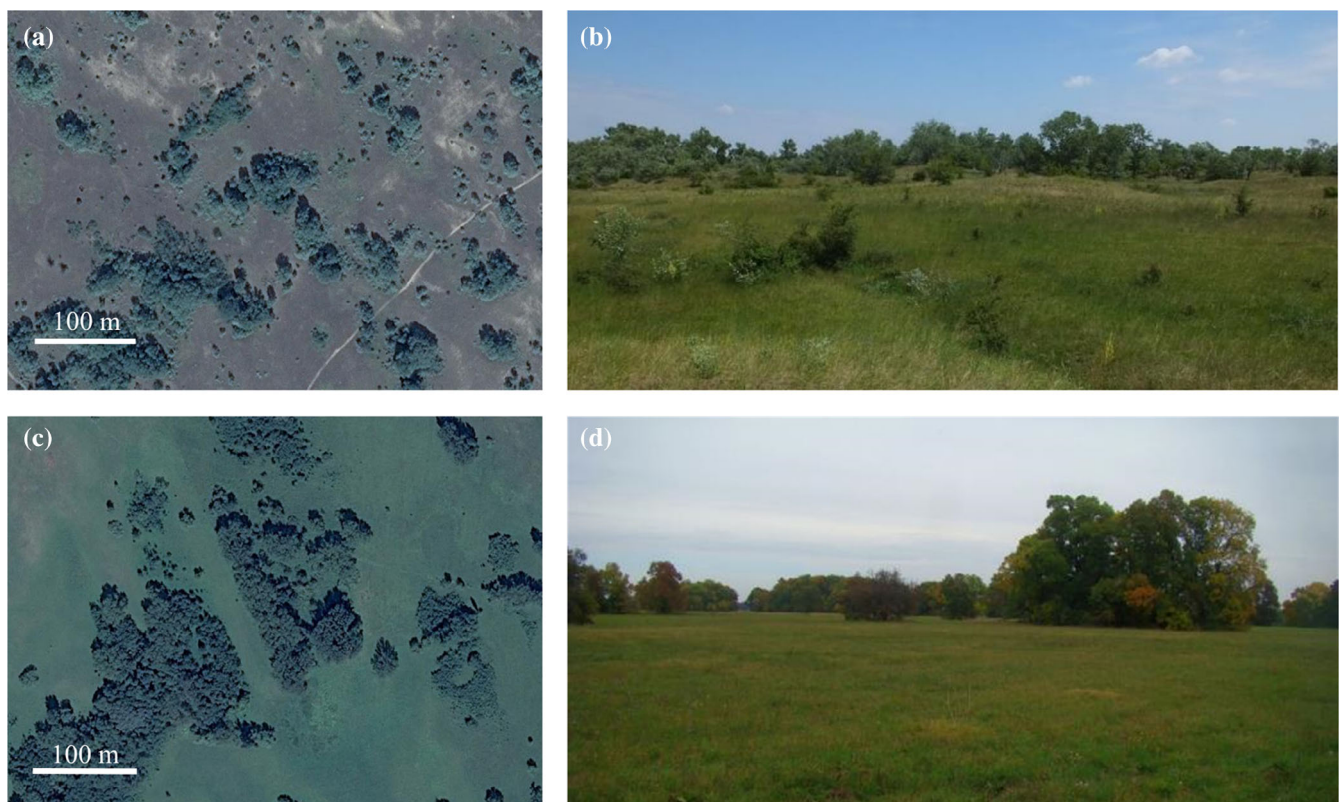
**FIGURE 1** Forest-steppes in Europe (after Dúbravková & Hajnalová, 2012) are represented with gray (left hand side) and the location of the sampling sites in central Hungary (right hand side). Dark gray: mesic forest-steppes; light gray: dry forest-steppes; black dots: mesic forest-steppe landscapes in Turjánvidék region; open circles: dry forest-steppes in Danube-Tisza Sandy Ridge

Europe. The forest-steppe zone is a separate vegetation belt in the transition between the zones of temperate forests and steppes in Europe and Asia. The Pannonian ecoregion, covers the westernmost forest-steppes, which comprise of relatively small forest fragments embedded in a grassland matrix resulting in structurally and microclimatically fine-scale mosaic ecosystem (Erdős, Ambarlı, et al., 2018). The term “fragment” refers to forest patches throughout the paper. Forest-steppes have different types, depending on soil and climatic conditions. The forest-steppe linked with calcareous sandy soil and the relatively humid mesic forest-steppes are present in the Pannonian ecoregion. We focused on both types, as both have the potential to preserve the valuable and different natural flora, fauna, and act as local biodiversity hotspots. Both types (i.e., dry forest-steppes and mesic mosaics) are formed naturally and they are usually managed extensively by grazing or mowing (Erdős, Ambarlı, et al., 2018; Tölgyesi et al., 2018). We selected 40 sites in two regions near six settlements, including 20 sites in extensive, dry, sandy forest-steppe region of the Kiskunság Sandy Ridge near the villages of Fülöpháza ( $n = 9$ ), Pirtó ( $n = 6$ ), and Tázlár ( $n = 5$ ), and 20 sites in the mesic forest-steppe mosaic of the Turjánvidék region near Páhi ( $n = 13$ ),

Tabdi ( $n = 5$ ), and Kiskőrös ( $n = 2$ ). The main feature of both forest-steppe regions is the patchy habitat structure, a mosaic of scattered trees and forest fragments embedded in a near natural grassland matrix (Figure 2). The size of the forest fragments ranges from a few trees and shrubs ( $30\text{--}50\text{ m}^2$ ) to several hectares, although the majority of forest fragments are smaller than  $5000\text{ m}^2$ . In the mesic region mowing occurs once a year, this inhibits bush and forest encroachment resulting in a stable landscape structure (Tölgyesi et al., 2015). Abandoned dry forest-steppes had been grazed at low intensity by sheep. The canopy of mesic fragments was characterized by *Fraxinus angustifolia* subsp. *danubialis* and *Quercus robur*. The dry fragments comprise of *Populus alba* trees, *Crataegus monogyna* and *Juniperus communis* bushes. Forestry activities have been absent in the forests of both forest-steppe types for more than half a century.

### Site selection and landscape metrics

We selected the study landscapes in the two regions using the QGIS software on the basis of satellite images so that they represent similar gradients of landscape



**FIGURE 2** Satellite images of the studied landscapes and typical pictures representing the sampled habitats (a) and (b) in dry forest-steppe, (c) and (d) in mesic forest-steppe

heterogeneity ranging from less than 5% to more than 50% of forest area within a 500 m radius buffer area, measured from the center of the focal fragment (forest habitat amount). We selected a 500-m buffer as several studies have supported that this is a scale at which landscape attributes affect plant, spider, and carabid diversity and composition (Gallé & Schwéger, 2014; Schmidt et al., 2005; Söderström et al., 2001; Weibull et al., 2003).

Sampling sites were situated at least 500 m from the edge of natural forest-steppe area, that is, far from arable land and built-up areas. The minimum distance between neighboring landscapes was 400 m (distance between closest sites was  $565 \pm 20.5$  m, mean  $\pm$  SEM). We excluded fragments with less than 500 m<sup>2</sup> area. We used the QGIS software to measure three variables: the size of the focal forest fragments (fragment size), the cumulative area of fragments within a 500 m radius buffer area around the sampling sites (forest habitat amount as compositional heterogeneity), and the shape of fragments with the cumulative edge length (configurational heterogeneity). For data analyses the above explanatory variables were mean-centered and divided by their standard deviation since they were defined on different scales (Legendre & Legendre, 2012).

## Vegetation sampling

In the sampled forest fragments, each sampling site consisted of four 1-m<sup>2</sup> quadrats resulting in a total of 160 quadrats (2 forest-steppe region  $\times$  20 landscapes in each region  $\times$  4 quadrats per site). We established relatively small quadrats due to the small size of fragments. The quadrats were located along a transect running parallel with the edge in the fragment, approximately 5–6 m from each other to reduce the confounding effect of autocorrelation (Appendix S1). All vascular plant species in the quadrats were identified to the species level and the presence/absence data of each species was recorded in early June 2014, the typical period for vegetation sampling in the region. Saplings and root sprouts of trees and shrubs were included if they were shorter than 50 cm. We assigned the recorded plant species according to their habitat association. We distinguished forest specialist plants and open-habitat plants according to Király (2009), and excluded species with no significant habitat affinity from the analyses.

## Arthropod sampling

Spiders and carabids were sampled with pitfall traps during three consecutive 7-day periods between late May

and late June 2014. We employed four pitfall traps per site made of plastic cups with a diameter of 8.5 cm. Traps were filled with 50% water—ethylene-glycol solution and a few drops of detergent were added. We placed a plastic funnel in each trap to eliminate vertebrate by-catches and to reduce the chance of arthropods escaping (Duelli et al., 1999). A plastic roof was also installed above the traps to prevent the dilution of the preservation fluid. Traps were installed in the ground 3 m from the vegetation survey plots (Appendix S1). We classified spider and carabid species according to their habitat association to forest specialist species and open-habitat species on the basis of literature data (Buchar & Ruzicka, 2002; Gesellschaft für Angewandte Carabidologie, 2009).

## Data analysis

Data of the four vegetation samples per sampling site were summed, resulting in 40 samples (2 forest-steppe region  $\times$  20 landscapes in each region). Spider and carabid species richness and abundances were summed over sampling periods and traps within each sampling site, resulting in 40 statistical samples for spiders. Carabid data were analyzed only in the mesic forest-steppe, because of the low catch rate in the dry forest-steppes, thus we had 20 statistical samples for carabids.

We analyzed the multivariate difference in plant and arthropod species composition of dry and mesic fragments with permutational multivariate analysis of variance (PerMANOVA) based on Bray–Curtis dissimilarity matrices with 5000 permutations using the vegan R package (Oksanen et al., 2015).

We performed a set of generalized linear mixed-effects models to evaluate the effects of fragment size (using the natural logarithm of fragment size), forest habitat amount, edge length, and their two-way interactions on (1) the species richness of forest specialist plants and the abundance of forest specialist arthropod species and (2) the species richness of open-habitat plants and the abundance of open-habitat arthropod species. In species richness models we used Poisson error term with the “glmer” function in R from the “lme4” package (Bates et al., 2015). For the models of the abundance data, we used negative binomial error term to account for overdispersion of data with “glmer.nb” function. According to the hierarchical nested structure of our sampling design, settlement (three for both dry forest-steppes and mesic mosaic) nested in region (forest-steppes and mesic mosaic) was used as random term in our models to account for the different management history and climatic effects and spatial autocorrelation of data in all models. We generated models with all possible

combinations of the fixed effects (i.e., fragment size, forest habitat amount, edge length, their second order interactions, and region) and compared them according to their Akaike's information criterion (AIC) values with the “dredge” function from the “MuMIn” package (Bartón, 2015). Model averaging was performed for competitive models ( $\Delta\text{AIC} \leq 6$  to incorporate the uncertainty arising from competitive models). For each parameter, we estimated AIC-weighted importance, and we also estimated the significance of the variables via Satterthwaite's degrees of freedom method with the “LmerTest” package (Kuznetsova et al., 2015). We used visreg package to visualize the significant main effects and interactions (Breheny & Burchett, 2016; Lüdecke, 2018). To assess correlations among forest habitat amount, fragment size and edge length, we calculated the variance inflation factors in the statistical models. The values ranged between 1.21 and 1.40, suggesting no significant multicollinearity.

## RESULTS

Dry forest-steppe was characterized by more and smaller fragments compared to the mesic forest-steppe. The mean number of fragments in dry forest-steppe was more than two times higher than in mesic forest-steppe ( $58.15 \pm 25.97$  mean  $\pm$  SEM vs.  $27.25 \pm 23.85$ , respectively), whereas the mean size of dry forest-steppe fragments was less than half the size of mesic forest-steppe fragments ( $0.41 \pm 0.31$  ha vs.  $1.17 \pm 1.08$  ha, respectively).

In total we recorded 169 plant species; 98 species in dry fragments and 87 species in mesic forest fragments. During the three sampling periods we collected 11,323 adult spiders belonging to 125 species; 3110 individuals of 71 species in dry forests and 8197 spiders of 86 species in mesic forests. We collected 8249 carabid beetles of 73 species in mesic forests. We recorded 98 plant, 41 spider, and 19 carabid species with affinity for open-habitats and 42 forest specialist plant, 31 forest specialist spider and 54 forest specialist carabid species (Appendix S2, S3 and S4).

The species composition of mesic and dry forest flora and fauna was very different. We detected significant multivariate differences of species composition between mesic and dry fragments for plants (PerMANOVA,  $R^2 = 0.398$ , pseudo- $F = 25.213$ ,  $p < 0.001$ ) and for spiders (PerMANOVA,  $R^2 = 0.414$ , pseudo- $F = 53.678$ ,  $p < 0.001$ ). Due to the low carabid abundance in the dry forest-steppes, carabid data were analyzed only in the mesic forest-steppe.

We found several significant effects of fragment size and landscape parameters on herbaceous plants,

carabids, and spiders of forest-steppes (Table 1). Supporting our hypothesis (1), forest habitat amount had a negative effect on the species richness of open-habitat plants ( $z = 2.163$ ,  $p = 0.030$ ; Figure 3a). We found a significant interaction effect of forest habitat amount and fragment size on open-habitat plant species richness with a less pronounced negative effect of forest habitat amount for large fragments ( $z = 2.342$ ,  $p = 0.019$ ; Figure 3b).

Fragment size and forest habitat amount interaction was important determinant of the abundance of forest specialist spiders, as the positive effect of forest habitat amount on forest specialist spiders was stronger in small fragments ( $z = 2.125$ ,  $p = 0.013$ ; Figure 4a), supporting our hypothesis (2). Cumulative edge length had a positive effect on forest spiders, and this effect was modified by interaction with fragment size. This indicated that the effect of edge length was positive in small fragments; however, it had a weak negative effect in large fragments ( $z = 2.858$ ,  $p = 0.002$ ; Figure 4b). Finally, supporting our hypothesis (1), forest habitat amount had a negative ( $z = 2.443$ ,  $p = 0.014$ ; Figure 4c), landscape configurational heterogeneity (i.e., cumulative edge length) had a positive effect on the abundance of open-habitat spider species ( $z = 3.375$ ,  $p < 0.001$ ; Figure 4d).

Partly supporting our hypothesis (3), fragment size exerted a significant negative effect on the abundance of open-habitat carabids ( $z = 3.666$ ,  $p < 0.001$ ; Figure 5a) and the effect of fragment size was less pronounced if landscape configuration was more complex ( $z = 2.313$ ,  $p = 0.020$ ; Figure 5b).

## DISCUSSION

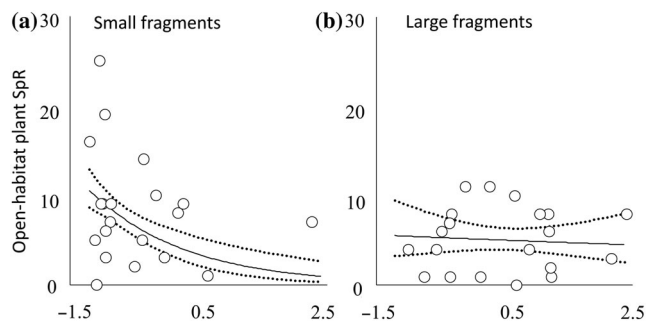
Our results showed that fragment size, landscape composition, and configuration affected together the biota of forest fragments of natural forest-steppes. We found that fragment size moderated the effect of landscape heterogeneity on plants, spiders, and carabids, and this effect was further modified by the habitat association of the species. Supporting our hypothesis (1), forest habitat amount had a negative effect on the species richness of open habitat plants and abundance of open-habitat spiders. Fragment size had a negative effect on the open-habitat carabids. Furthermore, edge length had an effect on the abundance of both open-habitat and forest spiders. Concerning hypothesis (2), forest habitat amount had a stronger positive effect on forest spider abundance of small fragments than that of large fragments, and in contrast open-habitat plant species richness was negatively affected by forest habitat amount, having a stronger decrease in small than large fragments. Our results partly supported hypothesis (3), hence the effect of fragment size showed a stronger

**TABLE 1** The effect of patch size and landscape variables on vegetation, spiders, and carabids, after multimodel averaging of best candidate models

| Model                                  | Multimodel estimate $\pm$ 95% CI | Importance (%) | $z$      |
|--|----------------------------------|----------------|----------|
| Vegetation, forest specialist richness |                                  |                |          |
| Patch size                             | $-0.106 \pm 0.193$               | 54             | 1.072    |
| Habitat amount                         | $0.174 \pm 0.182$                | 82             | 1.868    |
| Edge length                            | $-0.143 \pm 0.181$               | 63             | 1.542    |
| Patch size: Habitat amount             | $-0.130 \pm 0.160$               | 23             | 1.593    |
| Patch size: Edge length                | $0.024 \pm 0.196$                | 8              | 0.245    |
| Habitat amount: Edge length            | $-0.236 \pm 0.289$               | 26             | 1.599    |
| Vegetation, open species richness      |                                  |                |          |
| Patch size                             | $0.125 \pm 0.297$                | 85             | 0.825    |
| Habitat amount                         | $-0.286 \pm 0.312$               | 93             | 2.163*   |
| Edge length                            | $0.175 \pm 0.208$                | 62             | 1.649    |
| Patch size: Habitat amount             | $0.240 \pm 0.201$                | 63             | 2.342*   |
| Patch size: Edge length                | $0.134 \pm 0.225$                | 21             | 1.167    |
| Habitat amount: Edge length            | $0.230 \pm 0.274$                | 31             | 1.774    |
| Spiders, forest specialist abundance   |                                  |                |          |
| Patch size                             | $-0.148 \pm 0.245$               | 91             | 1.183    |
| Habitat amount                         | $0.083 \pm 0.276$                | 31             | 0.595    |
| Edge length                            | $0.199 \pm 0.174$                | 92             | 2.242*   |
| Patch size: Habitat amount             | $-0.263 \pm 0.243$               | 19             | 2.125*   |
| Patch size: Edge length                | $-0.246 \pm 0.169$               | 74             | 2.858**  |
| Spiders, open species abundance        |                                  |                |          |
| Patch size                             | $-0.033 \pm 0.120$               | 26             | 0.548    |
| Habitat amount                         | $-0.146 \pm 0.118$               | 89             | 2.443*   |
| Edge length                            | $0.191 \pm 0.111$                | 100            | 3.375*** |
| Patch size: Habitat amount             | $0.022 \pm 0.107$                | 3              | 0.401    |
| Patch size: Edge length                | $0.009 \pm 0.091$                | 3              | 0.207    |
| Habitat amount: Edge length            | $0.036 \pm 0.163$                | 16             | 0.434    |
| Carabids, forest specialist abundance  |                                  |                |          |
| Patch size                             | $0.031 \pm 0.236$                | 18             | 0.263    |
| Habitat amount                         | $-0.236 \pm 0.302$               | 60             | 1.528    |
| Edge length                            | $0.267 \pm 0.283$                | 72             | 1.848    |
| Patch size: Habitat amount             | $0.190 \pm 0.234$                | 2              | 1.591    |
| Patch size: Edge length                | $0.186 \pm 0.216$                | 4              | 1.684    |
| Habitat amount: Edge length            | $0.179 \pm 0.408$                | 6              | 0.857    |
| Carabids, open species abundance       |                                  |                |          |
| Patch size                             | $-0.305 \pm 0.162$               | 100            | 3.666*** |
| Habitat amount                         | $-0.141 \pm 0.207$               | 31             | 1.335    |
| Edge length                            | $-0.030 \pm 0.182$               | 28             | 0.328    |
| Patch size: Habitat amount             | $0.002 \pm 0.227$                | 3              | 0.020    |
| Patch size: Edge length                | $0.178 \pm 0.224$                | 16             | 2.312*   |

Note: Multimodel estimate  $\pm$  95% confidence interval; relative importance and  $z$  values are given.

\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

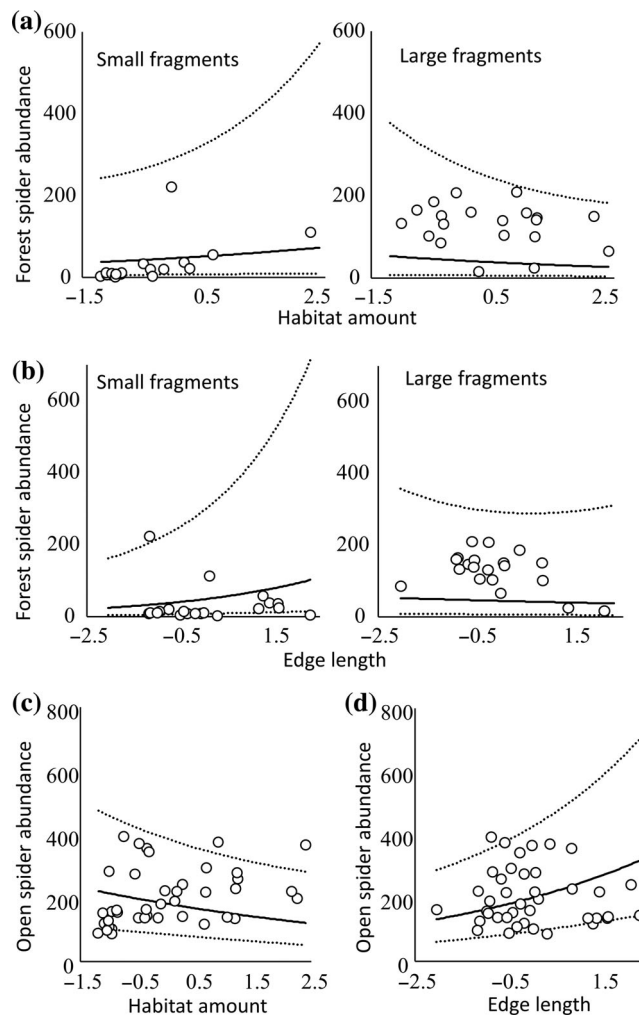


**FIGURE 3** Response of open-habitat plant species richness (SpR) to landscape variables predicted by the averaged linear mixed-effects models. The interactive effect of habitat amount and fragment size on open habitat species richness is shown. Dotted lines represent the 95% confidence intervals. Values for habitat amount are scaled. (a) Small fragments: size from 0.1 to 0.75 ha; (b) large fragments: from 0.9 to 3 ha

negative effect on the open-habitat carabids if landscape configuration was simple (i.e., the cumulative forest edge length was lower).

Our results showed that the naturally heterogeneous forest-steppe landscapes harbor high diversity, where we recorded almost 170 plant species, identified 125 spider and 73 carabid species. In general, the species pool of a landscape increases with increasing landscape heterogeneity (Dengler et al., 2014) due to the higher variation of available habitat patches (Lindenmayer & Fischer, 2013). Several Eastern-European and Central-Asian studies also demonstrated that small-scale landscape heterogeneity in forest-steppes has positive effects on plant (Feurdean et al., 2015; Kämpf et al., 2016) and invertebrate diversity (Dedyukhin, 2015; Hauck et al., 2014). Furthermore, number of different edge types and their length may also increase with increasing landscape heterogeneity (Ries et al., 2004). This in turn affects communities, populations, species interactions, and ecosystem processes resulting in a higher diversity of the landscape (Ries et al., 2004).

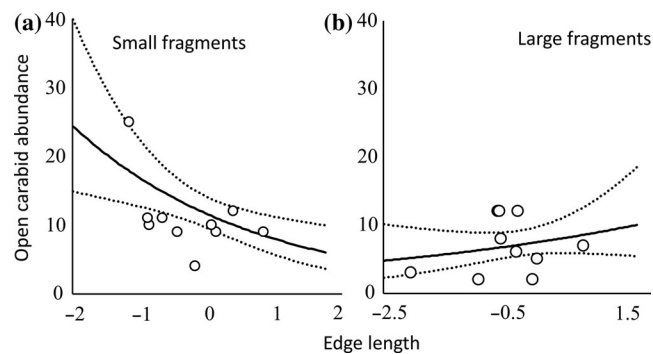
Generalist plants find more habitat types suitable than specialists, therefore they are presumably less affected by landscape filters due to their wide habitat breadth and high propagule availability (Deák et al., 2018). In contrast to generalists, the distribution of specialist plant species indicates naturally landscapes consisting of suitable and unsuitable habitats (Devictor et al., 2008; Gil-López et al., 2016). We detected rather low numbers of forest specialist plant species per site (in general only six). Forest specialist plant species represented less than 35% of the total plant species richness. Large forest patches should promote the occurrence of many forest specialist species (Kimberley et al., 2014). However, a major part of the relatively poor forest specialist species pool is



**FIGURE 4** Response of spiders to landscape variables predicted by the averaged linear mixed-effects models. (a) The interactive effect of habitat amount (i.e., amount of forest in the landscape) and fragment size on forest specialists. (b) The interactive effect of edge length and fragment size on forest specialist. (c) The effect of habitat amount (i.e., amount of forest in the landscape) on open-habitat spiders. (d) The effect of edge length on open-habitat spiders. Abundance values are shown on separate bar. Values for habitat amount and edge length are scaled. Dotted lines represent the 95% confidence intervals. Small fragments: size from 0.1 to 0.75 ha; large fragments: from 0.9 to 3 ha

presumably present even in the small fragments with low forest habitat amount. This is in line with Erdős, Kröel-Dulay, et al. (2018) who also found a relatively low number of forest specialist plant species in fragments of dry forest-steppe mosaics. However, the number of steppe specialist plant species is high in Central-European forest-steppes (Erdős, Ambarlı, et al., 2018; Erdős, Kröel-Dulay, et al., 2018). In contrast to the predictions of the habitat amount hypothesis (Fahrig, 2013) and island biogeography theory (MacArthur & Wilson, 1967), we found no effect on forest specialist plant





**FIGURE 5** Response of open-habitat carabids to landscape variables predicted by the averaged linear mixed-effects models. The interactive effect of fragment size and edge length is shown. Values for edge length are scaled. Dotted lines represent the 95% confidence intervals. (a) Small fragments: size from 0.1 to 0.75 ha; (b) large fragments: from 0.9 to 3 ha

species. However, we showed that open-habitat species richness was low in landscapes with high amount of forest habitat. Furthermore, the significant interaction between forest habitat amount and fragment size indicated that larger fragments have less open-habitat plant species if the forest habitat amount is high in the landscape.

We collected a high number of nonforest arthropods in the fragments, indicating the permeability of forest edges for open-habitat species. Spillover of organisms across habitat boundaries changes the species composition of the biota of forest fragments (Ruffell et al., 2017; Tölgyesi et al., 2018). The relatively small fragments and the open canopy (approximately 50%–80% canopy cover) of the dry forests of the present study experienced significant spillover from the adjacent grassland matrix, as also demonstrated for several arthropod assemblages (Rand et al., 2006). Matthews et al. (2014) found that the ratio of specialists to generalists generally increases with fragment area, thus nonforest species may respond positively to open habitat area, as they are able to utilize resources outside the fragment (Lindenmayer & Fischer, 2013). In the present study we also demonstrated the positive effect of landscape configurational heterogeneity on spider abundances, indicating that spider assemblages in forests are affected by higher rates of spillover from the adjacent grasslands if forest shape is more complex. Spillover may have a stronger effect on species composition in a specific interval of the habitat amount gradient (Martin et al., 2019).

Fragment size and landscape composition may have an interacting effect on the abundance and richness of species of various arthropod groups (e.g., Inclán et al., 2014; Öckinger et al., 2012; Tscharrntke et al., 2012; Watling & Donnelly, 2006). The interacting effect of

fragment size and forest habitat amount, which we confirmed for forest specialist spiders and open-habitat plant species, emphasize that small habitat fragments embedded in matrix-dominated landscapes are poorly connected. In large fragments, the increased resource availability and microhabitat diversity allow larger abundances of specialists (Ricklefs & Lovette, 1999). In contrast, specialist spiders and carabids are poorly represented in small fragments as they face a higher extinction rate due to stochastic effects, causing a decline in species richness (Genua et al., 2017; Lande, 1993). It has also been demonstrated that the species richness of spiders and carabid beetles may increase with decreasing fragment size as open-habitat species move into small fragments (Halme & Niemela, 1993; Usher et al., 1993). Generalist and open-habitat species may mask the decline in specialists in small fragments or when forest habitat amount is low if only species richness or abundances are measured rather than specialization; thus, the most frequently used metric to detect fragmentation effects, species richness, is confounded by compositional shifts in assemblage structure (Matthews et al., 2014).

Matrix quality can strongly influence the biodiversity of fragmented landscapes and may even override the influence of fragment area (Kupfer et al., 2006). The permeability of the matrix is measured by the structural similarity between fragments and any surrounding matrix, which may severely affect cross-matrix connectivity by constraining the probability of movement among fragments and colonization rates of populations (Prevedello & Vieira, 2010). Although spiders can colonize suitable habitat fragments by passive airborne dispersal (ballooning) and carabids by flying, many species rely on groundborne movements to traverse the matrix between forest fragments (Oxbrough & Ziesche, 2013). Dispersal processes may be more influenced by matrix permeability than distance between fragments (Watling et al., 2011), but this effect is negligible if the habitat amount is high (Ruffell et al., 2017). In the present study we consider grasslands relatively high-quality matrix for forest specialist biota, as well. The matrix is a natural element of the forest-steppe without significant human disturbance and the grassland matrix is a high-quality habitat for its specialized open habitat biota bearing a high nature conservation value. The nondisturbed grasslands may have a relatively high matrix permeability providing food and temporary shelter for forest arthropods.

Although our study was restricted to forest fragments, our findings revealed that fragment size, landscape compositional and configurational heterogeneity play a major role in shaping the diversity of both the herbaceous vegetation and the assemblages of spiders and carabids in the Central European forest-steppes. According to our

knowledge, our result is the first one to show that the diversity of forest-steppes depends not only on fragment size and landscape heterogeneity but also on their interaction, that is, landscape heterogeneity effect was modified by fragment size. In contrast to the habitat amount hypothesis, our results suggest that fragment size and landscape configuration substantially determine biodiversity patterns. Keeping the intact steppe matrix and the summed cover of forest fragments in the forest-steppe landscape is not enough to maximize diversity but an effective conservation strategy should also take into account the size and configuration of the forest fragments.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Gallé et al., 2021) are available from Zenodo: <https://doi.org/10.5281/zenodo.5668035>.

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