# THE EFFECT OF HABITAT FRAGMENTATION AND ROAD VERGES ON COMPOSITION OF PLANTS AND INVERTEBRATES IN THE GREAT HUNGARIAN PLAIN

**Ph.D. THESIS**

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**FACULTY OF SCIENCE AND INFORMATICS**

**2021**

**SZEGED**

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1. AICc values: Akaike's Information Criterion correction for small sample size
2. ANOSIM: Analysis of similarities
3. CWM: Community weighted mean
4. FD: Functional diversity
5. GLMMs: Generalised linear mixed models
6. Ind. Values (IndVal): Indicator values
7. LLEs: Linear landscape elements
8. NMDS: Non-metric multidimensional scaling
9. perMANOVA: Permutational multivariate analysis of variance

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## Note to reader

This is a manuscript-based thesis. Efforts have been made to integrate the research articles into the chapters to make one coherent thesis with caution. Various parts of the thesis like material and methods, results, and discussion are directly taken from the research articles.

Chapter 3: Gallé R, Tölgyesi C, Torma A, Bátori Z, Lőrinczi G, Szilassi P, Gallé-Szpisjak N, **Kaur H**, Makra T, Módra G, Batáry P (2021) Matrix quality and habitat type drive the diversity pattern of forest steppe fragment. Perspect Ecol Conserv (accepted)

Chapter 4: **Kaur H**, Torma A, Gallé-Szpisjak N, Seat J, Lorinczi G, Modara G, Galle R (2019) Road verges are important secondary habitats for grassland arthropods. J Insect Conserv 23, 899–907 https://doi.org/10.1007/s10841-019-00171-9

# Chapter 1: General Introduction

The main cause of biodiversity decrease is habitat fragmentation, habitat loss, and land-use change. Habitat fragmentation is defined as the disintegration of the large intact areas of a particular vegetation type into smaller fragments (Lord and Norton 1990; Franklin et al. 2002). This also creates a matrix between the fragmented patches that may be unsuitable for breeding, shelter, or for finding food for animals, and as habitats for plants (Jules and Shahani 2003; Makeeva et al. 2005; Prugh et al. 2008). Furthermore, matrix creates a dispersal barrier for organisms (Olff and Ritchie 2002), it interrupts the exchange of individuals between populations resulting in small population sizes and interbreeding, eventually leading to their extinction with time. Conversion of the continuous habitat into disjunct habitat fragments usually increases the length of the edges between fragments and the matrix, which may affect the properties of edges and the flora and fauna of the fragments (Murcia 2005). The effect of habitat fragmentation depends upon the species, how they perceive it (Fischer and Lindenmayer 2007).

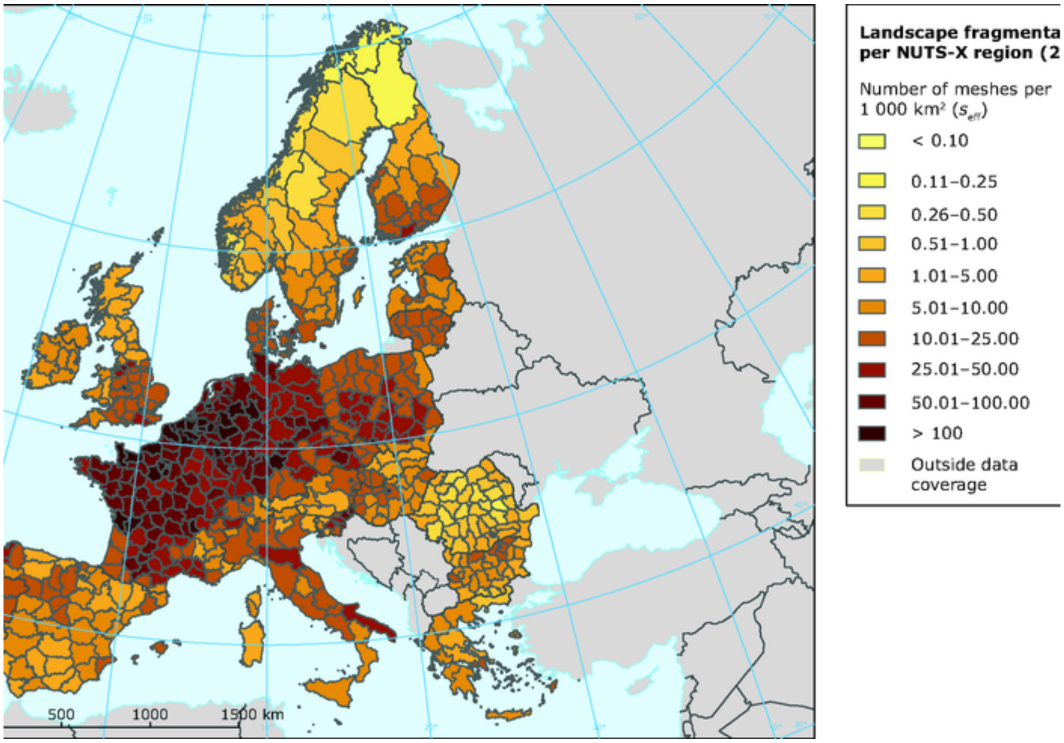


Fig. 1. Level of habitat fragmentation in Europe (Source: European Environmental agency /FOEN. 2011)

Hungarian forest-steppes of Kiskunság region is part of the large Eurasian forest-steppe region, which runs from the Pannonian lowland in the west (Europe) to China in the east (Asia) (fig.2). It is characterised by mosaics of native vegetation which includes poplar (*Populus alba*), oak forest patches (*Quercus robur, Q. pubscens*), and some shrub species such as *Crategus monogina* and *Juniperus communis,* with an open canopy embedded in dry grasslands dominated by drought-tolerant perennial grasses (e.g., *Festuca vaginata, Stipa borysthenica*) along with perennial herbs (e.g., *Alkanna tinctoria, Fumana procumbens*, and *Colchicum arenarium*) (Fekete et al. 2002; Erdős et al, 2015). It also includes the diversity of endemic, rare, and threatened plant species (e.g., *Dianthus diutinus, Artemisia pancicii, Astragalus wolgensis, Colchicum arenarium*), rare insects (e.g., *Myrmeleotettix antennatus, Hyponephele lupine*), and birds (e.g., *Coracias garrulus, Caprimulgus europaeus*) of community interest in the European Union (Habel et al. 2013; Kamp et al. 2016). Forest-steppes are recognized as important biodiversity hotspots (Habel et al. 2013; Dengler et al. 2012) and listed in the Habitats Directive (European Union 1992, codes: 91I0, 91N0, 6260). The climate in this region is continental (Erdős et al. 2018a). The area between the Tisza-Danube interfluve in southern Hungary receives mean annual precipitation between 500-550 mm, which is highest in June and November (Bohridi 1993). The annual mean temperature is ca. 10°C (Fekete et al. 2002). The bedrock is sandy and loess in nature. Steppe grasslands are open areas in sandy soil known to provide a relatively higher temperature of the soil surface that reaches up to 60°C and lower humidity during daytime than forests (Tölgyesi et al. 2020).

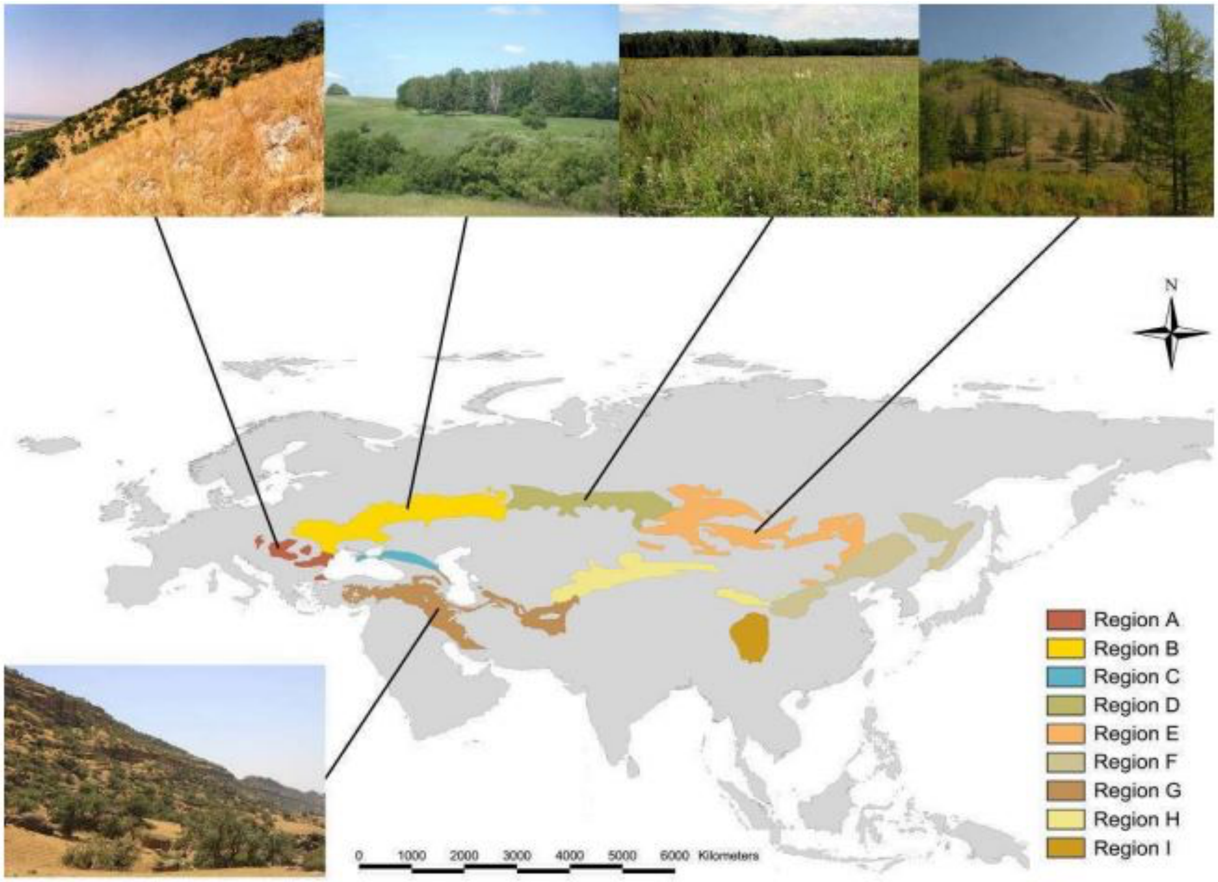


Fig. 2: The main forest-steppe region of Eurasia Southeast Europe (Region A), East Europe (Region B), North Caucasus and Crimea (Region C), West Siberia and North Kazakhstan (Region D), Inner Asia (Region E), Far East (Region F), Middle East (region G), Central Asia and Southwest Inner Asia (Region H), and Eastern Tibetan Plateau (Region I). (source: Erdős et al. 2019).

Anthropogenic activities leading to habitat modification, and habitat fragmentation are the main causes of biodiversity depletion in Hungary, as well. In the last few centuries, the majority of the natural forest and forest-steppes has been degraded or replaced with arable fields and tree plantations to meet the demands of the growing population, and to build new infrastructure, (Molnár et al. 2012). For example, by the end of the 20th-century majority of the natural forest-steppes in the Kiskunság region of the Hungarian Great Plain was replaced with plantations of pine (*Pinus sylvestris* and *P. nigra*) and black locust (*Robinia pseudoacacia*) (Rédei et al. 2008; Masón and Alía 2000; Erdős et al. 2018b) and become one of the most threatened habitats in Hungary (WWF report 2011). Grasslands were also destroyed during the previous century in Hungary. The formation of arable fields, construction advancement, and afforestation were the main drivers for grassland fragmentation and depletion. Natural grasslands changed to semi-natural grasslands due to overgrazing, mowing, and abandonment after intensive agricultural management (Biró et al. 2012).

Fragmentation of natural habitats not only depletes the native specialist species (Vandergast et al. 2004), but may also support invasive plant species, for example, forest-steppes in Hungary are invaded by species like *Asclepias syriaca*, *Solidago gigantea*, and *Ailanthus altissima* (Török et al. 2003). Invasive species can further reduce the fitness of the native species, also impacting the diversity, abundance, and intraspecific relations between the species (Barney et al. 2013). Fragmented and invaded habitats are generally occupied by generalist species of arthropods (Gibbs and Stanton 2001).

The quality of the landscape matrix around natural habitats is an important determinant of biodiversity. Low-quality matrix can restrict the movement of the species (Fischer and Lindenmayer 2007), whereas a high-quality matrix can provide temporary shelter. It can also provide passage for dispersal of species among the scattered habitat patches in the landscape (Gilbert et al.1998; Tscharntke et al. 2012). The functional properties of the matrix depend upon the level of human impact (Franklin 1993).

Connectivity of the fragmented patches in the matrix is important to minimize the adverse effect of habitat fragmentation. It is the property of landscape that emerge from the interaction between the landscape structure (landscape composition and configuration of landscape mosaic) and its function (Leitao et al. 2006). The role of linear landscape elements (LLE) such as road verges, hedgerows, powerlines corridors, and field margins are important in maintaining structural connectivity and conserving biodiversity (Hollmen et al. 2008; Noordijk et al. 2008; Hahn et al. 2014). They may provide corridors to facilitate free movement from one patch to another in highly modified landscapes. Occasionally, they may also act as suitable habitats themselves in degraded landscapes and provide appropriate habitats for many species, hence promoting biodiversity (McGuire et al. 2016). Indeed, road verges were shown to have an important role in conserving the arthropod fauna, rodents, and birds in highly modified habitats they can increase the connectivity, and minimise the fragmentation effect. (Joyce et al. 1999; Rondinini and Doncaster 2002). However, the effect of road verges can be negative as well. Creation of roads and road verges in native habitats may lead to fragmentation (Vermeulen 1994; Fuller et al. 2013).

The change in community composition, and structure of herbaceous vegetation are useful indicators of landscape changes such as, fragmentation, modification or grazing (Landsberg and Crowley 2004). Plants form an important component of terrestrial foodwebs as producers and provide primary structure of habitats for many species of arthropods. Arthropods are also widely used as indicator groups in conservation studies, as their communities are abundant and highly diverse in all types of terrestrial, and aquatic habitat. They interact with various other groups and are important mediators of ecosystems (Lavelle et al. 2006; Maleque et al. 2006). In our study, we focused on the vegetation and three arthropod taxa, spiders (Araneae), true bugs (Heteroptera), and ants (Hymenoptera: Formicidae).

Spiders are among the most abundant invertebrate predators, that play a decisive role in the regulation of other invertebrate communities in almost every terrestrial ecosystem including man-made habitats like planted forest (Clarke and Grant 1968; Moulder and Reichle 1972; Weeks and Holtzer 2000). The diversity of spider assemblages is affected by several habitat-scale environmental factors such as vegetation structure, moisture, and shading. Forest spiders are further affected by leaf litter cover, depth, and canopy cover (Ziesche and Roth 2008, Gallé et al. 2017b). Canopy cover and habitat structure provide them certain microclimatic and habitat conditions such as suitable temperature, moisture, and light intensity (Antvogel and Bonn 2008).

True bugs are the largest and most diverse group of hemimetabolous insects. They comprise phytophagous, zoophagous, and omnivorous feeders (Fauvel 1999). Their presence in particular habitat reflects the habitat condition. It primarily determined host plants for phytophagous and omnivorous species, whereas vegetation structure and prey availability specify the suitable habitat for zoophagous species (Gallé et al. 2010).

Ants are a highly diverse and abundant arthropod group, they are sensitive to change in the environment such as humidity, temperature, soil, and vegetation type (Hoffmann 2010). They play a complex role as predators, herbivores, seed-dispersal agents, and soil engineers (Hölldobler and Wilson 1990). Any change in their micro or macrohabitat such as shading effect, soil type, or vegetation cover directly affects their community structure in nature (Andersen et al. 2002). Ants respond quickly to changes in their habitat such as the clearing of forests (Majer et al. 1997), road construction (Lassau and Hochuli 2004), anthropogenic disturbances, or agricultural practices (Evans et al. 2011).

# Chapter 2: Aims

The purpose of this dissertation is to understand the species composition and diversity of arthropods in the highly modified landscape in the Great Hungarian Plain between Danube–Tisza Interfluve in southern Hungary. More specifically, we aimed to reveal:

(1) The effect of landscape quality and habitat type on the diversity pattern of flora and arthropod fauna of the Hungarian forest-steppe fragments (Chapter 3).

(2) The importance of road verges in the planted forest on conserving arthropod fauna of the Great Hungarian Plain (Chapter 4).

# Chapter 3

## Effect of landscape quality and habitat type on the diversity pattern of flora and arthropods of the Hungarian forest-steppe fragments

Landscape quality characterizes the compositional heterogeneity of the landscape, it considers both the quality of the matrix, and the habitat fragments within the landscape. Landscape quality is usually expressed as the sum of the area of different land cover types weighted by their suitability for organisms (Jeanneret et al. 2003; Löffler and Fartmann 2017; Galán-Acedo et al. 2019). It affects connectivity between habitat fragments (Watling et al. 2011), higher landscape quality assumes that landscape elements have a lower movement barrier effect and result in higher dispersal rates and lower isolation of fragments (Öckinger et al. 2012a). Regular immigration due to higher dispersal rates can help to avoid stochastic extinctions of populations with low abundance in small fragments, thus landscape quality may exert a stronger effect on small fragments than on large fragments.

This may also have a key effect on the variation of the species composition of habitat fragments, i.e., beta-diversity (Legendre 2008), which was first introduced by R.H. Whittaker (1960), who explained this as a ratio between the regional and local species diversity. Several frameworks exist to characterise the pattern of species distribution by partitioning beta diversity into its two components (Baselga 2012; Carvalho et al. 2013; Podani and Schmera 2011). Following that of Baselga (2012), the two components of beta diversity are, (1) species turnover, and (2) nestedness (Fig.3). Turnover is related to the replacement of species between communities by some other species due to the presence of any barrier or selective differentiation (Baselga et al. 2009), whereas nestedness expresses to what extent one community is a subset of another bigger one (Baselga and Orme 2012). Their relative importance may change according to the processes structuring metacommunities (Brendonck et al. 2015; Tonkin et al. 2016). Beta diversity and its nestedness component between connected habitats in relatively homogeneous landscapes is assumed to be low (Gianuca et al. 2017). Random extinctions may contribute to nestedness, however, increasing dispersal rates between fragments reduces differences in species composition resulting in homogenization of the metacommunity (Declerck et al. 2012; Samu et al 2018). Differences between the species composition of highly isolated fragments are mainly due to species turnover. Stochastic drift in species composition and the colonization of matrix species are the two main drivers of this phenomenon (Collins et al. 2017).

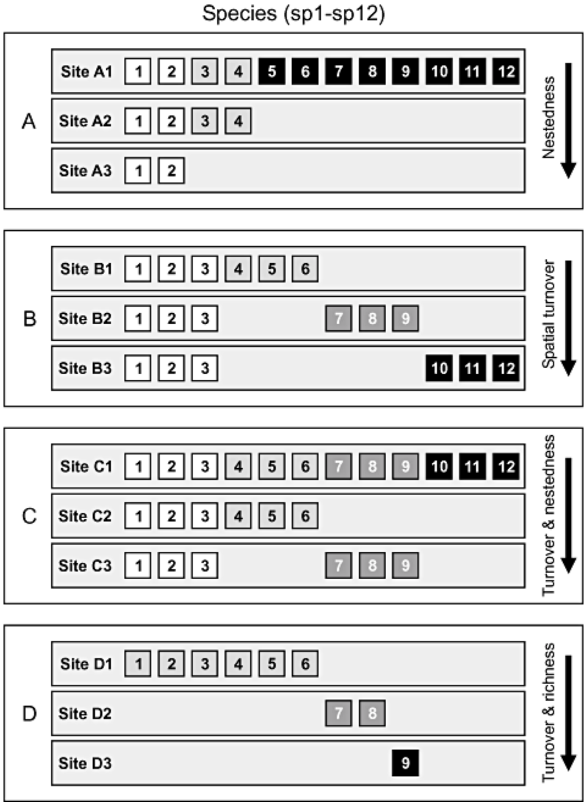


Fig.3 Hypothetical examples involving four islands (A–D) and three sampling sites in each. Biotas of sites A1–A3 are completely nested, because poorer biotas are subsets of richer biotas. Sites B1–B3 have the same richness (six species each) with three species common to all three sites and three species exclusive to each site, i.e., displaying a pattern of spatial turnover. Sites C1–C3 present both patterns, because C2 and C3 are subsets of C1 (nestedness), but some species are replaced between C2 and C3, which are not subsets of each other. Sites D1–D3 present spatial turnover and are not nested, but present differences in richness. Source: Andres Baselga, 2009 ( https://doi.org/10.1111/j.1466-8238.2009.00490.x)

Different habitat types create a gradient of plant and presumably invertebrate species richness in forest-steppe (Erdős et al. 2020), forests, and steppe grasslands have different physical conditions (Anenkhonov et al. 2015; Tölgyesi et al. 2018 a), resulting in different communities that harbour a high species diversity with numerous rare and endemic species. They are among the most threatened ecosystems in Central Europe due to habitat loss and fragmentation. As mentioned earlier, majority of forest-steppe mosaics of the region have been transformed into commercial plantations of exotic (mainly *Pinus sylvestris* and *P. nigra*), and native tree species (*Populus alba*) with low habitat heterogeneity (Erdős et al. 2018b). The dense canopy of plantations decreases the light availability on the forest floor resulting in lower understory biomass, moist, and sheltered microclimate, and a homogeneous habitat structure (Balandier et al. 2006). Contrarily, native forest-steppes are characterized by small-scale habitat heterogeneity and high microhabitat diversity, due to the dynamic mosaic structure of the two prevailing physiognomic units, forests, and steppes.

In the present study, we focused on plants, spiders, and ants. We aimed to understand current community composition and species richness patterns in highly modified forest-steppe regions by focusing on the three main habitat types, steppes, and forests of the forest-steppe fragments (hereafter 'steppes' and 'forests') and the most abundant habitat type of the landscape matrix, pine plantations (hereafter 'plantations'). More specifically, we tested the following hypotheses: (1) Steppes are more isolated than forests amidst the plantation-dominated landscape matrix, thus species turnover is larger and nestedness is smaller between steppe than between forest stands of isolated habitat fragments. (2) Increasing landscape quality (i.e., higher share of semi natural in the landscape) has a stronger positive effect on species richness of steppes than that of the forests, furthermore, it has a stronger positive effect on species richness of small fragment than large fragments.

## 3.1 **Material and methods**

### **3.1.1** Study region and Sampling design

Our study was conducted in the southern part of Hungary, in the Danube–Tisza Interfluve (47.1625°N, 19.5033°E, elevation approximately 100 m asl). The climate is continental with some Mediterranean influence (Borhidi 1993). Mean annual precipitation is 500–550 mm, which decreases from NW to SE, and the mean annual temperature is ca. 10 °C with a semi-arid period in late summer (Fekete et al. 2002). The dominant soil types are various calcareous soils with high sand and low moisture content. The main natural habitat type of the study region is a forest-steppe (Fig.4).

In our study region, only small and isolated forest-steppe fragments have been spared from large-scale landscape modification. We selected a total of 18 landscapes near the villages of Pirtó (n = 9), Kéleshalom (n = 4), and Bócsa (n = 5), and selected small forest-steppe fragments within each landscape, ranging from 0.2 to 6.0 hectares in size. We established a sampling site in the forest habitat and in the steppe habitat of each forest-steppe fragment and another site in their close vicinity in the landscape matrix, which was in all cases a pine plantation (n = 18 × 3 = 54 sampling sites) (Fig. 5a). We drew buffer circles with a radius of 500 m around each sampling site within the landscape with ArcGIS 10.1 software and measured the area of patches of different land cover types within the buffers using Google Earth satellite images. We applied five categories and gave the largest value to the highest quality patches: (1) highly disturbed land cover patches: arable fields, farm buildings, young plantations (less than 5 years old); (2) pine plantations; (3) intensively managed poplar plantations; (4) extensively grazed pastures and (5) intact forest-steppes (Gallé et al. 2017a, 2018b; Ingle et al. 2019) (Fig. 5b, c). We expressed the landscape quality by weighting the percentage cover of each land cover type with the rank of the given habitat type (Tölgyesi et al. 2014, Wildi 2016).

Fig. 4. Natural forest-steppes and their edge.

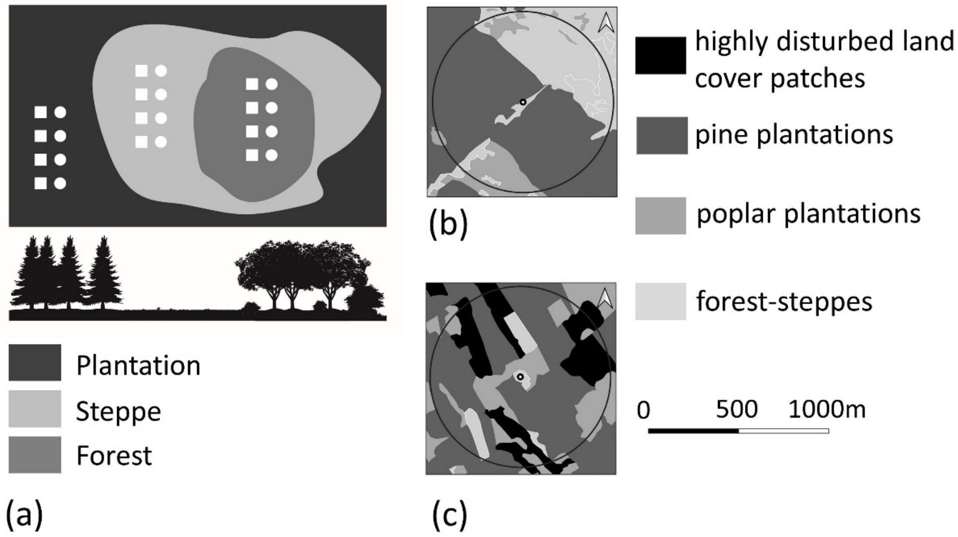


Fig 5. Study design. (a) sampling design, squares: botanical plots, circles: pitfall traps; (b) high-quality landscape; (c) low-quality landscape

### 3.1.2 Community sampling methods

We recorded all herbaceous plants and shrubs in four 2 m × 2 m plots in each sampling site and estimated their percentage cover in June 2018 (18 landscape × 3 habitat type × 4 replicates = 216 plots, Fig 5.a.). Plots were located in the centre of the forest and in steppe habitat and at least 30 meters from the edge in the case of pine plantations and were approximately 8 m apart from each other. We pooled the species data according to sampling sites resulting in 54 statistical samples.

We collected arthropods (spiders and ants) using pitfall traps (500-ml white plastic cups, 8.5 cm in diameter). We fitted the traps with transparent plastic funnels to reduce vertebrate bycatches and increase trapping efficiency (Császár et al. 2018). We filled them with 50% ethylene–glycol and water solution containing a few drops of odourless detergent to preserve the sample and to reduce the chance of escaping. We placed a plastic roof above each trap to prevent the dilution of the preservative. At each sampling site, we employed four pitfall traps, spaced 8 m apart, along a transect running parallel with the edge of the sampled habitat. The pitfall traps were placed circa. 1-2 meters from botanical plots (Fig. 5a). We installed a total of 216 traps (18 landscapes × 3 habitat type × 4 traps). We conducted sampling in three periods, from 4th to 18th May, from 14th to 26th June, and from 20th September to 5th October in 2018. We stored the collected invertebrates in 70% ethanol, and identified adult individuals to species level. For further analysis, we pooled the species data according to sampling sites, resulting in 54 statistical samples.

### 3.1.3 Data analysis

We compared the composition of plant, spider, and ant communities in the three habitats (i.e., forests, steppes, and plantations) with permutational multivariate analysis of variance (perMANOVA) using 5000 permutations. We visualized the community composition of the sampling sites with non-metric multidimensional scaling (NMDS) with Bray-Curtis distance using the vegan package (Oksanen et al.  2015) in R environment (R Core Team 2019). We applied Hellinger transformation on the data before the analysis (Legendre and Gallagher 2001). We used indicator value analysis to identify the characteristic species of plants, spiders and ants in forests, steppes, and plantations, with ‘labdsv’ package in R version 1.2.5042 (Roberts and Roberts 2016).

We evaluated possible correlations between spider, ant, and plant species composition with Mantel tests. We performed tests using Bray-Curtis distance matrices and 10000 permutations for forests, steppes, and plantations separately using the vegan package (Oksanen et al., 2015).

We calculated beta diversity for the natural habitat types, between forests, and between steppes, respectively, and decomposed it into turnover and nestedness components using two approaches. First, applying the incidence-based multiple-site dissimilarity approach, we calculated the replacement (related to turnover) and nestedness-resultant components for species compositional heterogeneity and overall beta diversity using R-package betapart (Baselga and Orme 2012) calculated with Sørensen dissimilarity index. Second, with abundance-based dissimilarity we separated balanced variation in abundance (related to turnover) and abundance gradients (related to nestedness) with Bray-Curtis dissimilarity index (Baselga 2017). We revealed the differences in turnover components of forests and steppes with 500 random sampling procedures. We resampled the two incidence-based and the two abundance-based multiple site dissimilarities for a subset of ten steppe and forest sites of the original data frame using the R-package betapart (Baselga and Orme 2012). We divided the turnover component with the total beta diversity for each random sample (Dobrovolski et al. 2012) and this turnover ratio was tested with one-way ANOVA to reveal differences between forests and steppes. We ran the above analysis for plant, spider, and ant data separately.

We categorized all species according to their habitat affinity to habitat specialist (i.e., grassland species for steppes and forest species for forests and plantations), and generalists. We used GLMMs (Generalised linear mix models) to determine the effect of habitat type (i.e., forest, steppe, and plantation), landscape quality (measured in 500 meters radius buffer), fragment size, and their first order interaction on the species richness and specialist species richness of the herb layer and arthropods with ‘village’ as random effect (true spatial replicates). Continuous fixed variables (i.e., matrix quality and forest-steppe size) were measured on different scales, thus, prior to analysis, they were ranged between 0 and 1. We used Poisson distribution error term in the models. We ran GLMMs for all possible combinations of predictor variables, and calculated AICc values (Akaike’s Information Criterion with correction for small sample size). We performed model averaging on models with a delta AICc $\leq 6$ of the best models (Burnham and Anderson 2002) using the R-package MuMIn (Barton 2012). To control the potential effect of outliers we used Cook’s distance for each sampling points and AICc values were checked again after the removal of influential points (Zuur et al. 2009).

## 3.2 **Results**

We recorded 164 plant species in the 54 sampling sites of the 18 landscapes. The most abundant graminoids were *Festuca vaginata*, *Stipa borysthenica* and *Carex liparicarpos*. Common forbs included *Teucrium chamaedrys*, *Potentilla arenaria* and *Euphorbia seguieriana* (Appendix Table 1). We collected 5595 adult spiders of 111 species. The most abundant ones were *Pardosa alacris*, *Alopecosa sulzeri*, and *Zelotes apricorum* (Appendix Table 1). Finally, we collected 8773 ants belonging to 32 species, with *Lasius psammophilus*, *Plagiolepis Taurica,* and *Myrmica sabuleti* being the most abundant species (Appendix 1).

Community composition of plants, spiders, and ants was influenced by habitat type (Fig. 6, Shepard diagrams for two dimensional MNDS plots are given in Appendix Figure 1). We found significant differences in the species composition of the three habitat types according to the perMANOVA analyses, with the most expressed differences between steppe and the other habitat types (Table 1). We identified high number of indicator species of forest (plants:19; spiders: 7, ants: 2 species) and steppes (plants: 24, spiders: 9, ants: 5 species), but relatively low number for plantations (plants:0; spiders: 6, ants: 4 species) (Appendix Table 1).

We found significant correlation between vegetation and spider community composition for forest and steppe sites, however spiders of plantations and ants did not show relationship with vegetation composition according to the perMANOVA analyses (Table 2).

The turnover component of beta diversity was higher for steppes than for forests both in the case of incidence-based and abundance-based approaches, i.e., we found higher patchiness of the steppe habitat compared to forests or plantations (Fig. 7, Table 3.). Plant species richness was highest in forests followed by steppes and it was the lowest in plantations according to the GLMM models, furthermore, landscape quality had a negative effect in small fragments, but this effect was positive in large fragments (Fig. 8, Appendix Table 2). We found higher specialist plants species richness in steppes followed by forests and plantations and we found similar interacting effect of landscape quality and fragment size to total plants species richness (Fig. 9, Appendix 3). We found higher species richness of spiders in steppes than is plantations and landscape quality had a positive effect on them (Fig. 10, Appendix Table 2). However, specialist spider species richness was the highest in steppes followed by plantations and forests (Fig. 11). We found no significant effects on ants, yet we detected more specialist ant species in plantations than in steppes (Appendix Table 2). Non-significant relations are plotted in Appendix Figure 2.

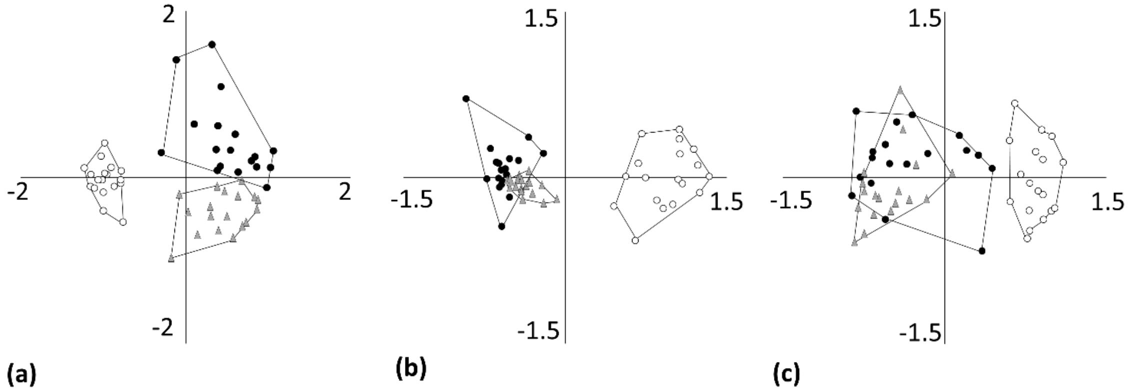


Fig. 6. Ordination plots of non-metric multidimensional scaling. (a) plants, (b) spiders, (c) ants. Open circles: steppes, grey triangles: forests, black dots: plantations. Stress values for all NMDS ordinations were low (vegetation: 0.15; spiders: 0.09; ants: 0.13). Shepard diagrams are given in Appendix 2.

Table 1. Pairwise differences between species composition of forests, grasslands, and pine plantations according to the perMANOVA analyses

| | Vegetation | | | Spiders | | | Ants | | |
|---|---|---|---|---|---|---|---|---|---|
| | $R^2$ | F | p | $R^2$ | F | p | $R^2$ | F | p |
| Steppe-forest | 0.388 | 21.59 | <0.001 | 0.542 | 40.38 | <0.001 | 0.434 | 26.12 | <0.001 |
| Forest-plantation | 0.148 | 5.79 | <0.001 | 0.119 | 4.61 | 0.002 | 0.107 | 4.07 | <0.001 |
| Plantation-steppe | 0.393 | 21.58 | <0.001 | 0.511 | 35.57 | <0.001 | 0. 370 | 20.05 | <0.001 |

[a] $**p < 0.01$, $***p < 0.001$

Table 2. Correlation between spider, ant community composition, and vegetation according to Mantel tests (Bray-Curtis distance, 10000 permutations)

| | Spiders - vegetation[a] | | Ants[a]-vegetation | |
|---|---|---|---|---|
| | Mantel r | p | Mantel r | p |
| Forests | 0.221 | 0.024 | 0.138 | 0.163 |
| Steppes | 0.225 | 0.020 | 0.050 | 0.291 |
| Plantations | 0.078 | 0.294 | 0. 067 | 0.708 |

[a] $^{**}p < 0.01$

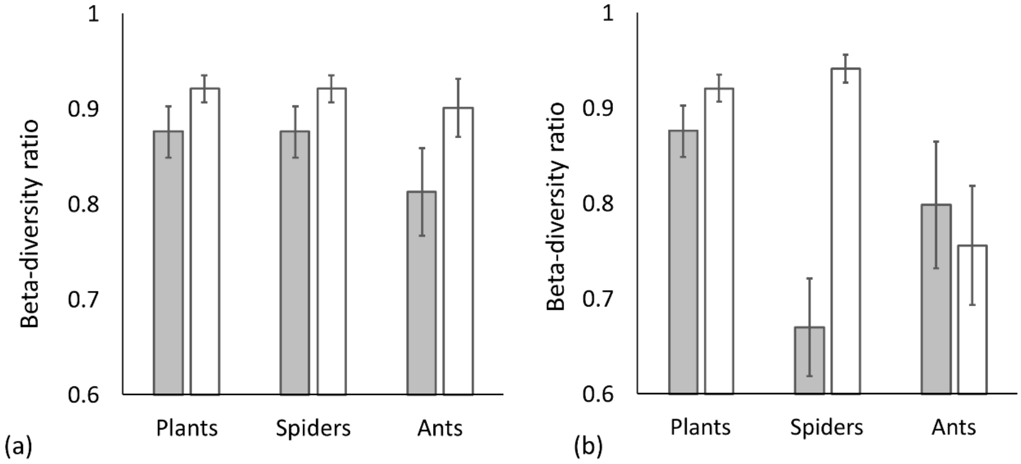


Fig. 7. The beta-diversity ratio measured as the ratio of turnover component and total beta diversity (a) abundance based approach, (b) incidence based approach. Grey bars represent forests (mean ± sd) and white bars represent steppes (mean ± sd). All differences are significant ($p<0.001$) according to the one-way ANOVAs.

Table 3. Differences in turnover ratios between forests and steppes according to the ANOVA.

| | Vegetation | | Spiders | | Ants | |
|---|---|---|---|---|---|---|
| | F | p | F | P | F | p |
| Incidence based turn-over ratio | 6067 | < 0.001 | 958.9 | < 0.001 | 1341 | < 0.001 |
| Abundance-based turnover ratio | 656.1 | < 0.001 | 12264 | < 0.001 | 137.4 | < 0.001 |

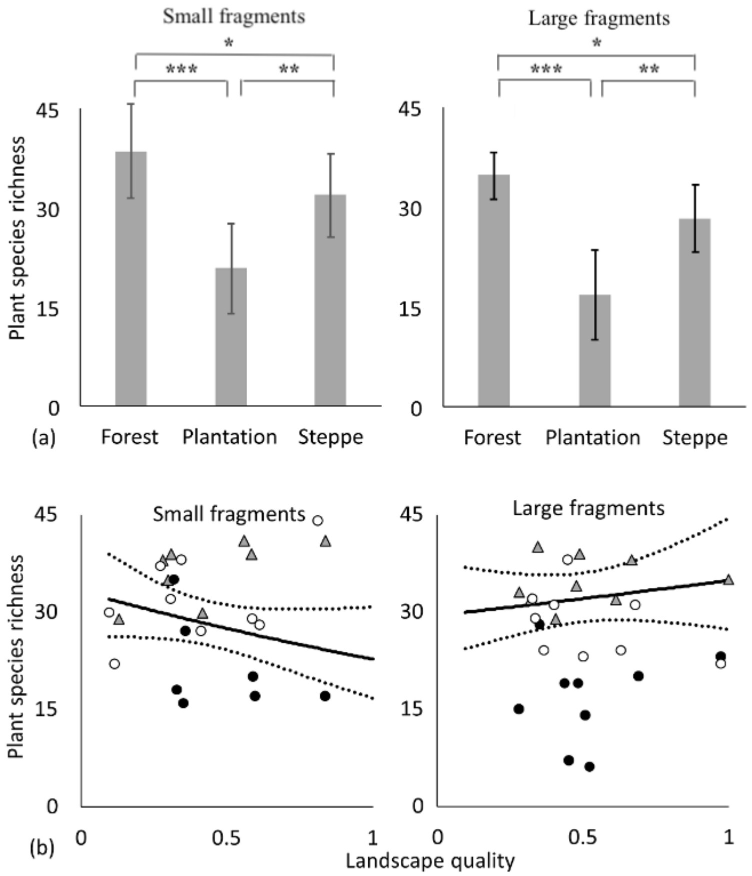


Fig. 8. Effect of habitat type, landscape quality, and fragment size on the species richness of plants. (a) interaction of fragment size and habitat type (mean ± sd), (b) interaction of landscape quality and fragment size. Small fragments: size from 0.24 to 0.75 hectares; Large fragments: size from 1.1 to 6.0 hectares. Values for landscape quality index are ranged between 0 and 1. Dotted lines represent the 95% CI intervals. Open circles: steppes, grey triangles: forests, black dots plantation

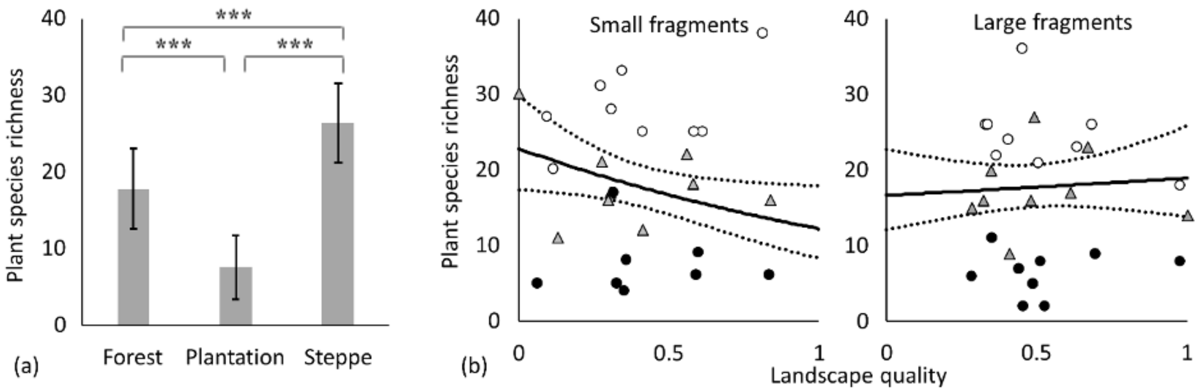


Fig. 9. Effect of habitat type, landscape quality, and fragment size on the species richness of specialist plants. (a) habitat type (mean ± sd), (b) interaction of landscape quality and fragment size. Small fragments: size from 0.24 to 0.75 hectares; Large fragments: size from 1.1 to 6.0 hectares. Values for landscape quality index are ranged between 0 and 1. Dotted lines represent the 95% CI intervals. Open circles: steppes, grey triangles: forests, black dots plantation.

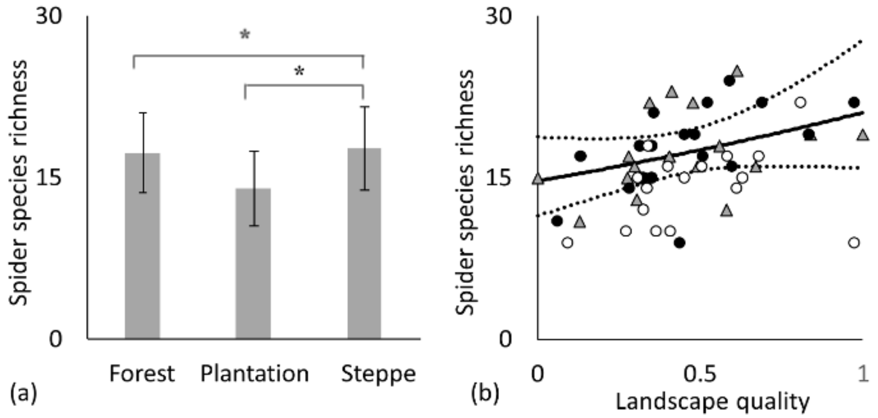


Fig. 10 Effect of habitat type and landscape quality on the species richness of spiders. (a) habitat type (mean ± sd), (b) landscape quality. Dotted lines represent the 95% CI intervals. Open circles: steppes, grey triangles: forests, black dots plantation.

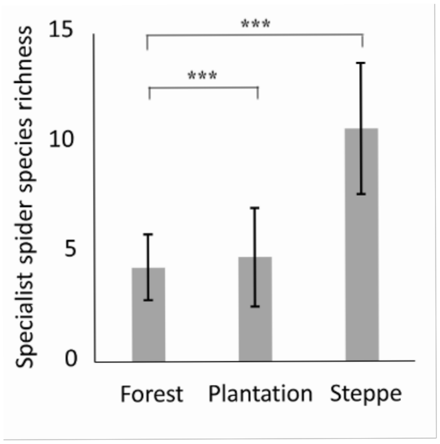


Fig. 11. Effect of habitat type on the species richness of specialist spiders (mean ± sd)

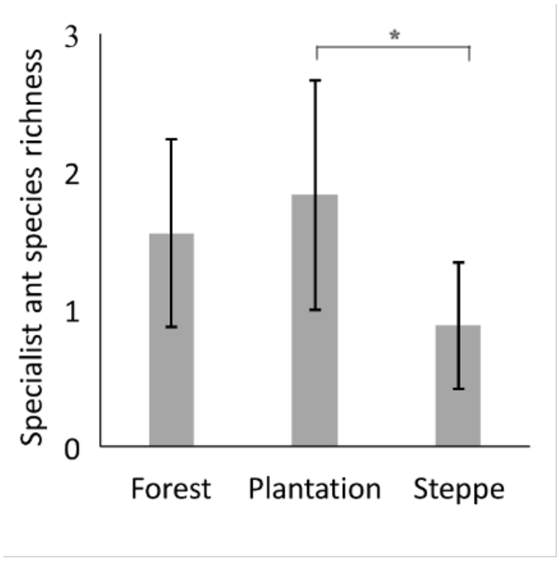


Fig. 12. Effect of habitat type on the species richness of specialist ants (mean ± sd)

### 3.3 Discussion and conclusions

The species composition of plantations was more similar to that of the forests than the steppes. We found higher turnover ratios for steppes than for forests for all taxa, indicating that steppes are more isolated than forests (hypothesis 1). We could not confirm hypothesis (2), as we did not find a stronger landscape quality effect on species richness of steppes compared to forests, although, landscape quality affected both plant and spider species richness.

We found a clear separation of the biota of focal habitat types. The composition of plants in the three habitat types was different. Numerous studies showed significant differences between the vegetation structure and plant species composition of forests, steppes in forest-steppe and plantation ecosystems (e.g Bátori et al. 2018; Erdős et al. 2014, 2018b). We found that the species richness of plantations was less than half of the species richness of the forests and this was true for the specialist species richness, presumably due to the thick and allelopathic litter layer of pine needles, and the low water and light availability in the forest floor of the plantations (Selvi et al. 2017; Tölgyesi et al. 2020). The dominant plant species of these plantations were mainly generalist, disturbance tolerant species (e.g., *Calamagrostis epigejos* and *Poa angustifolia*), and invasive (e.g., *Asclepias syriaca*), indicating that pine plantations are very low-quality secondary habitats for natural vegetation (Csecserits et al. 2016; Rédei et al. 2020).

The arthropod species composition of the three habitat types was also significantly different. However, plantations and forests have similar composition for both spiders and ants, according to NMDS. Interestingly, we found higher spider species richness in plantations than in steppes. Steppes formed on sandy soils are characterized by harsh microclimatic conditions with high and fluctuating ground temperature (maximum summer temperature of bare ground can exceed 60 °C) and low air humidity (Kovács-Láng et al. 2000; Erdős et al. 2014). The hot and dry conditions favour invertebrate species with certain trait state combinations (e.g. xerotolerant and thermophilous species), and serve as a strong environmental filter (Gallé et al. 2018b). A relatively small number of specialist invertebrate species can colonize such habitats (Gallé and Torma 2009). In line with Gallé et al. (2018a) and Ingle et al. (2019) the present study also suggests that forest generalist species constitute a large part of the fauna of plantations, and these species are unable to colonize forest-steppes.

We found that the turnover component had a high contribution (> 0.6) to beta diversity of forests, and even higher (> 0.9) for steppes for both incidence-based and abundance-based multiple-site dissimilarity approaches. Such remarkably high contribution of species replacement was observed for island butterflies in Malaysia (Yong et al. 2012) and spiders in China (Wu et al. 2017), suggesting a higher level of isolation for steppes than for forests. Low-quality landscapes with high habitat-matrix contrast may decrease functional connectivity by preventing movement of organisms between fragments (Vasudev et al. 2015, Reider et al 2018; Tölgyesi et al. 2018b). Community composition of plantations was more similar to forests than to steppes according to the NMDS ordinations, suggesting a higher habitat-matrix contrast and a less permeable landscape for the biota of grasslands than that of the forests. Communities in less permeable landscapes are more exposed to random shifts in community composition due to higher extinction rates and random colonization of species (Watling et al 2011). Therefore, these isolated communities have more divergent species compositions than communities for which the matrix is more permeable (Watling et al. 2011). Another possible explanation for the high turnover ratio between steppes could be the micro-habitat heterogeneity across the sampled grasslands. Small-scale differences in soil properties are known to affect vegetation in dry grasslands (Maestre and Cortina 2002, Zhou et al. 2008), and microhabitat structure affects spiders (Gallé et al. 2010; Heneberg and Řezáč 2014) and ants (Castracani et al. 2010) of arid grasslands. Presumably, low matrix permeability together with high microhabitat diversity resulted in the high turnover component of the beta diversity of steppes.

Landscape quality may have an interacting effect with fragment size, as increasing landscape quality may have a weaker effect on large fragments (Öckinger et al. 2012b). Increasing landscape quality had a positive effect on the plant species richness and specialist plant species richness of landscapes with large habitat fragments, however this effect was negative for landscapes with small fragment. Positive effect of high-quality matrix could occur by immigration of forest-steppe specialists to the habitat fragments (Rand et al. 2006). However, for small fragments, the lower probability of colonization of generalist and weed species from the matrix may have offset the positive effect of higher connectivity on forest-steppe specialists.

We found that increasing landscape quality had a positive effect on the species richness of spiders. Several studies also concluded that increasing landscape quality has a positive effect on the species richness of a habitat fragment, and this effect is the most expressed if the amount of suitable habitats and high quality matrix elements are low (Ruffell et al. 2017; Reider et al. 2018). This emphasizes the positive effect of increasing landscape quality for spiders, which are generally moderately good dispersers, even in high quality landscapes.

According to our findings, ant species richness was unaffected by habitat type, landscape quality and fragment size. This is in line with Dauber et al. (2003), who found that landscape quality explains relatively low variance in ant species richness, suggesting the importance of other factors, such as competition in shaping ant community structure (Hölldobler and Wilson 1990). Interference competition has an increasing importance in advanced successional stages (Gallé et al. 1998; Gibb 2011), such as in natural forest-steppe patches. However, habitat type had an effect on the species richness of specialist ants. In contrast to plants, we found higher specialist species richness in the plantations than in steppe habitats, numerous forest species colonised plantations presumably due to the thick litter layer and closed canopy.

Several landscape management strategies based on binary partitioning of landscape cover types were suggested to enhance connectivity between habitat patches in fragmented landscapes, such as stepping stones (Krosby et al. 2010; Saura et al 2014) and habitat corridors (Gilbert-Nortan et al. 2010, Haddad 2017). Our study emphasizes that landscape quality metrics may provide more insight into the distribution of organisms than binary metrics (Fischer and Lindenmayer 2007). Landscape perception is species specific and depends on numerous trait states (Rieder et al. 2018), however, detailed databases do not exist for all species groups of conservation importance. We argue that landscape quality assessment and evaluation for several taxonomic groups could help in developing landscape-wide conservation strategies.

The main implication of our study is that enhancing landscape quality by changing land use type and increasing the share of the fragmented natural habitat in the landscape would help to maintain habitat specialist species. Although it is economically not feasible to restore large forest-steppe areas in Central and Eastern Europe due to the growing demand for timber production, substituting the relatively poorly performing pine plantations with forest plantations of native tree species, such as silver poplar and establishing extensive pastures would support the native biota of forest-steppes. Furthermore, isolation of steppes could be mitigated by substituting the neighboring high contrast plantations with low contrast pastures.

# Chapter 4

## Importance of road verges in maintaining grassland arthropod fauna in the Great Hungarian Plain

Preservation of habitat specialist fauna in fragmented habitats requires conservation of natural habitat patches, and connectivity of fragments. Artificial linear landscape elements (LLEs) are landscape structures established for a special function such as transportation on roads and drainage by ditches, but they have a part covered by vegetation, which is not directly used for its original function, and may potentially constitute semi-natural habitats. It is shown that a significant proportion of native biota can survive in LLEs such as ditch banks (Torma et al. 2018) field margins, and hedgerows (Ernoult et al. 2013; Gallé et al. 2018a; Haaland et al. 2011; Morandin and Kremen 2013), road and railway verges (Henneberg et al. 2017; Jakobsson et al. 2018; Noordijk et al. 2009). These LLEs are important in conserving various arthropods and other animals as they can decrease isolation effect of fragmented habitats (Dover et al. 2000; Hinsley and Bellamy 2000; MacDonald 2003; Hollmen et al. 2008) and also, they function as corridors and refuges for species within highly modified landscapes (Zanden et al. 2013). Road verges between patches, for example, proved to have importance in conserving grassland specialist fauna in Ireland (Fuller et al. 2013) and also Noordijk et al. (2009) showed that apart from indigenous species of ants, spiders, ground beetles, bees, and butterflies, road verges were able to save several threatened species of bees in intensively used landscapes in the Netherlands. LLEs can help in increasing species movements across the fragment habitat (Gilbert-Nortan et al. 2010). Although, road verges in fragmented habitats usually undergo management activities like mowing and subsequently changing the composition of communities. Careful management and preservations of road-side verge can help to protect biota (Le Viol et al. 2008; Decleer et al. 2015).

To understand their potential role, we used functional diversity indices (FD), which explains the functions that a species can provide in an ecosystem and thereby able to predict the dynamics and stability of ecosystem. It has various measures that can be grouped as (1) single trait measures like CWM (community weighted mean trait values), where average of trait values weighted by the relative abundances of each species (Garnier et al. 2004); and (2) multivariate trait measure such as RaoQ (Rao's quadric entropy) that takes into accont different trait values assigned to the species based on the functions of interest in research question (Botta-Dukát 2005). Combination of both CWM and RaoQ indices can be effectively used to measure FD (Lavorel et al. 2008; Ricotta and Moretti, 2011).

We aimed to study the importance of linear landscape elements such as road verges on conserving grassland arthropod fauna Great Hungarian plain using (1) steppe component of forest-steppe patches (steppes), (2) pastures (moderately disturbed grassland habitats), and (3) road verges in exotic forest plantations. We focus on addressing the following questions:

(1) Do linear grassy stripes along road verges have a role in maintaining the steppe species of arthropods?

(2) Are the forest-steppe grasslands different from pastures in terms of arthropod species composition and functional diversity (functional trait composition, RaoQ diversity)?

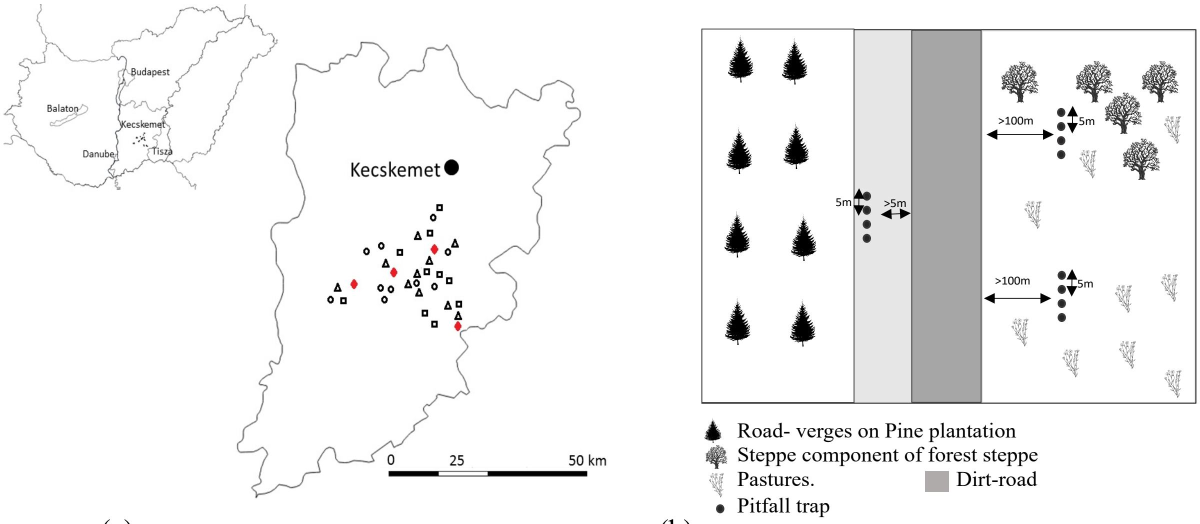
(3) Is there any difference in the species composition between the studied habitat types?

## 4.1 Materials and methods

### 4.1.1 Study sites and sampling design

Ten sites in each habitat, the steppe component of forest-steppes (F), pastures (P), and road verges (R) between pine forests were assigned for sampling, respectively. The vegetation of steppes consisted of drought tolerant tall grasses, mainly *Festuca vaginata* and *Stipa borysthenica* coupled with few dicots such as *Alkanna tinctoria, Dianthus serotinus, Fumana procumbens*, *Iris arenaria* and *Onosma arenaria*. Pastures were moderately grazed by sheep, they had more generalist plant species and less specialist steppe species. The vegetation of road verges consisted of generalist plant species along with some steppe grassland species such as *F. vaginata, S. borysthenica,* and *A. tinctoria*. We excluded potential sampling sites with significant cover of invasive plant species like *Asclepias syriaca*, *R. pseudoacacia,* and *Ailanthus altissima*. All study sites were in the range of approximately 50 km and were minimum 1 km apart and around four villages (Zsana, n = 5; Imrehegy, n = 3; Pirtó, n = 7; Tázlár, n = 15; Fig. 12.). In each site, four pitfall traps were arranged in a transect at 5 m intervals to sample ground-dwelling arthropods. Traps were 500 ml white plastic cups, 8.5 cm in diameter, and they were provided with a metal roof and plastic funnel to prevent the preservative from dilution by rain or entry of vertebrates (Császár et al. 2018).

We used 50/50 ethylene glycol/water mixture in pitfall traps as a preservative. In addition to pitfall traps, we also used sweep net technique to sample vegetation-dwelling arthropods. At each site, we collected 5 samples, each comprised of 25 sweeps along ca. 20 m transect. Pitfall traps were open twice between 6th and 16th June and between 11th and 26th September 2017, respectively. Sweep net sampling was done on the 16th of June and the 26th of September. Data were pooled per site for further analysis. We identified the collected invertebrates using the keys of Nentwig et al. (2019) for spiders, and key of Czechowski et al. (2012) for ants. To identify true bugs, we used various keys (Wagner and Weber 1964; Schuh et al. 1995; Matocq 2004; Rabitsch and Deckert 2007).



(a) (b)

Fig. 13. (a) Map of the study region. Road verges, steppe component of forest-steppe, pastures, and villages are represented by squares, circles, triangles, and red rhombus, respectively, in the Danube– Tisza Interfluve. (b) Schematic representation os sampling design.

### 4.1.2 Data analysis

We used three ecological traits to characterise the sampled arthropod species: moisture preference, shading tolerance, and dispersal ability (Table 4). Species were assigned with a specific value from 0 to maximum 3, 4 or 5 for each trait. If a given species fell under more than one category, then an averaged value was assigned. Generalist species or species with no data available in any trait category were excluded from further calculations. Species were considered as generalist if they fell under more than the half of the categories. All trait values were ranged between 0 and 1 to account for the different number of categories. We did not perform any statistical analysis on the dispersal ability of ants because the overwhelming majority of the collected species disperse only by nuptial flight. We calculated the single trait FD measure, community weighted mean (CWM) for all traits of the three arthropod groups, and we used the multivariate RaoQ index to characterize FD of our sampling sites with the FD package in R (Laliberté et al. 2014).

We used (generalised) linear mixed models to determine the effect of habitat type as fixed effect (i.e., F, P or R) and villages as random effect (true spatial replicates) on species richness and FD indices. We used negative binomial and Poisson error term for species richness after checking for overdispersion of data for spiders, true bugs, and ants respectively. We used Gaussian error term for CWM and RaoQ indices. Pairwise comparisons were carried out using the ‘relevel’ function in R.

We performed analysis of similarities (ANOSIM) based on Bray–Curtis dissimilarity matrices with 10,000 permutations to test the multivariate differences among the arthropod assemblages in the three habitats types using ‘anosim’ function of the vegan package in R (Oksanen et al. 2015). We visualized this data set with non-metric multidimensional scaling after Hellinger transformation of data (Legendre and Gallagher 2001) using vegan package 2.4-6. A maximum number of 20 random starts were used to search for a stable solution to fit into the two-dimensional plot. We also performed an indicator value analysis to identify the characteristic species in forest-steppe, pastures, and road verges (IndVal; Dufrene and Legendre 1997) with the ‘labdsv’ package (Roberts 2012).

Table 4. Functional diversity traits for spiders, true bugs, and ants.

| Spiders | True bugs | Ants |
|---|---|---|
| | Moisture preference | |
| Very dry: 1<br>Dry:2<br>Semi humid :3<br>Humid: 4<br>Very humid: 5<br>(Buchar and Ruzicka, 2002) | Very dry: 1<br>Dry: 2<br>Semi humid: 3<br>Humid: 4<br>Very humid: 5<br>(Wachmann et al. 2012) | Xerothermic: 1<br>Mesothermic and Xerothermic: 2<br>Mesothermic: 3<br>(Czechowski et al., 2012) |
| | Shading tolerance | |
| Open: 1<br>Semi open: 2<br>Partly shaded: 3<br>Shaded: 4<br>(Buchar and Ruzicka, 2002) | Open: 1<br>Semi open: 2<br>Partly shaded: 3<br>Shaded: 4<br>(Wachmann et al. 2012) | Open: 1<br>Semi open: 2<br>Shaded: 3<br>(Czechowski et al., 2012) |
| | Dispersal | |
| Not included in lists: 1<br>Members of the same family balloon: 2<br>Members of the same genus balloon: 3<br>Species known balloon: 4<br>(Bell et al., 2005, Blandenier et al., 2009) | Shortened-winged: 1<br>Predominantly shortened-winged: 2<br>Equally shortened-winged and macropterous species (including sexual dimorphism): 3<br>Predominantly macropterous species: 4<br>Macropterous species: 5<br>(Wachmann et al. 2012) | |

### 4.2 Results

We collected a total of 6983 spider individuals (out of which 1598 were adults and could be identified to species level and for all others that follow), 5537 adult true bugs and 16,425 adult ants from 114, 147, and 27 species, respectively (Appendix Table 3, 4, and 5). Altogether, we found 72 spider, 85 true bug, and 19 ant species in steppe component of forest-steppe; 51 spider, 87 true bug and 16 ant species in pastures; and 75 spider, 92 true bug, and 22 ant species in road verges. Among spiders, *Oxyopes heterophthalmus* (Latreille, 1804), *Tibellus macellus* (Simon, 1875) and *Zelotes longipes* (L. Koch, 1866) were the most common, comprising approximately 35% of all individuals. True bugs were largely represented by the rhopalids, and *Rhopalus parumpunctatus* (Schiling, 1829), and *Chorosoma gracile* (Josifov, 1968) were the most abundant species, together more than 27% of the total catch. The most abundant ant species were *Plagiolepis taurica* (Santschi, 1920), *Lasius psammophilus* (Seifert, 1992), and *Tetramorium cf. caespitum* (Linnaeus, 1758), accounting for approximately 70% of all individuals.

Linear stripes along the road verges had higher species richness of spiders, and ants than pastures, however, true bug species richness was similar in all three habitats (Table 5, Fig. 13). Road verges had higher spider FD (RaoQ) than the other two habitat types (Table 5 Fig. 14a). We also found higher moisture preference values in the road verges than in the other two habitat types for all arthropods, furthermore, CWM shading tolerance was also higher in the road verges for spiders and true bugs than in steppes and pastures (Table 5, Figs. 14, 15, and 16). The highest dispersal CWM values were also found in road verges for true bugs, however, we did not find any significant difference in the dispersal ability of spiders (Fig. 15c).

Table 5. Summary statistics of linear mix models for species richness and functional diversity of spiders, true bugs, and ants in steppe component of forest-steppes (F), pastures (P), and road verges (R). Model estimate ± 95% CI; z/t values are given. Significances marked with stars and significant results are marked in bolds. Degree of freedom is shown in brackets. SpR: Species richness

| | SpR$^{1,1,2}$ | RaoQ$^{3}$ | Moisture$^{3}$ (CWM) | Shading$^{3}$ (CWM) | Dispersal$^{3}$ (CWM) |
|---|---|---|---|---|---|
| | | | Spiders | | |
| F-P | - 0.305±0.231<br>**-2.573***(25) | -0.136±0.327<br>-0.819(26.98) | 0.002±0.023<br>0.186(26.56) | -0.03±0.049<br>-1.206(27) | 0.041±0.056<br>1.377(27) |
| F-R | 0.0295±0.217<br>0.264(25) | 0.364±0.329<br>**2.166** (26.6) | 0.030±0.256<br>**2.295***(26.8) | 0.097±0.049<br>**3.84*****(27) | 0.058±0.056<br>1.945(27) |
| P-R | 0.334±0.211<br>**3.095****(25) | 0.50±0.313<br>**3.117****(23.6) | 0.027±0.023<br>**2.266***(23.9) | 0.128±0.049<br>**5.04*****(27) | 0.016±0.056<br>0.568(27) |
| | | | True bugs | | |
| F-P | 0.047±0.231<br>0.404(25) | 0.255±0.341<br>1.438(26.41) | -0.053±0.058<br>-1.772(27) | -0.022±0.05<br>-0.796(27) | -0.087±0.066<br>**-2.54****(26) |
| F-R | -0.060±0.235<br>-0.505(25) | -0.028±0.352<br>-0.158(26.75) | 0.092±0.025<br>**3.045**(27)** | 0.075±0.05<br>**2.626****(27) | 0.115±0.066<br>**3.355****(25.5 |
| P-R | -0.108±0.233<br>-0.909(25) | -0.284±0.327<br>-1.702(24.17) | 0.145±0.025<br>**4.817*****(27) | 0.097±0.05<br>**3.422****(27) | 0.203±0.066<br>**5.903*****(25) |
| | | | Ants | | |
| F-P | -0.195±0.305<br>-1.247(26) | -0.264±0.666<br>-0.779(26.93) | -0.008±0.147<br>-0.118(26.91) | -0.059±0.115<br>-1.000(25.58) | |
| F-R | 0.279±0.272<br>**1.999***(26) | 0.296±0.672<br>0.865(26.96) | 0.234±0.147<br>**3.019***(26.98) | -0.036±0.115<br>0.618(24.79) | |
| P-R | 0.475±0.290<br>**3.209*****(26) | 0.561±0.635<br>1.731(23.48) | 0.243±0.139<br>**3.398****(23.7) | 0.022±0.115<br>0.382(24.8) | |

Models fitted with $^{1}$Poisson error term, $^{2}$negative binomial error term, $^{3}$Gaussian error term

Significance level: * <0.05, ** <0.01, *** <0.001

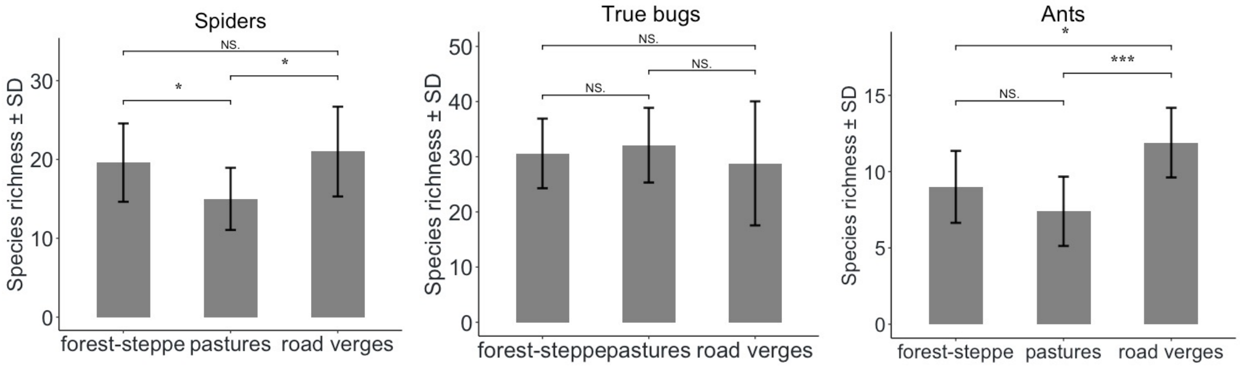


Fig. 14 Species richness of spiders, true bugs, and ants in steppe component of forest-steppe, pastures, and road verges. NS= Non significant, *<0.05, ** <0.01, *** <0.001

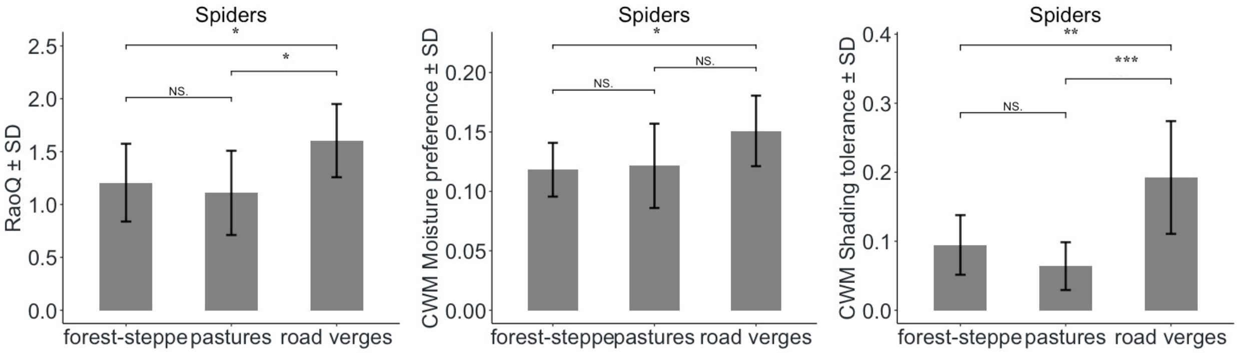


Fig. 15. Singnificant effects of habitat type on functional diversity of spiders, RaoQ, CWM moisture preference, and CWM shading tolerance of spiders in steppe component of forest-steppe, pastures and road verges in exotic pine plantations. NS= Non significant, *<0.05, ** <0.01, *** <0.001

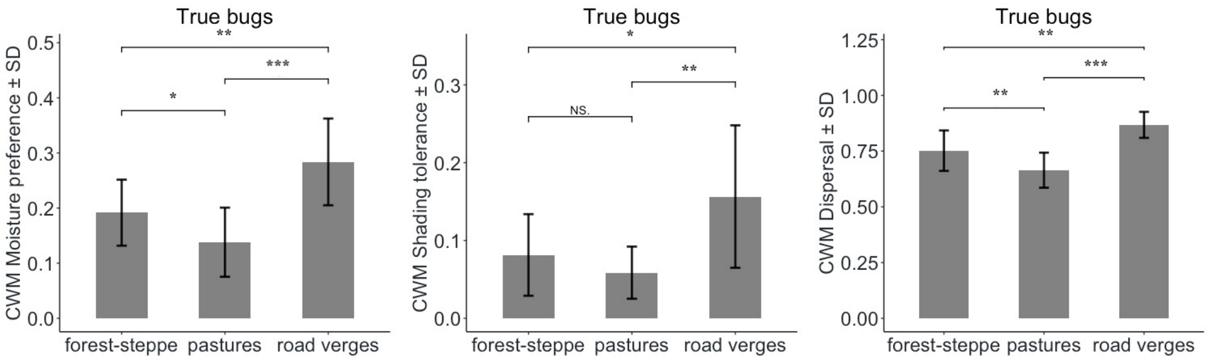


Fig. 16. Singnificant effects of habitat type on fuctional diversity of true bugs, CWM moisture preference, shading tolerance, and dispersal of true bugs in steppe component of forest-steppe, pastures, and road verges in exotic pine plantations. NS= Non significant, *<0.05, ** <0.01, *** <0.001

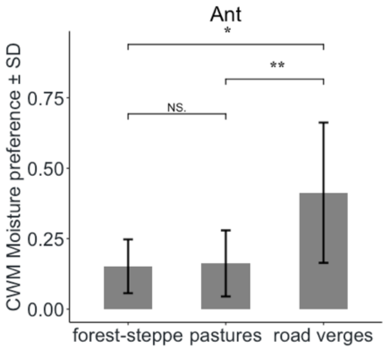


Fig. 17. Singnificant effects of habitat type on CWM moisture preference of ants in steppe component of forest-steppe, pastures, and road verges in exotic pine plantations. NS= Non significant, *<0.05, ** <0.01, *** <0.001

We found significant differences in the species composition of spiders (ANOSIM: $R = 0.282$, $p < 0.001$), true bugs (ANOSIM: $R = 0.4774$, $p < 0.001$), and ants (ANOSIM: $R = 0.211$, $p < 0.001$) between habitats. Road verges and pastures were the most distinct habitat pair, with little overlap between them according to the NMDS scatterplot (Fig. 17). Significant indicator species in all three habitats were found for true bugs (19), followed by spiders (15), and ants (6) (Table 5). Majority of the indicator value species of true bugs in road verges were dry grassland species (e.g., *D. spinolae, N. tipularis,* and *Catoplatus carthusianus*), wet meadow (e.g., *L. simulans*) along with some habitat generalist species (e.g., *Palomena prasina*). Spiders were represented by xerothermic (e.g., *Z. electus, Z. apricorum* and *P. minimus*), habitat generalist (e.g., *T. terricola, Pardosa alacris,* and *Zodarion germanicum*), grassland species (e.g., *M. acalypha*) and forest species (e.g., *P. tincta*). Ants' community in road verges comprised of generalist (e.g., *T. unifasciatus*), xerothermic grassland (e.g., *Temnothorax interruptus*), and dry forest species (e.g., *Formica sanguinea*).

Table 6. List of indicator species of spiders, true bugs, and ants in road verges, steppe component of forest-steppe, and pastures indicator values (IndVal) and p-values are given.

| Species | Indval | P values | Habitat |
|---|---|---|---|
| | Spiders | | |
| *Mangora acalypha* | 0.656 | 0.002 | Road verge |
| *Pardosa alacaris* | 0.56 | 0.003 | Road verge |
| *Zelotes apricorum* | 0.557 | 0.004 | Road verge |
| *Zodarion germanicum* | 0.557 | 0.029 | Road verge |
| *Titanoeca schineri* | 0.495 | 0.003 | Road verge |
| *Zelotes electus* | 0.495 | 0.002 | Road verge |
| *Phrurolithus minimus* | 0.454 | 0.026 | Road verge |
| *Platnickina tincta* | 0.4 | 0.023 | Road verge |
| *Trochosa tericola* | 0.4 | 0.022 | Road verge |
| *Phylloneta impressa* | 0.533 | 0.004 | Steppe |
| *Simitidion simile* | 0.44 | 0.029 | Steppe |
| *Alopecosa psammophila* | 0.433 | 0.036 | Steppe |
| *Heliophanus lineiventris* | 0.740 | >0.001 | Pasture |
| *Zelotes segrex* | 0.588 | 0.002 | Pasture |
| *Agyneta rurestris* | 0.490 | 0.008 | Pasture |
| | True bugs | | |
| *Palomena prasina* | 0.79 | <0.001 | Road verge |
| *Dimorphopterus spinolae* | 0.639 | 0.001 | Road verge |
| *Lygaeus simulans* | 0.635 | 0.004 | Road verge |
| *Aelia acuminate* | 0.615 | 0.002 | Road verge |
| *Catoplatus carthusianus* | 0.512 | 0.023 | Road verge |
| *Neides tipularius* | 0.563 | 0.037 | Road verge |
| *Agramma minutum* | 0.422 | 0.017 | Steppe |
| *Stenodema calcarata* | 0.375 | 0.047 | Steppe |
| *Emblethis ciliatus* | 0.737 | 0.002 | Pasture |
| *Menaccarus Arenicola* | 0.708 | <0.001 | Pasture |
| *Chorosoma gracil* | 0.603 | 0.003 | Pasture |
| *Spathocera obscur* | 0.56 | 0.003 | Pasture |
| *Nysius ericae* | 0.54 | 0.004 | Pasture |
| *Trigonotylus pulchellu* | 0.529 | 0.009 | Pasture |
| *Parapiesma silenes* | 0.5 | 0.041 | Pasture |
| *Acetropis carinata* | 0.444 | 0.022 | Pasture |
| *Chorosoma gracil* | 0.603 | 0.003 | Pasture |
| *Oxycarenus pallen* | 0.387 | 0.041 | Pasture |

Table 5. continued

| | | | |
|---|---|---|---|
| Ants | | | |
| *Formica fusca* | 0.88 | >0.001 | Road verge |
| *Temnothorax unifasciatus* | 0.880 | >0.001 | Road verge |
| *Temnothorax interruptus* | 0.5 | 0.008 | Road verge |
| *Formica sanguinea* | 0.497 | 0.009 | Road verge |
| *Cataglyphis aenescens* | 0.556 | 0.018 | Pasture |
| *Lasius psammophilus* | 0.547 | 0.033 | Pasture |

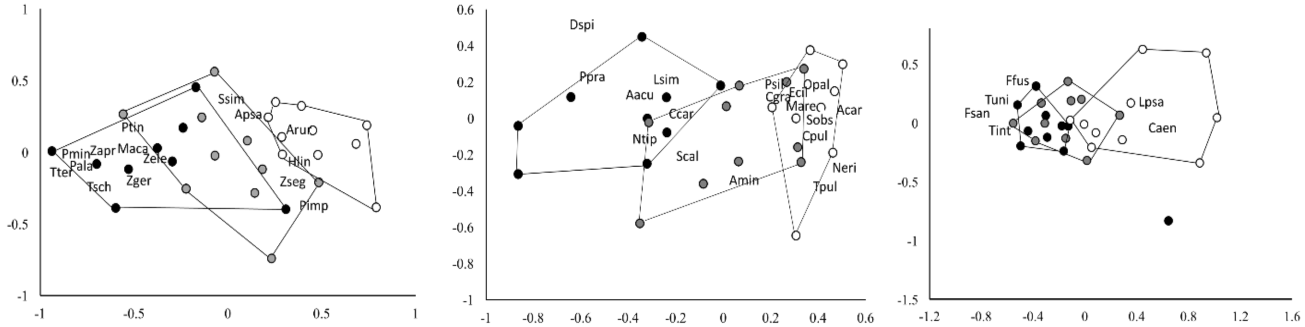


Fig. 18. NMDS ordination of sampling sites (dots) and significant indicator species for spiders (A), true bugs (B), and ants (C). Black dots: road verges; grey dots: steppe component of forest-steppe; open circles: pastures. Species names are abbreviated with the first letter of the genus name and the first three letters of the species name (see table 3. for further details).

### 4.3 Discussion and conclusions

In this research we aimed to assess the importance of road verges in maintaining the arthropod fauna of forest-steppes. We compared species composition and FD of steppe component of forest-steppe and pastures with road verges. We observed higher species richness in road verges than in pastures for spiders and ants. In line with Schirmel et al. (2016), we also found high FD values for spiders and different trait composition for all taxa in road verges when compared with forest-steppes and pastures. The characteristic species composition and the high number of indicator species for pastures and forest-steppes suggest that road verges do not serve as habitat for several grassland and forest-steppe species, in spite of the fact that numerous specialist species were found in the road verges, as well. We found that the steppe component of forest-steppes has higher species richness of spiders than pastures, and we found differences in species composition of the two habitat types for all taxa based on the multivariate analyses. The role of road verges in maintaining arthropod biodiversity within intensively managed landscape is increasingly recognised (Schaffers et al. 2012; Reck and van der Ree 2015), as they may serve as linear habitats and dispersal corridors for weak-flying insects (Vermeulen 1994) and overwintering habitat for several specialists (Schaffers et al. 2012; Gallé et al. 2018a). In native forests, however, road verges may have a negative impact on the biota, fragmenting forest habitats by exerting barrier effects on the forest specialist species (Yamada et al. 2010). Furthermore, they may also support invasive species (Smith et al. 2007). In our study, road verges were inhabited partly by forest species from pine plantations [e.g., spiders: *P. alacris* (C. L. Koch, 1833) and *Z. germanicum* (C. L. Koch, 1837), ants: *F. sanguinea* (Latreille, 1798)]. The higher CWM shading values in road verges as compared to pastures also indicated the relatively high number of forest species. Besides forest species, we also collected open habitat generalists [e.g., spiders: *O. heterophthalmus* (Latreille, 1804), true bugs: *P. prasina* (Linnaeus, 1761), ants: *T. interruptus* (Schenck, 1852)] and several steppe species [e.g., spiders: *Gnaphosa mongolica* (Simon, 1895), true bugs: *C. carthusianus* (Goeze, 1778)]. Thus, road verges between exotic plantations may act as secondary habitats for several specialist arthropod species. In line with these results, Koivula (2003) found that the narrow forest roadside verges are preferred by open-habitat and generalist carabid beetles.

Pine plantation forests have a relatively simple habitat structure due to the closed canopy (Gallé et al. 2014). Compared to the interior of exotic plantations, road verges between exotic forests have more open spaces, which can regulate microhabitat conditions, species composition of vascular plants and structure of the vegetation (Mullen et al. 2003; Smith et al. 2007). The dense vegetation along road verges provides high diversity of potential food for true bugs and ants, and it substantially increases the number of potential web attachment points for web-building spiders and may increase the species richness. Moisture preference CWM values were consistently highest in road verges for all the studied taxa. This may correspond with a temperature gradient. Sandy dry pastures of the Kiskunság region often exhibit very high surface temperature during summer that can reach 60 °C (Erdős et al. 2014), and as a consequence of evaporation, there is a very low soil water content near the soil surface. These climatic parameters act as strong environmental filters (Entling et al. 2007), and as a consequence, sandy pastures have a specialized, thermophilous and xerotolerant fauna. This environmental filter reduces the diversity of trait values, resulting in low RaoQ values (Gallé et al. 2018b). Certainly, this does not imply the higher conservation value of road verges compared to steppes of forest-steppe and pastures.

Road verges were associated with the highest dispersal trait values for true bugs according to the linear mixed models. These narrow grassy strips in pine plantations are low quality secondary habitats for the forest-steppe fauna of true bugs, and the regular disturbance may preclude the effective colonization of several wingless species. Dispersal ability clearly influences the colonization of true bugs (Moir et al. 2005), resulting in higher dispersal trait values of true bugs in more disturbed habitats (Torma et al. 2019). Well dispersing species with developed wings can travel long distances (presumably several kilometres, see Kiritani and Sasaba 1969), but they probably travel as far as necessary to locate the nearest host plant or suitable habitat patch (Tillman et al. 2009). The type of vegetation and land use primarily affects the species composition and richness of true bug assemblages (Zurbrügg and Frank 2006; Torma and Császár 2013; Torma et al. 2017), thus, besides dispersal limitation, specialized habitat requirements of species and the density of potential host plants may be the most important determinants of colonization pattern of true bugs in road verges.

Our study emphasizes the importance of road verges in exotic plantations for the conservation of arthropod diversity. With the change of natural habitats to exotic or semi-natural forests, it is important to maintain every aspect of this grassland habitat that has the capability to protect this unique biodiversity. Our results indicate that road verges should be considered an important reserve for grassland specialists, as they provide secondary linear habitats for many arthropod species. Road verges are often maintained by forestry management, and this disturbance may reduce their conservation capabilities. We suggest the maintenance of these grassy strips in order to preserve arthropod biodiversity.

# Summary

In fragmented landscapes, fragment size, quality of the landscape around fragmented patches, and connectivity between them play an important role in conserving the biodiversity. The majority of the natural forest-steppes in the Great Hungarian Plain have been modified due to anthropogenic activities and replaced with exotic plantations. This thesis aimed to understand the species composition and diversity of plants and arthropods (spiders, true bugs, and ants) in these specific habitats namely natural forest patches of forest-steppes, grassland component of forest-steppes, and the main type of the landscape matrix, exotic pine plantations in Kiskunság region of southern Hungary.

To understand the diversity pattern of flora and fauna we calculated the beta diversity and ran multivariate analysis on forest, steppe component of forest-steppe and matrix around fragmented patches considering size, and quality around the patches. Species turnover was higher for steppes than for forests, indicating a higher degree of isolation for steppes than forests. We ran GLM models to identify influential variables for species richness and grassland specialist species richness of plants, spiders, and ants. We found that increasing landscape quality increased plant species richness of small fragments, and also positively affected spider species richness. Our findings suggest that improving landscape quality by planting native trees instead of exotic plantations and establishing extensively managed grasslands would help to preserve the threatened forest-steppe biota.

In the second study, we aimed to understand the importance of linear landscape elements like road verges in conserving biodiversity. Here, we sampled steppe component of forest-steppe, pastures, and road verges between exotic pine plantations. We calculated the functional diversity of spiders, true bugs, and ants. We used Generalized linear mixed models and Non-metric multidimensional scaling to visualize the composition of arthropods in the given habitats. We found higher FD values for spiders and different trait composition for all taxa in road verges, when compared with forest-steppes and pastures. Numerous specialist species from forest-steppe and grassland were found in the road verges, and forest-steppes had a higher species richness of spiders than pastures. This indicates that road verges should be considered as an important refuge for grassland specialist arthropods.

# Összefoglalás

Az emberi tájhasználat egyre intenzívebbé válása meghatározóan befolyásolta az Alföld tájszerkezetét, a erdőssztyeppek jelentős részét erdőületvénykere cserélték, melynek következménye a természetes előhelyek erőteljes fragmentációja. A megmarad erdőssztyeppfoltok mennyisége, térbeli elrendezésük és a foltokat körülvevő táji mátrix minősége valószínűleg jelentősen befolyásolja a tájszintű biodiverzitást. Jelen dolgozat célja, hogy feltárjuk (1) a táji mátrix hatását az élőhelyfoltok természetvédelmei értekére, diverzitásmegtartó képességére. (2) a vonalas tájelemek másodlagos élőhelyként betöltött szerepét az erdőssztyepp élővilágának megőrzésében. A dolgozat első vizsgálatához 18 tájat jelöltünk ki, minden esetben mintát vettünk az erdőssztyepp erdő komponensében, a természetes gyepen valamint a táji mátrix domináns elemében, egy fenyőültetvényben. A különböző gyepek béta diverzitását vizsgálva gyepek turnover/teljes béta diverzitás aránya magasabb volt, mint természetes erdőké, mely alapján a gyepek erősebben izolált élőhelyek, mint az erdők. A táji mátrix szignifikáns pozitív hatással volt a pókközösségek fajszámára és jelentősen befolyásolta az élőhely-méret hatását a növények esetén. A második vizsgálat során földutakat szegélyező gyepsávok ízeltlábú közösségeit hasonlítottuk össze természetes erdőssztyepp gyepekkel és mérsékelten zavart legelőkkel. A földutak szegélye a gyepekétől jelentősen eltérő ízeltlábú faunával rendelkezik, funkcionális diverzitása magasabb, a fenyőerdőkre jellemző generalisták jelenléte miatt. Azonban számos specialista faj is előfordul ezeken az élőhelyeken, hangsúlyozva a földutak szegélyének másodlagos élőhelyként betöltött szerepét. A táji mátrix minőségének emelkedése a megmaradt természetes foltok megőrzése mellet új foltok kialakításával és őshonos fafajú ültetvények létrehozásával érhető el, így hozzájárulva az értékes flóra és fauna megőrzéséhez.

## Financial Support

Hardeep Kaur was supported by the Stipendium Hungaricum Scholarship and Stipendium dissertation scholarship of Tempus Public Foundation. This work was supported by the Hungarian National Research, Development and Innovation Office; Grant Id: NKFIH-FK-131379, and Grant Id Id NKFH- FK-124579 respectively.

## Acknowledgments

In preparation for my Ph.D. thesis, I took the help and guidance of some respected persons, who deserve my deepest gratitude. As the completion of my Ph.D. thesis gave me so much pleasure, so I would like to expand my gratitude to all those who directly and indirectly guided me in writing my thesis. However, this is not at all an individual effort, it is a long and continuous collaboration of people, thoughts, inspirations, and immense supports. I would like to acknowledge all those here for their valuable contributions.

Firstly, and most importantly I would like to express my deepest or sincere gratitude to my respected supervisors **Dr. Gallé Robert** and **Dr. Torma Atilla** for their continuous support, patience, motivation, and, immense knowledge. They gave me the opportunity to make this start which has culminated in the current shape. I see them as the kindest pillar of strength, motivation and knowledge who has never ceased to motivate me. Scientific knowledge providing me the freedom to explore the world of science. This dissertation would not have the shape it is currently in without his unwavering support, tireless efforts, and insightfulness of my supervisors.

I would like to express my sincere gratitude especially to **Dr. Gallé Róbert** who supported me in all difficult times throughout my tenure as a student and as well as a foreigner in a new country. Without the support of him, it would have been immensely difficult to achieve this milestone. Here, I would also like to thank **Dr. Lipnszki Zoltan** who introduced me to Dr. Gallé Robert and suggested me continue my studies under his supervision.

A special mention is due for **Dr. Batáry Peter** who has been my support towards the end of my Ph.D. journey and gave me opportunity to continue my studies in Vacratot. His supportive, facilitative nature and calm demeanor have motivated me to achieve my current and future endeavors. My sincere thanks also go to **Dr. Lőrinczi Gabor**, **Dr. Batori Zoltan,** and **Dr. Tölgyesi Csaba** for their collaboration, courses and positivity that they brought.

Likewise, many thanks to **Nikolett Gallé-Szpisjak**, whose's hardwork has provided us with all identification data on time, her immense support during field works, and lastly, teaching me identification of the spider families is irreplicable. I also would like to extend my thanks to **Seat Jelena** and **Gabor Modra** for their identification work. I would like to acknowledge my all labmates and peers from Szeged and Vacratot for their indirect support and friendship.

Last but not the least, I would like to thank my family: my parents **Charanjeet Kaur** and **Bhupinder Singh**, my husband **Maciej Mieczyslaw Dudek**, my twin **Amandeep Kaur**, brother **Jagvir Singh**, my in-law family **Alina Dudek** and **Mieczyslaw Dudek,** and to all my friends for supporting me spiritually throughout my Ph.D. and my life in general. I am also acknowledging to them, to whom I forgot to mention their name. A special thank to my son **Wojciech Waryam Dudek** who was a constant source of inspiration for me. I am extremely grateful to the almighty God for the good health and wellbeing that were necessary to complete this Ph.D. dissertation.

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## Publication List MTMT Id: 10071558

**Kaur H**, Torma A, Gallé-Szpisjak N, Seat J, Lorinczi G, Modara G, Galle R (2019) Road verges are important secondary habitats for grassland arthropods. J Insect Conserv 23, 899–907 https://doi.org/10.1007/s10841-019-00171-9 **Impact factor 2.262**

Gallé R, Tölgyesi C, Torma A, Bátori Z, Lőrinczi G, Szilassi P, Gallé-Szpisjak N, **Kaur H**, Makra T, Módra G, Batáry P. Matrix quality and habitat type drive the diversity pattern of forest-steppe fragments. Perspect Ecol Conserv (accepted) **Impact factor 4.677**

## Publications not related to thesis

Gallé R, Tölgyesi C, Császár P, Bátori Z, Gallé-Szpisjak N, **Kaur H**, Maák I, Torma A, Batáry P, (2021) Landscape structure is a major driver of plant and arthropod diversity in natural European forest fragments. Ecosphere (accepted). **Impact factor: 3.171**

Ingle K, Gallé-Szpisjak N, **Kaur H**, Gallé R (2019) Forest type interacts with milkweed invasion to affect spider communities. Insect Conserv Diver 12: 321-328 https://doi.org/10.1111/icad.12346 **Impact factor:2.729**

Ingle K, **Kaur H**, Gallé-Szpisjak N, Bürgés J, Szabó A, Gallé R (2020) Winter-Active Spider Fauna is Affected by Plantation Forest Type. Environ Entomol 49:601–606 https://doi.org/10.1093/ee/nvaa025 **Impact Factor: 1.586**

## Presentations

**Kaur H**, Gallé R, Torma A ‘Road verges as important secondary habitats for grassland arthropods’ 5thStudent conference on conservation science Tihany, Balaton Limnological Institute, Centre for Ecological Research H-8237,3 Klebelsberg Kuno str. Tihany, Hungary, 27-31 August 2019.

Šeat J, **Kaur H**, Gallé R, Torma A ‘The role of road verges as secondary linear habitats for forest-steppe heteroptera, 8th European Hemiptera Congress Zawiercie, Katowice Poland, 24-29 June 2018.

## Poster

**Kaur H**, Gallé R Road verges functionally important or not? 31st European Congress of Arachnology, Vác, Hungary, 08–13 July 2018.

### Other scientific work

Training on **‘Assessing multi-taxon diversity in forest ecosystems’** by European cooperation in science and technolog**.** Arezzo, Italy, 28-30 Sep 2021.

Summer school on **‘Aegean seminars for computational ecology and evolution 2018’** by the ecology and evolutionary biology society of Turkey**. Venue:** Izmir institute of technology, Izmir, Turkey, 16-22 Sep 2019.

## Declaration

As the responsible author of the scientific publication, I certify that the results reported in the Ph.D. dissertation and the following publication were not used to acquire any Ph.D. degree previously and will not be used in the future either.

Kaur H, Torma A, Gallé-Szpisjak N, Seat J, Lőrinczi G, Módra G, Gallé R (2019) Road verges are important secondary habitats for grassland arthropods. J Insect Conserv 23, 899–907 https://doi.org/10.1007/s10841-019-00171-9

Gallé R, Tölgyesi C, Torma A, Bátori Z, Lőrinczi G, Szilassi P, Gallé-Szpisjak N, **Kaur H**, Makra T, Módra G, Batáry P. Matrix quality and habitat type drive the diversity pattern of forest-steppe fragments. Perspect Ecol Conserv (accepted)

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## Supplement material

**Appendix Table 1. List of species. Cumulative cover values are given for plants, cumulative abundance values are given for spiders and ants.**

| *PLANTS* | forest | plantation | steppe | IndVal | p | Habitat type |
|---|---|---|---|---|---|---|
| *Achillea pannonica* | 1.1 | 0 | 0.7 | 0.068 | 0.53 | forest |
| *Acinos arvensis* | 1.4 | 1 | 0 | 0.130 | 0.422 | forest |
| *Alkanna tinctoria* | 0.4 | 1.9 | 28.3 | 0.771 | 0.001 | steppe |
| *Allium vineale* | 1.5 | 0.3 | 0 | 0.046 | 1 | forest |
| *Alyssum alyssoides* | 0 | 0 | 2.2 | 0.056 | 1 | steppe |
| *Alyssum tortuosum* | 0.3 | 0 | 3.4 | 0.408 | 0.001 | steppe |
| *Anchusa officinalis* | 1.2 | 0 | 0 | 0.111 | 0.343 | forest |
| *Anthemis ruthenica* | 0 | 0 | 0.1 | 0.056 | 1 | steppe |
| *Anthriscus caucalis* | 5 | 0 | 0 | 0.056 | 1 | forest |
| *Anthriscus cerefolium* | 8.1 | 1 | 0 | 0.099 | 0.578 | forest |
| *Arabidopsis thaliana* | 0.1 | 0 | 0 | 0.056 | 1 | forest |
| *Arabis auriculata* | 0.2 | 0 | 0 | 0.056 | 1 | forest |
| *Arenaria serpylliphilia* | 0.3 | 0.7 | 4.8 | 0.782 | 0.001 | steppe |
| *Artemisia campestris* | 0.7 | 0 | 25.7 | 0.433 | 0.001 | steppe |
| *Asclepias syriaca* | 16.7 | 24.4 | 31.2 | 0.281 | 0.862 | plantation |
| *Asparagus officinalis* | 17.2 | 3.5 | 0.5 | 0.811 | 0.001 | forest |
| *Asperula cynanchica* | 0.4 | 4 | 0 | 0.051 | 1 | plantation |
| *Aster linosyris* | 2.5 | 0 | 0 | 0.056 | 1 | forest |
| *Ballota nigra* | 0.6 | 0 | 0 | 0.056 | 1 | forest |
| *Bassia laniflora* | 0.1 | 0 | 2.4 | 0.640 | 0.001 | steppe |
| *Berberis vulgaris* | 21.8 | 4.3 | 0 | 0.557 | 0.001 | forest |
| *Botriochloa ischaemum* | 0.7 | 0 | 20.1 | 0.429 | 0.002 | steppe |
| *Bromus squarrosus* | 0.3 | 0 | 0.2 | 0.067 | 0.753 | forest |
| *Bromus sterilis* | 128.5 | 11.7 | 0 | 0.560 | 0.001 | forest |
| *Bromus tectorum* | 2.6 | 6.3 | 1.8 | 0.164 | 0.547 | plantation |
| *Buglossoides arvensis* | 0.5 | 0 | 0.4 | 0.049 | 0.772 | steppe |
| *Calamagrostis epigeios* | 213.1 | 31.1 | 4.4 | 0.810 | 0.001 | forest |
| *Camelina microcarpa* | 1.5 | 0 | 0 | 0.056 | 1 | forest |
| *Capsella bursa-pastoris* | 0.4 | 0 | 0 | 0.111 | 0.292 | forest |
| *Carduus nutans* | 0.1 | 0 | 0 | 0.056 | 1 | forest |
| *Carex flacca* | 39 | 8.2 | 0 | 0.138 | 0.235 | forest |
| *Carex liparicarpos* | 296.4 | 175.8 | 39.5 | 0.579 | 0.008 | forest |
| *Carex stenophylla* | 1.5 | 0.2 | 1.2 | 0.092 | 0.598 | steppe |

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|---|---|---|---|---|---|---|
| *Carlina vulgaris* | 0.5 | 0 | 0 | 0.111 | 0.301 | forest |
| *Celtis occidentalis* | 54 | 8 | 0 | 0.871 | 0.001 | forest |
| *Centaurea arenaria* | 2.1 | 0.3 | 14.6 | 0.811 | 0.001 | steppe |
| *Cephalanthera rubra* | 0.9 | 0 | 0 | 0.056 | 1 | forest |
| *Cerastium semidecandrum* | 1.3 | 0 | 10 | 0.492 | 0.001 | steppe |
| *Chenopodium album* | 0.4 | 0.3 | 0 | 0.095 | 0.619 | forest |
| *Chondrilla juncea* | 2 | 0.1 | 0.5 | 0.342 | 0.013 | forest |
| *Conyza canadensis* | 0.1 | 0.2 | 0 | 0.037 | 1 | plantation |
| *Crataegus monogyna* | 62.5 | 0.8 | 0.3 | 0.983 | 0.001 | forest |
| *Crepis foetida* | 0.2 | 0.2 | 1.9 | 0.459 | 0.002 | steppe |
| *Cruciata pedemontana* | 2 | 0 | 0 | 0.056 | 1 | forest |
| *Cynodon dactylon* | 31.7 | 27.6 | 39.6 | 0.289 | 0.695 | steppe |
| *Cynoglossum officinale* | 6.6 | 9.2 | 0.2 | 0.447 | 0.013 | plantation |
| *Dactylis glomerata* | 0.3 | 0 | 0 | 0.056 | 1 | forest |
| *Daucus carota* | 0 | 0.1 | 0 | 0.056 | 1 | plantation |
| *Dianthus serotinus* | 4.4 | 1.5 | 1.5 | 0.165 | 0.209 | forest |
| *Echinops ruthenicus* | 16 | 0 | 0 | 0.056 | 1 | forest |
| *Elymus repens* | 12.2 | 2 | 0 | 0.095 | 0.71 | forest |
| *Epipactis atrorubens* | 0.5 | 0 | 0 | 0.167 | 0.107 | forest |
| *Equisetum ramosissima* | 0.2 | 0.3 | 1.1 | 0.076 | 0.6 | steppe |
| *Erigeron canadensis* | 0 | 0.3 | 0.1 | 0.125 | 0.33 | plantation |
| *Erophila verna* | 0.1 | 0.2 | 10.1 | 0.971 | 0.001 | steppe |
| *Eryngium campestre* | 19.5 | 1.6 | 7.1 | 0.461 | 0.209 | forest |
| *Erysimum diffusum* | 0.2 | 0 | 2.7 | 0.414 | 0.001 | steppe |
| *Euonymus eurpaeus* | 3 | 0 | 0 | 0.222 | 0.026 | forest |
| *Euphorbia cyparissias* | 40.6 | 3.2 | 3.3 | 0.575 | 0.004 | forest |
| *Euphorbia seguieriana* | 16.7 | 1.4 | 102.2 | 0.802 | 0.001 | steppe |
| *Fallopia convulvulus* | 0.2 | 0.1 | 0 | 0.074 | 0.778 | forest |
| *Festuca pseudovina* | 5 | 0 | 15.5 | 0.042 | 1 | steppe |
| *Festuca rupicola* | 1.1 | 0 | 65.2 | 0.164 | 0.142 | steppe |
| *Festuca vaginata* | 105.2 | 8.5 | 1184 | 0.912 | 0.001 | steppe |
| *Festuca wagneri* | 0 | 0 | 25 | 0.056 | 1 | steppe |
| *Fumana procumbens* | 0.1 | 0.2 | 49.5 | 0.884 | 0.001 | steppe |
| *Gagea pusilla* | 0 | 0 | 0.3 | 0.056 | 1 | steppe |
| *Galium aparine* | 2.3 | 0.2 | 0 | 0.409 | 0.002 | forest |
| *Galium verum* | 43.9 | 0.3 | 4.3 | 0.553 | 0.001 | forest |
| *Geranium pusillum* | 0.2 | 0 | 0 | 0.056 | 1 | forest |
| *Geranium robertianum* | 0.1 | 4.2 | 0 | 0.109 | 0.522 | plantation |
| *Geum urbanum* | 3 | 0 | 0 | 0.056 | 1 | forest |
| *Gleditsia triacanthos* | 2.4 | 1.6 | 0 | 0.267 | 0.08 | forest |
| *Gypsophila arenaria* | 0.1 | 0 | 0.2 | 0.037 | 1 | steppe |
| *Hedera helix* | 35.5 | 0 | 0 | 0.111 | 0.331 | forest |
| *Helianthemum ovatum* | 0.3 | 0 | 0.9 | 0.042 | 1 | steppe |
| *Hieracium auricoluides* | 4 | 0.5 | 0 | 0.049 | 1 | forest |

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|---|---|---|---|---|---|---|
| *Hieracium umbellatum* | 4.4 | 0.8 | 0.1 | 0.092 | 0.868 | forest |
| *Holosteum umbellatum* | 0.2 | 0 | 23.7 | 0.992 | 0.001 | steppe |
| *Hypericum perforatum* | 0 | 0 | 0.5 | 0.056 | 1 | steppe |
| *Iris arenaria* | 0 | 0 | 3.3 | 0.056 | 1 | steppe |
| *Juglans regia* | 0 | 1.5 | 0 | 0.056 | 1 | plantation |
| *Juniperus communis* | 63.3 | 7.5 | 1 | 0.735 | 0.001 | forest |
| *Koeleria glauca* | 0.5 | 1.3 | 74.4 | 0.434 | 0.008 | steppe |
| *Lappula squarrosa* | 0.1 | 0 | 0 | 0.056 | 1 | forest |
| *Leontodon hispidus* | 8.2 | 0.1 | 0 | 0.110 | 0.344 | forest |
| *Ligustrum vulgare* | 115.6 | 5.9 | 0 | 0.846 | 0.001 | forest |
| *Linaria genistifolia* | 0.5 | 0.6 | 0.9 | 0.100 | 0.531 | steppe |
| *Linum hirsutum* | 2.5 | 0 | 3.5 | 0.032 | 1 | steppe |
| *Lithospermum officinale* | 3.8 | 1 | 0 | 0.264 | 0.019 | forest |
| *Medicago falcata* | 28.1 | 0 | 0 | 0.278 | 0.008 | forest |
| *Medicago lupulina* | 0.4 | 0 | 0 | 0.111 | 0.342 | forest |
| *Medicago minima* | 0.2 | 1.3 | 5.3 | 0.433 | 0.016 | steppe |
| *Melica transsilvanica* | 1.3 | 0.4 | 0 | 0.042 | 1 | forest |
| *Minuartia glaucina* | 0.2 | 0 | 3.2 | 0.680 | 0.001 | steppe |
| *Muscari comosum* | 0.6 | 0.9 | 0.3 | 0.037 | 0.929 | forest |
| *Mycelis muralis* | 0 | 4 | 0 | 0.111 | 0.312 | plantation |
| *Myosotis stricta* | 0.1 | 0 | 1.1 | 0.306 | 0.007 | steppe |
| *Ononis spinosa* | 0.7 | 0 | 0.2 | 0.043 | 1 | forest |
| *Onosma arenaria* | 0.5 | 0 | 0.4 | 0.074 | 0.756 | steppe |
| *Ornithogalum umbellatum agg.* | 0.1 | 0 | 0.1 | 0.028 | 1 | forest |
| *Parthenocissus quinquefolia* | 0.1 | 0.1 | 0 | 0.028 | 1 | forest |
| *Phleum phleoides* | 0 | 0 | 0.1 | 0.056 | 1 | steppe |
| *Pimpinella saxifraga* | 47.9 | 0.1 | 1 | 0.272 | 0.013 | forest |
| *Pinus nigra* | 4.9 | 1 | 0.1 | 0.227 | 0.106 | forest |
| *Pinus sylvestris* | 2.6 | 1.8 | 0 | 0.164 | 0.372 | forest |
| *Poa angustifolia* | 91.2 | 8.8 | 1 | 0.853 | 0.001 | forest |
| *Poa bulbosa* | 5.3 | 0.2 | 186.9 | 0.917 | 0.001 | steppe |
| *Polygala comosa* | 2.7 | 0 | 4.7 | 0.141 | 0.179 | steppe |
| *Polygonatum latifolium* | 1.5 | 0 | 0 | 0.056 | 1 | forest |
| *Polygonatum odoratum* | 5.2 | 0 | 0 | 0.167 | 0.11 | forest |
| *Polygonum arenarium* | 0.2 | 0 | 1.6 | 0.691 | 0.001 | steppe |
| *Populus canescens* | 13.3 | 3.1 | 66.7 | 0.580 | 0.002 | steppe |
| *Potentilla arenaria* | 5.9 | 1.6 | 124.6 | 0.786 | 0.001 | steppe |
| *Prunus sp.* | 6.1 | 0.4 | 0 | 0.156 | 0.22 | forest |
| *Prunus spinosa* | 18.3 | 0 | 0 | 0.611 | 0.001 | forest |
| *Pulsatilla nigricans* | 3 | 0.1 | 0 | 0.054 | 1 | forest |
| *Pyrus pyraster* | 0.3 | 0 | 0 | 0.056 | 1 | forest |
| *Quercus cerris* | 3.9 | 0.5 | 0 | 0.148 | 0.506 | forest |

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|---|---|---|---|---|---|---|
| *Quercus robur* | 0.2 | 0.2 | 0 | 0.056 | 0.75 | forest |
| *Ranunculus polyanthemos* | 1 | 0 | 0 | 0.056 | 1 | forest |
| *Rhamnus catharticus* | 14.4 | 0.4 | 0 | 0.703 | 0.001 | forest |
| *Robinia pseudoacacia* | 3.4 | 3.6 | 0 | 0.162 | 0.238 | forest |
| *Rosa canina agg.* | 6.5 | 0 | 0 | 0.389 | 0.003 | forest |
| *Salix rosmarinifolia* | 1.1 | 0 | 0 | 0.111 | 0.315 | forest |
| *Sambicus nigra* | 0.5 | 0 | 0 | 0.056 | 1 | forest |
| *Saxifraga tridactylites* | 0.2 | 0 | 0.4 | 0.111 | 0.298 | steppe |
| *Scabiosa ochroleuca* | 4.7 | 1.2 | 10 | 0.559 | 0.004 | steppe |
| *Scirpoides holoschoenus* | 0.2 | 1 | 8.7 | 0.195 | 0.131 | steppe |
| *Secale sylvestris* | 0.8 | 0.1 | 26.2 | 0.591 | 0.001 | steppe |
| *Sedum urvillei* | 0 | 0 | 2.2 | 0.278 | 0.007 | steppe |
| *Senecio vernalis* | 1.2 | 0.4 | 0.2 | 0.074 | 0.897 | forest |
| *Seseli annuum* | 15.6 | 0.6 | 0 | 0.214 | 0.075 | forest |
| *Seseli osseum* | 5.5 | 0 | 3.6 | 0.034 | 1 | forest |
| *Silene alba* | 4.2 | 4.2 | 0.1 | 0.082 | 0.733 | forest |
| *Silene conica* | 0 | 0 | 0.3 | 0.111 | 0.326 | steppe |
| *Silene otites* | 0.8 | 0.2 | 13.7 | 0.362 | 0.004 | steppe |
| *Solanum dulcamara* | 0 | 1.2 | 0 | 0.111 | 0.32 | plantation |
| *Solidago virgaaurea* | 14.5 | 2.3 | 0.3 | 0.424 | 0.016 | forest |
| *Sporobolus cryptandrus* | 0 | 0 | 6 | 0.056 | 1 | steppe |
| *Stachys recta* | 0.2 | 0 | 0 | 0.056 | 1 | forest |
| *Stellaria media* | 5.2 | 0.1 | 0 | 0.164 | 0.245 | forest |
| *Stipa borysthenica* | 44.1 | 1.1 | 680 | 0.938 | 0.001 | steppe |
| *Syrenia cana* | 0.1 | 0 | 1 | 0.202 | 0.09 | steppe |
| *Taraxacum sp.* | 59.8 | 21.3 | 0 | 0.696 | 0.001 | forest |
| *Teucrium chamaedrys* | 107.9 | 27.8 | 22.2 | 0.494 | 0.004 | forest |
| *Thesium arvense* | 3.5 | 0 | 3.6 | 0.192 | 0.252 | forest |
| *Thlaspi perfoliata* | 1 | 0 | 0 | 0.167 | 0.095 | forest |
| *Thymus pannonicus* | 3.9 | 0 | 11.3 | 0.165 | 0.356 | steppe |
| *Tragopogon dubium* | 3.7 | 0.1 | 0 | 0.216 | 0.059 | forest |
| *Tragopogon floccosus* | 1 | 0 | 5.1 | 0.372 | 0.01 | steppe |
| *Tragopogon orientale* | 0.1 | 0 | 0 | 0.056 | 1 | forest |
| *Trifolium repens* | 1 | 0 | 0 | 0.056 | 1 | forest |
| *Ulmus minor* | 0.3 | 0 | 0 | 0.056 | 1 | forest |
| *Verbascum lychnitis* | 2.2 | 0.4 | 3.2 | 0.123 | 0.573 | steppe |
| *Veronica hederifolia* | 0.2 | 0 | 0 | 0.111 | 0.312 | forest |
| *Veronica praecox* | 2.2 | 0 | 0.8 | 0.074 | 0.878 | steppe |
| *Vicia angustifolia* | 8.1 | 0 | 0 | 0.333 | 0.004 | forest |
| *Vicia hirsuta* | 0.6 | 0 | 0.1 | 0.190 | 0.075 | forest |
| *Vicia tetrasperma* | 0.1 | 0 | 0 | 0.056 | 1 | forest |
| *Vincetoxicum hirundinaria* | 1.5 | 0 | 1 | 0.033 | 1 | forest |
| *Viola hirta* | 18 | 0 | 0 | 0.056 | 1 | forest |
| *Viola kitaibeliana* | 1.1 | 3.1 | 1.8 | 0.183 | 0.804 | steppe |

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|---|---|---|---|---|---|---|
| *Viola rupestris* | 8.7 | 0.3 | 0 | 0.429 | 0.002 | forest |

| *SPIDERS* | forest | plantation | steppe | IndVal | p | Habitat type |
|---|---|---|---|---|---|---|
| *Nemesia pannonica* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Pholcus opilionoides* | 1 | 1 | 0 | 0.028 | 1 | steppe |
| *Dysdera hungarica* | 2 | 3 | 0 | 0.100 | 0.361 | plantation |
| *Harpactea rubicunda* | 6 | 19 | 0 | 0.549 | 0.001 | plantation |
| *Ero furcata* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Eresus kollari* | 1 | 0 | 4 | 0.190 | 0.044 | steppe |
| *Asagena phalerata* | 6 | 10 | 1 | 0.163 | 0.209 | plantation |
| *Dipoena melanogaster* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Enoplognatha serratosignata* | 0 | 0 | 1 | 0.059 | 0.325 | steppe |
| *Enoplognatha thoracica* | 57 | 39 | 2 | 0.549 | 0.001 | steppe |
| *Episinus truncatus* | 0 | 5 | 0 | 0.222 | 0.031 | plantation |
| *Euryopis flavomaculata* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Euryopis quinqueguttata* | 1 | 0 | 6 | 0.203 | 0.023 | steppe |
| *Steatoda albomaculata* | 0 | 0 | 3 | 0.176 | 0.027 | steppe |
| *Acartauchenius scurrilis* | 0 | 0 | 4 | 0.118 | 0.091 | steppe |
| *Agyneta rurestris* | 2 | 0 | 0 | 0.111 | 0.32 | steppe |
| *Canariphantes nanus* | 10 | 51 | 0 | 0.511 | 0.001 | plantation |
| *Centromerus sylvaticus* | 2 | 5 | 0 | 0.198 | 0.051 | plantation |
| *Ceratinella brevis* | 2 | 4 | 0 | 0.111 | 0.255 | plantation |
| *Gongylidiellum murcidum* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Hylyphantes graminicola* | 0 | 0 | 1 | 0.059 | 0.301 | steppe |
| *Mermessus trilobatus* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Metopobactrus ascitus* | 1 | 4 | 0 | 0.178 | 0.088 | plantation |
| *Palliduphantes pillichi* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Panamomops mengei* | 15 | 57 | 1 | 0.520 | 0.001 | plantation |
| *Sintula spiniger* | 0 | 0 | 2 | 0.118 | 0.097 | steppe |
| *Tapinocyba insecta* | 2 | 8 | 0 | 0.267 | 0.018 | plantation |
| *Tenuiphantes flavipes* | 0 | 5 | 0 | 0.056 | 1 | plantation |
| *Trichoncus hackmani* | 3 | 10 | 0 | 0.299 | 0.005 | plantation |
| *Trichopterna cito* | 0 | 3 | 2 | 0.065 | 0.778 | plantation |
| *Walckenaeria alticeps* | 0 | 3 | 0 | 0.167 | 0.1 | plantation |
| *Araneus sturmi* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Cercidia prominens* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Zilla diodia* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Alopecosa cuneata* | 0 | 0 | 1 | 0.059 | 0.312 | steppe |
| *Alopecosa farinosa* | 0 | 0 | 1 | 0.059 | 0.31 | steppe |
| *Alopecosa psammophila* | 5 | 2 | 34 | 0.683 | 0.001 | steppe |
| *Alopecosa pulverulenta* | 0 | 0 | 1 | 0.059 | 0.291 | steppe |
| *Alopecosa sulzeri* | 542 | 175 | 55 | 0.700 | 0.001 | steppe |
| *Arctosa figurata* | 3 | 0 | 1 | 0.123 | 0.299 | steppe |

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|---|---|---|---|---|---|---|
| *Arctosa lutetiana* | 182 | 43 | 4 | 0.794 | 0.001 | steppe |
| *Aulonia albimana* | 0 | 16 | 0 | 0.056 | 1 | plantation |
| *Hogna radiata* | 0 | 0 | 1 | 0.059 | 0.34 | steppe |
| *Pardosa alacris* | 1270 | 1351 | 22 | 0.511 | 0.009 | plantation |
| *Pardosa prativaga* | 3 | 0 | 1 | 0.056 | 1 | steppe |
| *Trochosa hispanica* | 3 | 1 | 1 | 0.033 | 1 | steppe |
| *Trochosa robusta* | 1 | 2 | 0 | 0.074 | 0.57 | plantation |
| *Trochosa ruricola* | 3 | 3 | 0 | 0.083 | 0.482 | steppe |
| *Trochosa terricola* | 75 | 85 | 2 | 0.466 | 0.004 | plantation |
| *Agelena labyrinthica* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Eratigena agrestis* | 0 | 0 | 3 | 0.118 | 0.112 | steppe |
| *Hahnia nava* | 0 | 2 | 0 | 0.056 | 1 | plantation |
| *Hahnia pusilla* | 0 | 11 | 0 | 0.333 | 0.001 | plantation |
| *Argenna subnigra* | 0 | 2 | 0 | 0.111 | 0.331 | plantation |
| *Lathys stigmatisata* | 0 | 2 | 0 | 0.111 | 0.303 | plantation |
| *Titanoeca schineri* | 53 | 41 | 17 | 0.447 | 0.039 | steppe |
| *Titanoeca spominima* | 0 | 0 | 2 | 0.059 | 0.344 | steppe |
| *Cheiracanthium effossum* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Cheiracanthium elegans* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Zora pardalis* | 2 | 1 | 3 | 0.091 | 0.48 | steppe |
| *Zora spinimana* | 0 | 2 | 1 | 0.073 | 0.762 | plantation |
| *Anyphaena accentuata* | 5 | 0 | 0 | 0.167 | 0.091 | steppe |
| *Agroeca cuprea* | 6 | 16 | 1 | 0.347 | 0.014 | plantation |
| *Phrurolithus festivus* | 2 | 15 | 0 | 0.294 | 0.015 | plantation |
| *Phrurolithus minimus* | 52 | 38 | 0 | 0.481 | 0.002 | steppe |
| *Clubiona comta* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Zodarion germanicum* | 50 | 21 | 20 | 0.347 | 0.226 | steppe |
| *Zodarion rubidum* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Berlandina cinerea* | 1 | 0 | 12 | 0.327 | 0.003 | steppe |
| *Callilepis nocturna* | 1 | 1 | 16 | 0.421 | 0.001 | steppe |
| *Callilepis schuszteri* | 24 | 3 | 7 | 0.465 | 0.002 | steppe |
| *Drassodes lapidosus* | 10 | 1 | 13 | 0.252 | 0.109 | steppe |
| *Drassodes pubescens* | 2 | 0 | 1 | 0.056 | 1 | steppe |
| *Drassyllus praeficus* | 1 | 1 | 5 | 0.213 | 0.036 | steppe |
| *Drassyllus villicus* | 77 | 61 | 6 | 0.504 | 0.001 | steppe |
| *Gnaphosa mongolica* | 6 | 5 | 120 | 0.916 | 0.001 | steppe |
| *Haplodrassus bohemicus* | 0 | 0 | 5 | 0.294 | 0.006 | steppe |
| *Haplodrassus dalmatensis* | 0 | 0 | 1 | 0.059 | 0.301 | steppe |
| *Haplodrassus signifer* | 0 | 0 | 2 | 0.118 | 0.097 | steppe |
| *Haplodrassus silvestris* | 2 | 0 | 0 | 0.111 | 0.328 | steppe |
| *Micaria dives* | 0 | 0 | 4 | 0.176 | 0.027 | steppe |
| *Phaeocedus braccatus* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Sernaokorba sp* | 0 | 1 | 2 | 0.030 | 0.775 | steppe |
| *Trachyzelotes pedestris* | 29 | 14 | 0 | 0.412 | 0.01 | steppe |

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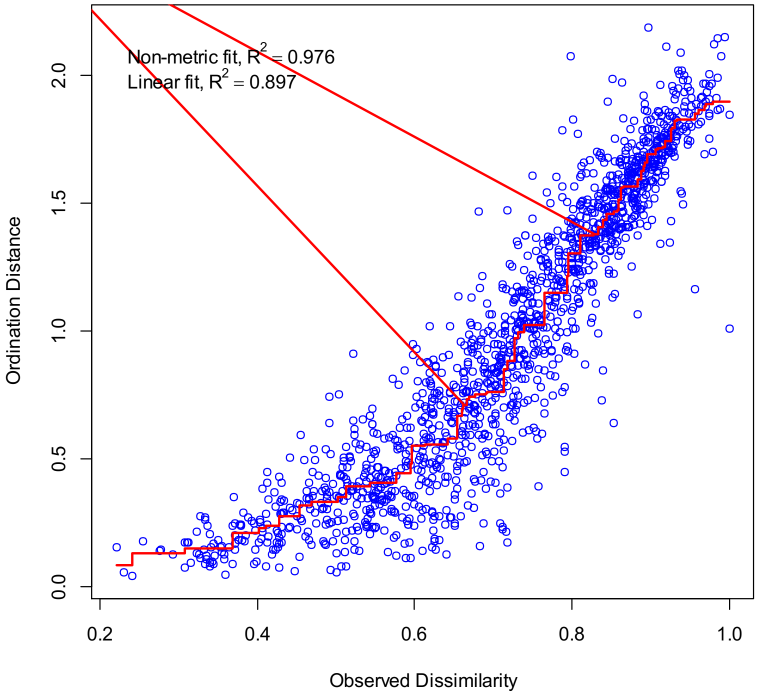
|---|---|---|---|---|---|---|
| *Zelotes apricorum* | 99 | 136 | 5 | 0.566 | 0.001 | plantation |
| *Zelotes electus* | 1 | 3 | 19 | 0.442 | 0.002 | steppe |
| *Zelotes exiguus* | 0 | 9 | 0 | 0.167 | 0.104 | plantation |
| *Zelotes longipes* | 2 | 0 | 52 | 0.849 | 0.001 | steppe |
| *Zelotes segrex* | 0 | 0 | 60 | 0.941 | 0.001 | steppe |
| *Philodromus fuscomarginatus* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Thanatus arenarius* | 0 | 0 | 1 | 0.059 | 0.331 | steppe |
| *Philodromus dispar* | 0 | 2 | 0 | 0.111 | 0.299 | plantation |
| *Thanatus formicinus* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Philodromus margaritatus* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Ozyptila atomaria* | 1 | 0 | 1 | 0.030 | 0.774 | steppe |
| *Ozyptila praticola* | 14 | 0 | 0 | 0.333 | 0.002 | steppe |
| *Synema ornatum* | 0 | 0 | 1 | 0.059 | 0.32 | steppe |
| *Xysticus audax* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Xysticus kochi* | 0 | 0 | 16 | 0.529 | 0.001 | steppe |
| *Xysticus lendli* | 0 | 0 | 1 | 0.059 | 0.32 | steppe |
| *Xysticus luctator* | 10 | 11 | 0 | 0.204 | 0.13 | plantation |
| *Xysticus ninnii* | 0 | 0 | 1 | 0.059 | 0.323 | steppe |
| *Xysticus pseudolanio* | 0 | 1 | 0 | 0.056 | 1 | plantation |
| *Xysticus robustus* | 4 | 2 | 0 | 0.111 | 0.222 | steppe |
| *Aelurillus v-insignitus* | 0 | 0 | 11 | 0.235 | 0.009 | steppe |
| *Euophrys frontalis* | 8 | 6 | 4 | 0.181 | 0.303 | steppe |
| *Evarcha falcata* | 4 | 5 | 0 | 0.154 | 0.172 | plantation |
| *Neon reticulatus* | 0 | 3 | 0 | 0.111 | 0.304 | plantation |
| *Pellenes nigrociliatus* | 0 | 0 | 19 | 0.529 | 0.001 | steppe |
| *Sittiflor zimmermanni* | 4 | 0 | 1 | 0.132 | 0.242 | steppe |
| *Synageles hilarulus* | 0 | 0 | 2 | 0.118 | 0.108 | steppe |

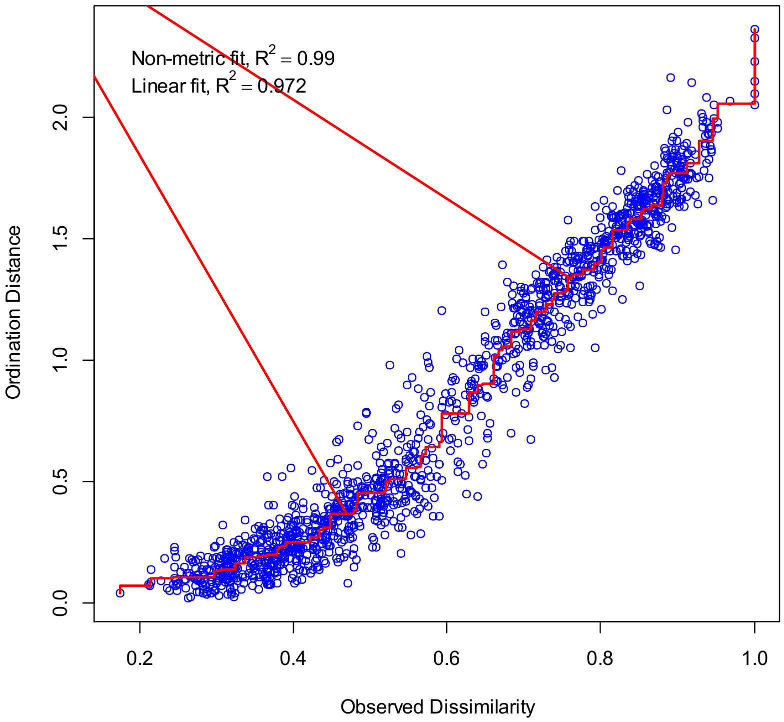
| *ANTS* | forest | plantation | steppe | IndVal | p | Habitat type |
|---|---|---|---|---|---|---|
| *Camponotus fallax* | 1 | 1 | 0 | 0.028 | 1 | steppe |
| *Camponotus vagus* | 141 | 58 | 52 | 0.562 | 0.001 | steppe |
| *Cataglyphis aenescens* | 0 | 0 | 92 | 0.500 | 0.001 | steppe |
| *Colobopsis truncata* | 1 | 0 | 0 | 0.056 | 1 | steppe |
| *Dolichoderus quadripunctatus* | 7 | 0 | 0 | 0.167 | 0.113 | steppe |
| *Formica cunicularia* | 6 | 24 | 133 | 0.544 | 0.001 | steppe |
| *Formica fusca* | 328 | 500 | 27 | 0.585 | 0.001 | plantation |
| *Formica polyctena* | 0 | 2 | 1 | 0.037 | 1 | plantation |
| *Formica pratensis* | 0 | 19 | 0 | 0.056 | 1 | plantation |
| *Formica rufa* | 0 | 6 | 2 | 0.167 | 0.104 | plantation |
| *Formica rufibarbis* | 0 | 3 | 39 | 0.361 | 0.004 | steppe |
| *Formica sanguinea* | 2 | 7 | 2 | 0.106 | 0.452 | plantation |
| *Lasius alienus* | 11 | 22 | 64 | 0.073 | 0.879 | steppe |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lasius bombycina* | 71 | 65 | 36 | 0.092 | 0.911 | steppe |
| *Lasius carniolicus* | 0 | 1 | 42 | 0.163 | 0.25 | steppe |
| *Lasius distinguendus* | 2 | 0 | 0 | 0.056 | 1 | steppe |
| *Lasius niger* | 0 | 2 | 0 | 0.056 | 1 | plantation |
| *Lasius platythorax* | 1 | 52 | 14 | 0.259 | 0.017 | plantation |
| *Lasius psammophilus* | 63 | 230 | 3055 | 0.912 | 0.001 | steppe |
| *Myrmica rubra* | 10 | 2 | 1 | 0.043 | 1 | steppe |
| *Myrmica sabuleti* | 1117 | 250 | 9 | 0.722 | 0.001 | steppe |
| *Myrmica scabrinodis* | 17 | 2 | 0 | 0.099 | 0.509 | steppe |
| *Plagiolepis taurica* | 24 | 64 | 1364 | 0.887 | 0.001 | steppe |
| *Ponera coarctata* | 0 | 2 | 0 | 0.111 | 0.315 | plantation |
| *Solenopsis fugax* | 6 | 11 | 17 | 0.167 | 0.432 | steppe |
| *Tapinoma subboreale* | 11 | 0 | 2 | 0.141 | 0.378 | steppe |
| *Temnothorax affinis* | 1 | 1 | 0 | 0.028 | 1 | steppe |
| *Temnothorax crassispinus* | 8 | 21 | 0 | 0.362 | 0.009 | plantation |
| *Temnothorax interruptus* | 2 | 3 | 4 | 0.074 | 0.946 | steppe |
| *Temnothorax unifasciatus* | 75 | 220 | 1 | 0.743 | 0.001 | plantation |
| *Tetramorium atratulum* | 0 | 2 | 2 | 0.056 | 1 | plantation |
| *Tetramorium cf. caespitum* | 52 | 110 | 177 | 0.348 | 0.068 | steppe |

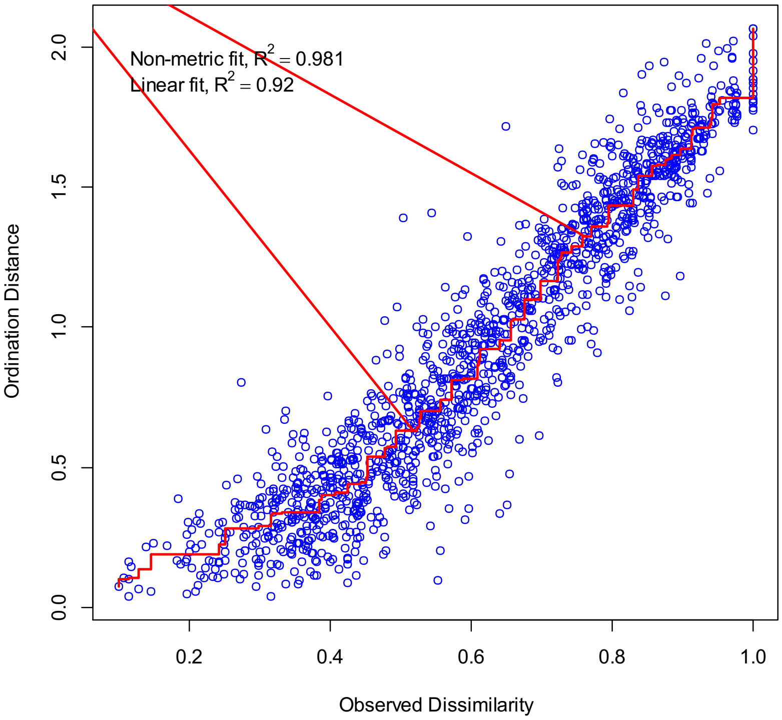
**Appendix Figure 1**. Goodness of Non-metric multidimensional scaling



Appendix 1a. Shepard diagram for two dimensional MNDS plot for vegetation



Appendix 1b. Shepard diagram for two dimensional MNDS plot for vegetation



Appendix 1c. Shepard diagram for two dimensional MNDS plot for ants

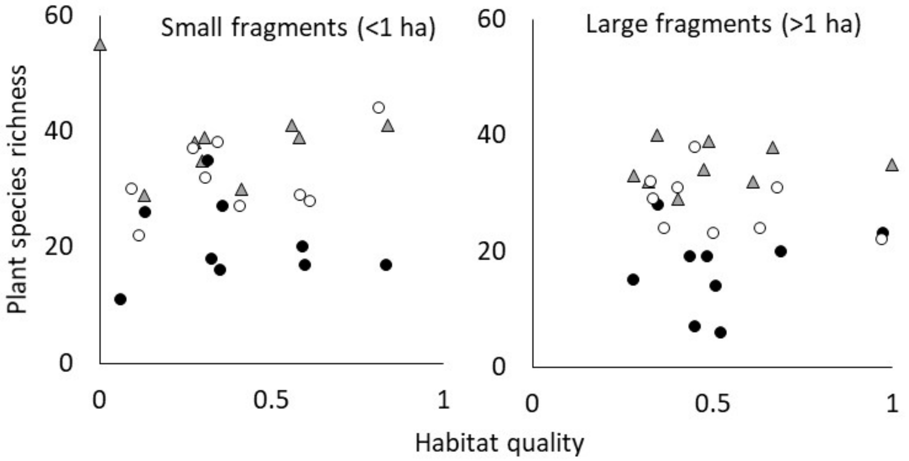
**Appendix Table 2.** Summary table for GLMM results after multi-model averaging of best candidate models showing the importance of each explanatory variable on species richness

| Variable[a] | Relative importance(%) | Multimodel estimate ± 95% CI | z value[b] | p value |
|---|---|---|---|---|
| **Plants** | | | | |
| Forest – Plantation | 100 | -0.605 ± 0.210 | 5.662 | <0.001*** |
| Forest – Steppe | 100 | -0.184 ± 0.160 | 2.257 | 0.024* |
| Steppe – Plantation | 100 | -0.421 ± 0.256 | 3.230 | 0.001** |
| Size | 49 | -0.135 ±.0.202 | 0.492 | 0.623 |
| Landscape quality | 39 | -0.215 ± 0.610 | 0.692 | 0.488 |
| Landscape quality: size | 21 | 0.892 ± 0.785 | 2.227 | 0.025* |
| Size: Forest – Plantation | 20 | -0.360 ± 0.486 | 1.450 | 0.147 |
| Size: Forest – Steppe | 20 | 0.035 ± 0.142 | 0.882 | 0.377 |
| Size: Steppe – Plantation | 20 | -0.537 ± 0.499 | 2.117 | 0.034* |
| **Specialist plants** | | | | |
| Forest – Plantation | 100 | -0.937 ± 0.247 | 7.453 | <0.001*** |
| Forest – Steppe | 100 | 0.390 ± 0.166 | 4.624 | <0.001*** |
| Steppe – Plantation | 100 | -1.327 ± 0.042 | 10.375 | <0.001*** |
| Size | 60 | -0.272 ± 0.672 | 1.443 | 0.149 |
| Landscape quality | 56 | -0.552 ± 0.750 | 0.794 | 0.427 |
| Landscape quality: size | 41 | 1.193 ± 0.936 | 2.505 | 0.012* |
| Size: Forest – Plantation | 6 | 0.194 ± 0.750 | 0509 | 0.610 |
| Size: Forest – Steppe | 6 | 0.167 ± 0.481 | 0.682 | 0.495 |
| Size: Steppe – Plantation | 6 | -0.362 ± 0.417 | 0.990 | 0.322 |
| Landscape quality: Forest – Plantation | 2 | 0.274 ± 0.992 | 0.542 | 0.587 |
| Landscape quality: Forest – Steppe | 2 | 0.136 ± 0.638 | 0.418 | 0.675 |

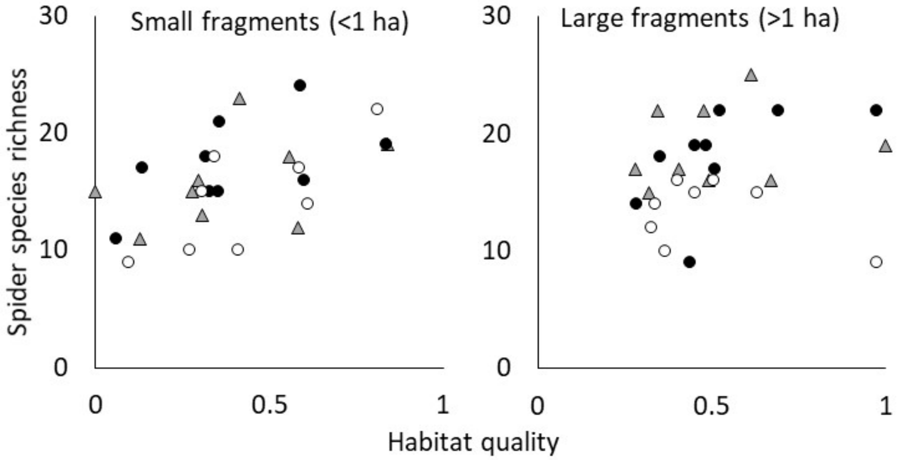
| | | | | |
|---|---|---|---|---|
| Landscape quality: Steppe – Plantation | 2 | 0.138 ± 0.967 | 0.280 | 0.779 |
| **Spiders** | | | | |
| Landscape quality | 96 | 0.398 ± 0.337 | 2.319 | 0.020* |
| Forest – Plantation | 94 | 0.005 ± 0.186 | 0.055 | 0.956 |
| Forest – Steppe | 94 | -0.228 ± 0.234 | 1.997 | 0.045* |
| Steppe – Plantation | 94 | 0.244 ± 0.239 | 2.167 | 0.030* |
| Size | 28 | -0.037 ± 0.484 | 0.192 | 0.847 |
| Landscape quality: size | 6 | 0.321 ± 0.742 | 0.674 | 0.500 |
| Size: Forest – Plantation | 5 | 0.232 ± 0.503 | 0.850 | 0.395 |
| Size: Forest – Steppe | 5 | 0.492 ± 0.566 | 1.702 | 0.088 |
| Size: Steppe – Plantation | 5 | -0.194 ± 0.734 | 0.905 | 0.365 |
| Landscape quality: Forest – Plantation | 5 | -0.232 ± 0.535 | 0.850 | 0.395 |
| Landscape quality: Forest – Steppe | 5 | -0.198 ± 0.687 | 0.565 | 0.571 |
| Landscape quality: Steppe – Plantation | 5 | -0.025 ± 0.736 | 0.453 | 0.650 |
| **Specialist spiders** | | | | |
| Forest – Plantation | 100 | 0.065 ± 0.638 | 0.317 | 0.751 |
| Forest – Steppe | 100 | 0.911 ± 0.320 | 5.581 | <0.001*** |
| Steppe – Plantation | 100 | -0.845 ± 0.339 | 4.895 | <0.001*** |
| Landscape quality | 55 | 0.323 ± 0.651 | 0.973 | 0.330 |
| Size | 34 | 0.086 ± 0.794 | 0.286 | 0.330 |
| Landscape quality: size | 5 | 0.711 ± 1.607 | 0.867 | 0.386 |
| Size: Forest – Plantation | 7 | 0.484 ± 1.140 | 0.904 | 0.366 |
| Size: Forest – Steppe | 7 | 0.501 ± 0.920 | 1.067 | 0.286 |
| Size: Steppe – Plantation | 7 | -0.017 ± 0.882 | 0.038 | 0.970 |

| | | | | |
|---|---|---|---|---|
| Landscape quality: Forest – Plantation | 2 | 0.759 ± 1.216 | 1.106 | 0.269 |
| Landscape quality: Forest – Steppe | 2 | 0.171 ± 1.723 | 0.284 | 0.777 |
| Landscape quality: Steppe – Plantation | 2 | 0.588 ± 1.127 | 0.987 | 0.324 |
| **Ants** | | | | |
| Size | 35 | -0.182 ± 0.383 | 0.932 | 0.351 |
| Landscape quality | 26 | 0.057 ± 0.503 | 0.224 | 0.823 |
| Forest – Plantation | 16 | 0.149 ± 0.243 | 1.190 | 0.234 |
| Forest – Steppe | 16 | 0.054 ± 0.257 | 0.429 | 0.670 |
| Steppe – Plantation | 16 | 0.094 ± 0.241 | 0.764 | 0.445 |
| Landscape quality: size | 3 | 0.407 ± 1.451 | 0.551 | 0.582 |
| **Specialist ants** | | | | |
| Forest – Plantation | 70 | 0.163 ± 0.515 | 0.622 | 0.533 |
| Forest – Steppe | 70 | -0.560 ± 0.629 | 1.743 | 0.081 |
| Steppe – Plantation | 70 | 0.723 ± 0.834 | 2.318 | 0.020* |
| Size | 30 | -0.314 ± 0.776 | 0.792 | 0.428 |
| Landscape quality | 24 | 0.123 ± 1.012 | 0.240 | 0.815 |

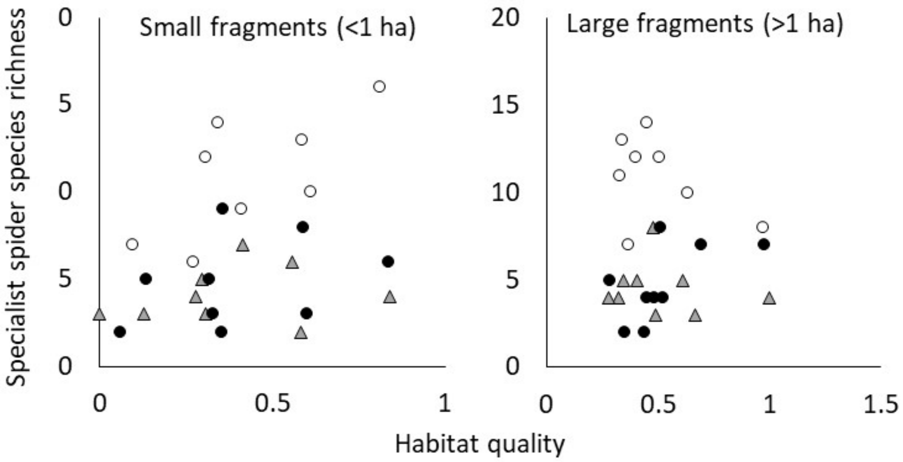
**Appendix Figure 2.** Non-significant effect of habitat type, landscape quality and fragment size



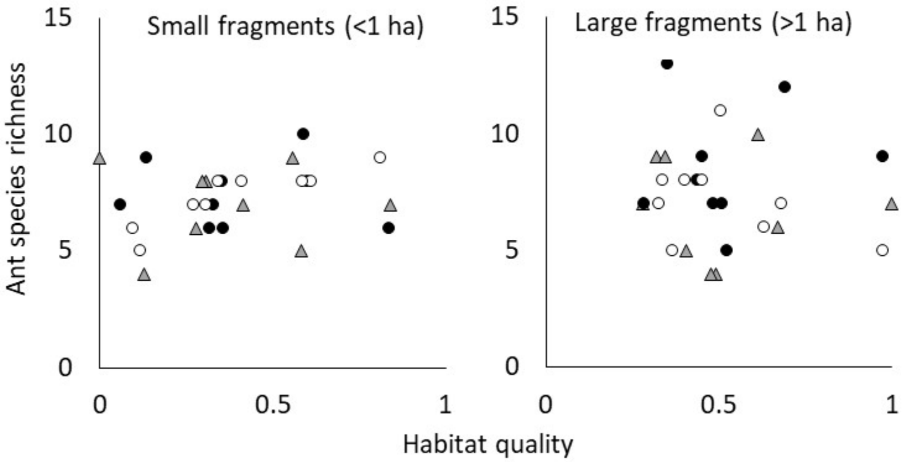
Appendix 2a. Species richness of vegetation. Open circles: steppes, grey triangle: forests, black dots: plantations



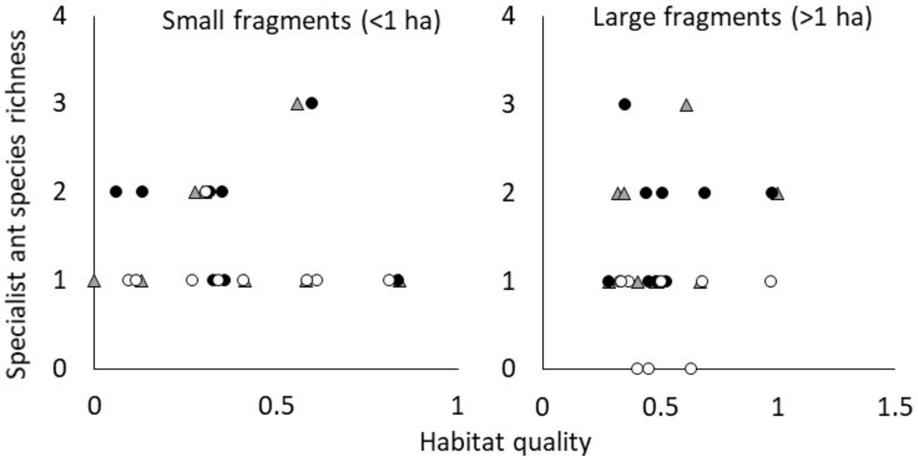
Appendix 2b. Species richness of spiders. Open circles: steppes, grey triangle: forests, black dots: plantations



Appendix 2c. Species richness of specialist spiders. Open circles: steppes, grey triangle: forests, black dots: plantations



Appendix 2d. Species richness of ants. Open circles: steppes, grey triangle: forests, black dots: plantations



Appendix 2e. Species richness of specialist ants. Open circles: steppes, grey triangle: forests, black dots: plantations

**Appendix Table 3. list of spider species, individuals found in road verges, forest- steppe and pasturs.**

| | Road verge | Forest-steppe | Pasture |
|---|---|---|---|
| *Uloborus walckenaerius* Latreille, 1806 | 32 | 23 | 9 |
| *Asagena phalerata* (Panzer, 1801) | 1 | 0 | 0 |
| *Cryptachaea riparia* (Blackwall, 1834) | 0 | 0 | 1 |
| *Enoplognatha thoracica* (Hahn, 1833) | 3 | 0 | 0 |
| *Episinus truncatu Latreille*, 1809 | 2 | 0 | 0 |
| *Euryopis quinqueguttata Thorell*, 1875 | 2 | 2 | 0 |
| *Neottiura bimaculata* (Linnaeus, 1767) | 1 | 0 | 0 |
| *Neottiura suaveolens* (Simon, 1880) | 0 | 0 | 2 |
| *Phylloneta impressa* (L. Koch, 1881) | 0 | 2 | 16 |
| *Platnickina tincta* (Walckenaer, 1802) | 4 | 0 | 0 |
| *Simitidion simile* (C. L. Koch, 1836) | 4 | 11 | 0 |
| *Steatoda albomaculata* (De Geer, 1778) | 1 | 0 | 0 |
| *Theridion uhligi Martin*, 1974 | 0 | 3 | 2 |
| *Agyneta rurestris* (C. L. Koch, 1836) | 1 | 1 | 9 |
| *Araeoncus humilis* (Blackwall, 1841) | 1 | 0 | 1 |
| *Bathyphantes gracilis* (Blackwall, 1841) | 1 | 0 | 1 |
| *Ceratinella brevis* (Wider, 1834) | 2 | 0 | 0 |
| *Erigone dentipalpis* (Wider, 1834) | 0 | 0 | 1 |
| *Gnathonarium dentatum* (Wider, 1834) | 1 | 0 | 0 |
| *Gongylidiellum murcidu* Simon, 1884 | 1 | 0 | 1 |
| *Linyphia triangularis* (Clerck, 1757) | 1 | 1 | 0 |
| *Oedothorax apicatus* (Blackwall, 1850) | 1 | 0 | 0 |
| *Panamomops mengei Simon*, 1926 | 2 | 1 | 0 |
| *Tenuiphantes tenuis* (Blackwall, 1852) | 1 | 0 | 1 |
| *Trichopterna cito* (O. P.-Cambridge, 1873) | 1 | 0 | 0 |

| | | | |
|---|---|---|---|
| *Walckenaeria alticeps* (Denis, 1952) | 1 | 0 | 0 |
| *Walckenaeria furcillata* (Menge, 1869) | 0 | 0 | 1 |
| *Pachygnatha degeeri* Sundevall, 1830 | 0 | 1 | 0 |
| *Araneus diadematus* Clerck, 1757 | 5 | 0 | 0 |
| *Araneus sturmi* (Hahn, 1831) | 1 | 0 | 0 |
| *Araneus triguttatu* (Fabricius, 1775) | 0 | 0 | 1 |
| *Argiope bruennichi* (Scopoli, 1772) | 0 | 1 | 0 |
| *Argiope lobata* (Pallas, 1772) | 0 | 1 | 0 |
| *Cercidia prominens* (Westring, 1851) | 0 | 1 | 0 |
| *Gibbaranea ullrichi* (Hahn, 1835) | 0 | 1 | 0 |
| *Hypsosinga albovittata* (Westring, 1851) | 0 | 12 | 12 |
| *Hypsosinga heri* (Hahn, 1831) | 0 | 0 | 4 |
| *Hypsosinga sanguinea* (C. L. Koch, 1844) | 1 | 1 | 2 |
| *Mangora acalypha* (Walckenaer, 1802) | 73 | 15 | 1 |
| *Neoscona adianta* (Walckenaer, 1802) | 0 | 0 | 1 |
| *Alopecosa cuneata* (Clerck, 1757) | 0 | 1 | 0 |
| *Alopecosa farinosa* (Herman, 1879) | 1 | 0 | 0 |
| *Alopecosa psammophila* Buchar, 2001 | 5 | 13 | 3 |
| *Alopecosa schmidti* (Hahn, 1835) | 0 | 0 | 2 |
| *Alopecosa sulzeri* (Pavesi, 1873) | 9 | 4 | 1 |
| *Arctosa figurata* (Simon, 1876) | 0 | 2 | 0 |
| *Arctosa leopardus* (Sundevall, 1833) | 0 | 1 | 0 |
| *Arctosa lutetiana* (Simon, 1876) | 25 | 4 | 0 |
| *Aulonia albimana* (Walckenaer, 1805) | 1 | 1 | 0 |
| *Pardosa alacris* (C. L. Koch, 1833) | 42 | 3 | 0 |
| *Trochosa terricola* Thorell, 1856 | 17 | 0 | 0 |
| *Xerolycosa miniata* (C. L. Koch, 1834) | 0 | 2 | 0 |
| *Dolomedes fimbriatus* (Clerck, 1757) | 0 | 0 | 1 |
| *Pisaura mirabilis* (Clerck, 1757) | 0 | 0 | 1 |

| | | | |
|---|---|---|---|
| *Eratigena agresti* (Walckenaer, 1802) | 2 | 2 | 0 |
| *Oxyopes heterophthalmus* (Latreille, 1804) | 83 | 97 | 142 |
| *Oxyopes ramosus* (Martini & Goeze, 1778) | 1 | 0 | 1 |
| *Titanoeca schineri* L. Koch, 1872 | 19 | 4 | 0 |
| *Zora pardalis* Simon, 1878 | 1 | 3 | 0 |
| *Zora spinimana* (Sundevall, 1833) | 1 | 0 | 0 |
| *Phrurolithus festivus* (C. L. Koch, 1835) | 16 | 6 | 0 |
| *Phrurolithus minimus* C. L. Koch, 1839 | 20 | 2 | 0 |
| *Clubiona brevipes* Blackwall, 1841 | 0 | 1 | 0 |
| *Zodarion germanicum* (C. L. Koch, 1837) | 55 | 13 | 1 |
| *Aphantaulax trifasciata* (O. P.-Cambridge, 1872) | 0 | 1 | 0 |
| *Berlandina cinerea* (Menge, 1872) | 2 | 5 | 9 |
| *Callilepis nocturna* (Linnaeus, 1758) | 3 | 4 | 4 |
| *Callilepis schuszteri* (Herman, 1879) | 5 | 3 | 0 |
| *Drassodes lapidosus* (Walckenaer, 1802) | 1 | 0 | 0 |
| Drassyllus lutetianus (L. Koch, 1866) | 2 | 0 | 0 |
| *Drassyllus praeficus* (L. Koch, 1866) | 7 | 6 | 0 |
| *Drassyllus villicus* (Thorell, 1875) | 2 | 0 | 0 |
| *Gnaphosa mongolica* Simon, 1895 | 10 | 16 | 12 |
| *Haplodrassus bohemicus* Miller & Buchar, 1977 | 3 | 5 | 0 |
| *Haplodrassus signifer* (C. L. Koch, 1839) | 1 | 0 | 0 |
| *Micaria dives* (Lucas, 1846) | 4 | 4 | 2 |
| *Micaria fulgens* (Walckenaer, 1802) | 0 | 3 | 0 |
| *Poecilochroa variana* (C. L. Koch, 1839) | 0 | 1 | 0 |
| *Sernokorba* sp. Kamura, 1992 | 1 | 0 | 0 |
| *Zelotes apricorum* (L. Koch, 1876) | 13 | 1 | 0 |
| *Zelotes electus* (C. L. Koch, 1839) | 17 | 6 | 1 |
| *Zelotes exiguus* (Müller & Schenkel, 1895) | 1 | 0 | 1 |

| | | | |
|---|---|---|---|
| *Zelotes longipes* (L. Koch, 1866) | 32 | 42 | 43 |
| *Zelotes segrex* (Simon, 1878) | 1 | 13 | 20 |
| *Philodromus cespitum* (Walckenaer, 1802) | 0 | 0 | 1 |
| *Philodromus collinus* C. L. Koch, 1835 | 1 | 1 | 0 |
| *Pulchellodromus ruficapillus* (Simon, 1885) | 0 | 0 | 1 |
| *Thanatus arenarius* L. Koch, 1872 | 0 | 1 | 0 |
| *Tibellus macellus* Simon, 1875 | 64 | 29 | 30 |
| *Ebrechtella tricuspidata* (Fabricius, 1775) | 0 | 1 | 0 |
| *Ozyptila atomaria* (Panzer, 1801) | 0 | 0 | 1 |
| *Runcinia grammica* (C. L. Koch, 1837) | 1 | 5 | 4 |
| *Synema ornatum* (Thorell, 1875) | 6 | 12 | 7 |
| *Thomisus onustus* Walckenaer, 1805 | 11 | 16 | 18 |
| *Xysticus audax* (Schrank, 1803) | 1 | 0 | 0 |
| *Xysticus cristatus* (Clerck, 1757) | 0 | 1 | 0 |
| *Xysticus kempeleni* Thorell, 1872 | 1 | 1 | 0 |
| *Xysticus kochi* Thorell, 1872 | 1 | 1 | 5 |
| *Xysticus lendli* Kulczyński, 1897 | 0 | 6 | 7 |
| *Xysticus ninnii* Thorell, 1872 | 2 | 8 | 3 |
| *Aelurillus v-insignitus* (Clerck, 1757) | 0 | 1 | 2 |
| *Carrhotus xanthogramma* (Latreille, 1819) | 0 | 1 | 0 |
| *Euophrys frontalis* (Walckenaer, 1802) | 8 | 2 | 1 |
| *Evarcha arcuata* (Clerck, 1757) | 4 | 4 | 0 |
| *Evarcha falcata* (Clerck, 1757) | 8 | 2 | 0 |
| *Heliophanus cupreus* (Walckenaer, 1802) | 5 | 2 | 0 |
| *Heliophanus lineiventris* Simon, 1868 | 2 | 19 | 60 |
| *Neon rayi* (Simon, 1875) | 0 | 2 | 0 |
| *Pellenes nigrociliatus* (Simon, 1875) | 3 | 2 | 2 |
| *Philaeus chrysops* (Poda, 1761) | 0 | 0 | 2 |
| *Salticus zebraneus* (C. L. Koch, 1837) | 0 | 1 | 0 |

| | | | |
|---|---|---|---|
| *Sittiflor zimmermanni* (Simon, 1877) | 1 | 1 | 1 |
| *Synageles hilarulus* (C. L. Koch, 1846) | 2 | 3 | 4 |
| *Talavera aequipes* (O. P.-Cambridge, 1871) | 0 | 3 | 0 |

**Appendix Table 4.** List of true-bug species ,individuals found in road verges, forest- steppe and pasturs.

| | Road verge | Forest-steppe | Pasture |
|---|---|---|---|
| *Adelphocoris lineolatus* (Goeze, 1778) | 4 | 9 | 10 |
| *Acalypta gracilis* (Fieber, 1844) | 18 | 128 | 159 |
| *Acalypta marginata* (Wolff, 1804) | 5 | 2 | 0 |
| *Acetropis (Acetropis) carinata* (Herrich-Schäffer, 1841) | 0 | 3 | 24 |
| *Adelphocoris lineolatus* (Goeze, 1778) | 0 | 3 | 3 |
| *Aelia acuminata* (Linnaeus, 1758) | 40 | 13 | 12 |
| *Aelia rostrata* Boheman, 1852 | 5 | 6 | 13 |
| *Agramma (Agramma) confusum* (Puton, 1879) | 1 | 0 | 0 |
| *Agramma (Agramma) minutum* Horvath, 1874 | 0 | 14 | 5 |
| *Amblytylus nasutus* (Kirschbaum, 1856) | 0 | 2 | 0 |
| *Antheminia lunulata* (Goeze, 1778) | 0 | 3 | 2 |
| *Aradus ribauti* Wagner, 1956 | 0 | 1 | 0 |
| *Beosus maritimus* (Scopoli, 1763) | 2 | 0 | 0 |
| *Beosus quadripunctatus* (Muller, 1766) | 1 | 0 | 0 |
| *Berytinus (Berytinus) clavipes* (Fabricius, 1775) | 0 | 1 | 0 |
| *Berytinus (Lizinus) geniculatus* (Horvath, 1885) | 2 | 1 | 4 |
| *Berytinus (Berytinus) minor* (Herrich-Schäffer, 1835) | 0 | 0 | 1 |
| *Brachycarenus tigrinus* (Schilling, 1829) | 0 | 3 | 4 |

| | | | |
|---|---|---|---|
| *Byrsinus flavicornis* (Fabricius, 1794) | 1 | 1 | 2 |
| *Campylomma verbasci* (Meyer-Dür, 1843) | 3 | 0 | 0 |
| *Canthophorus melanopterus* (Herrich-Schäffer, 1835) | 0 | 0 | 2 |
| *Capsus ater* (Linnaeus, 1758) | 1 | 0 | 0 |
| *Carpocoris (Carpocoris) pudicus* (Poda, 1761) | 12 | 11 | 4 |
| *Carpocoris (Carpocoris) purpureipennis* (De Geer, 1773) | 0 | 2 | 0 |
| *Catoplatus carthusianus* (Goeze, 1778) | 30 | 2 | 9 |
| *Charagochilus (Charagochilus) gyllenhalii* (Fallen, 1807) | 0 | 2 | 0 |
| *Chartoscirta cocksii* (Curtis, 1835) | 0 | 0 | 2 |
| *Chlamydatus (Euattus) pullus* (Reuter, 1870) | 1 | 1 | 7 |
| *Chorosoma gracile* Josifov, 1968 | 57 | 199 | 390 |
| *Copium clavicorne* (Linnaeus, 1758) | 1 | 4 | 1 |
| *Coranus* sp. | 1 | 2 | 5 |
| *Corizus hyoscyami* (Linnaeus, 1758) | 1 | 0 | 0 |
| *Corythucha arcuata* (Say, 1832) | 4 | 0 | 5 |
| *Deraeocoris (Deraeocoris) ruber* (Linnaeus, 1758) | 21 | 7 | 0 |
| *Deraeocoris (Camptobrochis) serenus* (Douglas & Scott, 1868) | 1 | 0 | 0 |
| *Deraeocoris (Deraeocoris) ventralis* Reuter, 1904 | 1 | 0 | 0 |
| *Derephysia (Paraderephysia) cristata* (Panzer, 1806) | 0 | 1 | 3 |
| *Dicranocephalus albipes* (Fabricius, 1781) | 10 | 29 | 43 |
| *Dictyla echii* (Schrank, 1782) | 1 | 2 | 0 |
| *Dictyla rotundata* (Herrich-Schäffer, 1835) | 0 | 0 | 2 |
| *Dimorphopterus doriae* (Ferrari, 1874) | 16 | 3 | 8 |
| *Dimorphopterus spinolae* (Signoret, 1857) | 53 | 5 | 0 |
| *Dolycoris baccarum* (Linnaeus, 1758) | 9 | 1 | 2 |
| *Emblethis ciliatus* Horvath, 1875 | 11 | 46 | 160 |

|  |  |  |  |
|---|---|---|---|
| *Emblethis verbasci* (Fabricius, 1803) | 1 | 0 | 6 |
| *Europiella albipennis* (Fallen, 1829) | 97 | 68 | 6 |
| *Eurydema (Eurydema) oleracea* (Linnaeus, 1758) | 1 | 0 | 0 |
| *Eurydema (Eurydema) ornata* (Linnaeus, 1758) | 4 | 3 | 5 |
| *Eurygaster dilaticollis* Dohrn, 1860 | 9 | 74 | 50 |
| *Eurygaster maura* (Linnaeus, 1758) | 0 | 2 | 1 |
| *Eurygaster testudinaria* (Geoffroy, 1785) | 0 | 0 | 1 |
| *Galeatus spinifrons* (Fallen, 1807) | 0 | 0 | 2 |
| *Gampsocoris culicinus* Seidenstucker, 1948 | 0 | 7 | 1 |
| *Geocoris (Geocoris) grylloides* (Linnaeus, 1761) | 8 | 10 | 15 |
| *Globiceps (Kelidocoris) flavomaculatus* (Fabricius, 1794) | 1 | 0 | 1 |
| *Graphosoma lineatum* (Linnaeus, 1758) | 1 | 0 | 5 |
| *Hallodapus suturalis* (Herrich-Schäffer, 1837) | 28 | 3 | 12 |
| *Jalla dumosa* | 0 | 2 | 0 |
| *Kalama tricornis* (Schrank, 1801) | 0 | 1 | 0 |
| *Lasiacantha capucina* (Germar, 1837) | 0 | 1 | 2 |
| *Lasiacantha gracilis* (Herrich-Schäffer, 1830) | 1 | 23 | 7 |
| *Leptopterna ferrugata* (Fallen, 1807) | 0 | 7 | 3 |
| *Liorhyssus hyalinus* (Fabricius, 1794) | 0 | 3 | 3 |
| *Lygaeosoma sardeum* Spinola, 1837 | 3 | 5 | 2 |
| *Lygaeus equestris* (Linnaeus, 1758) | 1 | 0 | 0 |
| *Lygaeus simulans* Deckert, 1985 | 103 | 24 | 35 |
| *Lygus pratensis* (Linnaeus, 1758) | 1 | 1 | 0 |
| *Lygus rugulipennis* Poppius, 1911 | 5 | 0 | 1 |
| *Macroplax preyssleri* (Fieber, 1837) | 5 | 25 | 47 |
| *Megaloceroea recticornis* (Geoffroy, 1785) | 2 | 3 | 1 |
| *Megalocoleus naso* (Reuter, 1879) | 0 | 9 | 2 |

| | | | |
|---|---|---|---|
| *Megalonotus hirsutus* Fieber, 1861 | 0 | 2 | 1 |
| *Megalonotus sabulicola* (Thomson, 1870) | 2 | 0 | 0 |
| *Melanocoryphus albomaculatus* (Goeze, 1778) | 1 | 0 | 0 |
| *Melanocoryphus tristrami* (Douglas & Scott, 1868) | 1 | 1 | 2 |
| *Menaccarus arenicola* (Scholz, 1847) | 37 | 73 | 267 |
| *Metopoplax origani* (Kolenati, 1845) | 3 | 0 | 1 |
| *Microporus nigrita* (Fabricius, 1794) | 1 | 0 | 0 |
| *Monosteira unicostata* (Mulsant & Rey, 1852) | 1 | 3 | 0 |
| *Monosynamma bohemanni* (Fallen, 1829) | 0 | 2 | 3 |
| *Myrmecoris gracilis* (R.F. Sahlberg, 1848) | 1 | 0 | 1 |
| *Myrmus miriformis* (Fallen, 1807) | 5 | 0 | 0 |
| *Nabis (Nabis) pseudoferus* Remane, 1949 | 21 | 13 | 11 |
| *Nabis (Nabis) punctatus* A. Costa, 1847 | 2 | 3 | 2 |
| *Nabis (Nabis) rugosus* (Linnaeus, 1758) | 2 | 1 | 0 |
| *Neides tipularius* (Linnaeus, 1758) | 112 | 37 | 30 |
| *Neottiglossa leporina* (Herrich-Schäffer, 1830) | 18 | 1 | 15 |
| *Nysius cymoides* (Spinola, 1837) | 3 | 5 | 9 |
| *Nysius ericae* (Schilling, 1829) | 0 | 1 | 9 |
| *Nysius senecionis* (Schilling, 1829) | 3 | 1 | 1 |
| *Nysius thymi* (Wolff, 1804) | 7 | 1 | 2 |
| *Ochetostethus opacus* (Scholtz, 1847) | 0 | 1 | 0 |
| *Odontoscelis (Odontoscelis) lineola* Rambur, 1839 | 1 | 3 | 8 |
| *OscaOncochila scapularis* (Fieber, 1844) | 14 | 27 | 32 |
| *Orius (Orius) niger* (Wolff, 1811) | 2 | 10 | 15 |
| *Orthocephalus bivittatus* Fieber, 1864 | 1 | 1 | 0 |
| *Orthocephalus proserpinae* (Mulsant & Rey, 1852) | 2 | 0 | 0 |
| *Ortholomus punctipennis* (Herrich-Schäffer, 1838) | 6 | 11 | 3 |

|  |  |  |  |
|---|---|---|---|
| *Oxycarenus (Euoxycarenus) pallens* (Herrich-Schäffer, 1850) | 2 | 0 | 64 |
| *Palomena prasina* (Linnaeus, 1761) | 305 | 78 | 2 |
| *Parapiesma kochiae* (Becker, 1867) | 4 | 4 | 14 |
| *Parapiesma silenes* (Horvath, 1888) | 5 | 19 | 40 |
| *Peribalus (Peribalus) strictus* (Fabricius, 1803) | 1 | 0 | 0 |
| *Phimodera humeralis* (Dalman, 1823) | 12 | 44 | 132 |
| *Phymata (Phymata) crassipes* (Fabricius, 1775) | 0 | 2 | 0 |
| *Phytocoris (Ktenocoris) insignis* Reuter, 1876 | 6 | 9 | 0 |
| *Picromerus bidens* (Linnaeus, 1758) | 1 | 0 | 0 |
| *Pionosomus opacellus* Horvath, 1895 | 28 | 33 | 32 |
| *Plagiognathus (Plagiognathus) fulvipennis* (Kirschbaum, 1856) | 63 | 41 | 13 |
| *Plinthisus (Plinthisus) longicollis* Fieber, 1861 | 2 | 1 | 0 |
| *Polymerus (Poeciloscytus) brevicornis* (Reuter, 1879) | 19 | 32 | 4 |
| *Polymerus (Poeciloscytus) cognatus* (Fieber, 1858) | 0 | 0 | 1 |
| *PuniPolymerus (Poeciloscytus) unifasciatus* (Fabricius, 1794) | 0 | 5 | 0 |
| *Polymerus (Poeciloscytus) vulneratus* (Panzer, 1806) | 0 | 1 | 1 |
| *Polymerus (Polymerus) nigrita* (Fallen, 1807) | 1 | 0 | 0 |
| *Prostemma (Prostemma) sanguineum* (Rossi, 1790) | 2 | 0 | 0 |
| *Prostemma (Prostemma) sanguineum* (Rossi, 1790) | 1 | 0 | 0 |
| *Psacasta (Cryptodontus) neglecta* (Herrich-Schäffer, 1837) | 0 | 0 | 1 |
| *Pyrrhocoris apterus* (Linnaeus, 1758) | 1 | 0 | 0 |
| *Raglius alboacuminatus* (Goeze, 1778) | 2 | 0 | 0 |
| *Raglius confusus* (Reuter, 1886) | 9 | 26 | 3 |
| *Rhacognathus punctatus* (Linnaeus, 1758) | 0 | 2 | 0 |
| *Rhopalus (Rhopalus) parumpunctatus* Schilling, 1829 | 461 | 179 | 206 |

| | | | |
|---|---|---|---|
| *Rhynocoris (Rhynocoris) iracundus* (Poda, 1761) | 1 | 2 | 0 |
| *Rhyparochromus vulgaris* (Schilling, 1829) | 0 | 0 | 1 |
| *Rubiconia intermedia* (Wolff, 1811) | 45 | 27 | 5 |
| *Sciocoris (Aposciocoris) microphthalmus* Flor, 1860 | 1 | 0 | 0 |
| *Sciocoris (Sciocoris) cursitans* (Fabricius, 1794) | 5 | 12 | 18 |
| *Sciocoris (Sciocoris) sulcatus* Fieber, 1851 | 1 | 0 | 0 |
| *Spathocera obscura* (Germar, 1842) | 0 | 5 | 20 |
| *ScalStenodema (Brachystira) calcarata* (Fallen, 1807) | 12 | 0 | 4 |
| *Stenotus binotatus* (Fabricius, 1794) | 44 | 0 | 0 |
| *Stephanitis (Stephanitis) pyri* (Fabricius, 1775) | 2 | 1 | 1 |
| *Stictopleurus abutilon* (Rossi, 1790) | 1 | 0 | 0 |
| *Stictopleurus pictus* (Fieber, 1861) | 2 | 0 | 0 |
| *Stictopleurus punctatonervosus* (Goeze, 1778) | 0 | 2 | 0 |
| *Stygnocoris sabulosus* (Schilling, 1829) | 15 | 0 | 0 |
| *Strongylocoris niger* (Herrich-Schäffer, 1835) | 2 | 0 | 0 |
| *Syromastus rhombeus* (Linnaeus, 1767) | 5 | 3 | 3 |
| *Thyreocoris scarabaeoides* (Linnaeus, 1758) | 1 | 0 | 0 |
| *Tingis (Tingis) grisea* Germar, 1835 | 0 | 0 | 1 |
| *Trigonotylus caelestialium* (Kirkaldy, 1902) | 0 | 1 | 28 |
| *Trigonotylus pulchellus* (Hahn, 1834) | 2 | 0 | 15 |
| *Tropidophlebia costalis* (Herrich-Schäffer, 1850) | 6 | 0 | 4 |
| *Vilpianus galii* (Wolff, 1802) | 0 | 2 | 4 |
| *Xanthochilus quadratus* (Fabricius, 1798) | 1 | 1 | 9 |
| *Zicrona caerulea* Linnaeus, 1758 | 0 | 0 | 1 |

**Appendix Table 5. List of ant species, individuals found in road verges, forest- steppe and pasturs.**

| | Road verge | Forest-steppe | Pasture |
|---|---|---|---|
| *Camponotus vagus* | 43 | 35 | 9 |
| *Cataglyphis aenescens* | 33 | 173 | 471 |
| *Formica cunicularia* | 245 | 202 | 343 |
| *Formica fusca* | 119 | 12 | 3 |
| *Formica pratensis* | 2 | 0 | 11 |
| *Formica rufa* | 186 | 0 | 0 |
| *Formica rufibarbis* | 53 | 25 | 97 |
| *Formica sanguinea* | 217 | 1 | 0 |
| *Lasius bombycina* | 465 | 255 | 608 |
| *Lasius carniolicus* | 0 | 15 | 0 |
| *Lasius niger* | 46 | 65 | 13 |
| *Lasius nitidigaster* | 0 | 1 | 0 |
| *Lasius psammophilus* | 661 | 1104 | 2132 |
| *Myrmica sabuleti* | 309 | 4 | 1 |
| *Myrmica schencki* | 19 | 0 | 1 |
| *Plagiolepis taurica* | 602 | 2048 | 2583 |
| *Polyergus rufescens* | 1 | 0 | 0 |
| *Solenopsis fugax* | 39 | 49 | 20 |
| *Tapinoma madeirense* | 14 | 25 | 452 |
| *Temnothorax affinis* | 5 | 3 | 0 |
| *Temnothorax crassispinus* | 4 | 0 | 0 |
| *Temnothorax interruptus* | 20 | 4 | 0 |
| *Temnothorax unifasciatus* | 134 | 3 | 0 |
| *Tetramorium cf. caespitum* | 776 | 143 | 1516 |
| *Tetramorium hungaricum* | 0 | 0 | 5 |