



# Ground-dwelling spider assemblages as indicators of urbanization in Tisza River floodplain forest patches

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## Abstract

We evaluated the impacts of urbanization on ground-dwelling spiders in isolated floodplain forest patches of the Tisza River system (Szeged, Hungary) along a rural-suburban-urban gradient. We investigated how human-mediated landscape acts as an ecological filter shaping assemblage-level functional traits, including habitat affinity, microclimatic preferences, and hunting strategies. Generalized linear modeling revealed that overall species richness and the richness of forest specialists remained statistically uniform across the urban-rural continuum. However, intensive urban forest management (canopy thinning and leaf litter removal) induced marked shifts in assemblage composition driven by microclimatic desiccation. While moisture-dependent, disturbance-sensitive forest taxa were suppressed in the urban forest patches, the opening of the habitat's vegetation facilitated the establishment of dry-adapted (xerophilous), light-associated (photophilous), and open-habitat spiders. Indicator species analysis (IndVal) corroborated this structural turnover: *Piratula hygrophila* and *Liocranoeca striata* characterized undisturbed rural and suburban habitats, whereas *Tenuiphantes tenuis*, *Drassyllus pusillus*, *Pardosa agrestis*, and *Zelotes apricorum* emerged as distinct urban specialists. Our findings demonstrate that urbanization triggers a functional substitution of specialized riverine fauna with ubiquitous generalists. To preserve the unique biodiversity and ecological integrity of these vulnerable riparian remnants, local forest management intensity should be moderated, prioritizing the retention of dense canopy cover, and natural forest floor structure.

**Keywords** Diversity · Pitfall traps · Habitat affinity · Human disturbance · Species richness · IndVal

## Introduction

Today, urbanization is a critical anthropogenic disturbance, posing a threat to the survival of numerous native species. The impacts of urbanization considerably affect terrestrial ecosystems, making it crucial to evaluate, and comprehend the related effects on biodiversity (McKinney 2002; Gál et al. 2008). Two considerable consequences of it are the reduction and alteration of habitats, which are the primary causes of the well-documented decline in habitat structural and functional diversity in urbanized environments (Eötvös

et al. 2020). Furthermore, urbanization substantially modifies local environmental conditions by altering habitat structure, vegetation cover, microclimate, soil characteristics, and resource availability; thereby, influencing the composition and diversity of biological communities (Papp et al. 2020). If the global trend of increasing population density continues and all areas change due to urban expansion, the modified land cover will expand by 1.2 million km<sup>2</sup> by 2030 (Seto et al. 2012). Urban areas are expanding rapidly worldwide, with their spatial extent increasing approximately twice as fast as population growth (Angel et al. 2011). This expansion leads to substantial habitat transformation, fragmentation, and changes in local environmental conditions, including vegetation structure, microclimate, and resource availability, thereby affecting biodiversity and the composition of ecological communities.

Urbanization is an ongoing process hypothesized to considerably impact suburban environments, potentially decreasing species abundance and diversity (Piano et al. 2019). On both local and global scales, the expansion of

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urban areas results in the loss of biodiversity and the conversion or loss of natural habitats (McDonald et al. 2008). Additionally, urbanization decreases species richness of many species, which is particularly noticeable in densely populated cities and intensively managed areas (McKinney 2008; Niemelä and Kotze 2009). The continued expansion of urban areas is expected to increase habitat transformation and fragmentation, making it increasingly important to understand how biological communities respond to urbanization (Seto et al. 2012). Urbanization is often associated with homogenization (loss of species richness) by the overpopulation of generalist species that can lead to a decrease in biodiversity (Hernández-Téllez et al. 2023). However, some studies have concluded that urbanization can occasionally increase diversity by facilitating the establishment of non-native species that displace native ones (McKinney 2002, 2006). Urban areas often exhibit exceptionally high habitat heterogeneity because they contain a mosaic of land-use types, including parks, gardens, remnant forest patches, built-up areas, roadsides, and vacant lots (Savard et al. 2000; Thompson et al. 2003). This environmental mosaic creates a wide variety of microhabitats and resource conditions within relatively small spatial scales, allowing species with different ecological requirements to coexist. Consequently, urban landscapes may support high beta diversity and, in some cases, elevated overall species richness compared to more homogeneous rural environments, particularly for taxa capable of maintaining viable populations in small habitat patches (Niemelä 1999; Wania et al. 2006).

An international project called GlobeNet (Global Network for Monitoring Landscape Change) was established in 1998 to monitor the impact of urbanization on biodiversity in various countries around the world (Niemelä et al. 2000). The GlobeNet project identified a gradient of rural-suburban-urban forest habitats representing different levels of human disturbance (Pickett et al. 2001). The primary objective of the project is to investigate the related effects using a commonly used sampling method (pitfall trapping), which targets various groups of terrestrial arthropods such as terrestrial isopods, spiders, and rove beetles, while most of the studies conducted within the project have focused on ground beetles (Niemelä et al. 2002; Ishitani et al. 2003; Magura et al. 2004, 2008b, c; d, 2010a; Sadler et al. 2006; Elek and Lövei 2007; Gaublot et al. 2008; Tóthmérész et al. 2011). Later on, research on other arthropod taxa has been included (spiders: Alaruikka et al. 2002; Magura et al. 2008d, 2010b; Horváth et al. 2012, 2014; Lövei et al. 2018; terrestrial isopods: Hornung et al. 2007; Vilisics et al. 2007; Magura et al. 2008a; d; rove beetles: Magura et al. 2013).

Spiders are widely recognized as sensitive indicators of environmental change because their distribution and assemblage composition respond rapidly to alterations in habitat

structure, microclimatic conditions, vegetation complexity, and disturbance intensity. Factors such as canopy openness, litter depth, humidity, vegetation stratification, and land-use intensity can strongly influence spider assemblages by affecting prey availability, shelter, dispersal opportunities, and microhabitat suitability. Consequently, spider assemblages have frequently been used to assess the ecological effects of forest management, habitat degradation, agricultural intensification, and urbanization (Benhadi-Marin et al. 2020; Košulič et al. 2021; Michalko et al. 2023; Hamřík et al. 2024). Urbanization alters habitat structure and microclimatic conditions through changes in vegetation cover, canopy closure, and disturbance regimes, leading to shifts in spider diversity, functional composition, and behavior (Dahirel et al. 2019). Given their sensitivity to these environmental gradients, spiders represent a suitable model group for investigating the ecological consequences of urbanization in forest habitats.

While numerous studies have investigated macro-invertebrate response along urbanization gradients, the vast majority have focused on stable, terrestrial ecosystems such as temperate upland forests, urban parks, or residential lawns. Consequently, how urbanization impacts highly dynamic, moisture-dependent, and intrinsically disturbed ecosystems remains poorly understood. This study addresses this critical gap by examining ground-dwelling spider assemblages within the isolated, semi-natural floodplain forest patches of the Tisza River system in and around Szeged. Riparian floodplain forests are unique ecological corridors characterized by specialized, humidity-dependent, and disturbance-sensitive fauna adapted to historical hydrological regimes.

The primary novelty of this research lies in its comprehensive integration of habitat affinity, fine-scale microclimatic preferences (moisture and light), hunting strategies, and assemblage-level fidelity (via IndVal analysis) into a unified framework of urbanization-driven ecological filtering. Rather than evaluating isolated species metrics, we explore how human-mediated landscape modification, manifested through local canopy thinning, understory clearing, and subsequent microclimatic desiccation, acts as a selective environmental sieve. By examining these mechanisms in a riparian context, this study provides critical, scale-appropriate insights into the ecological filtering pressures of expanding cities and establishes clear, localized management guidelines to buffer and protect vulnerable riverine biodiversity within urban forest remnants.

Our study aimed to evaluate the effects of urbanization on ground-dwelling spider assemblages. Several hypotheses have been developed to explain the consequences of various human disturbances on arthropod communities. We tested the following hypotheses:

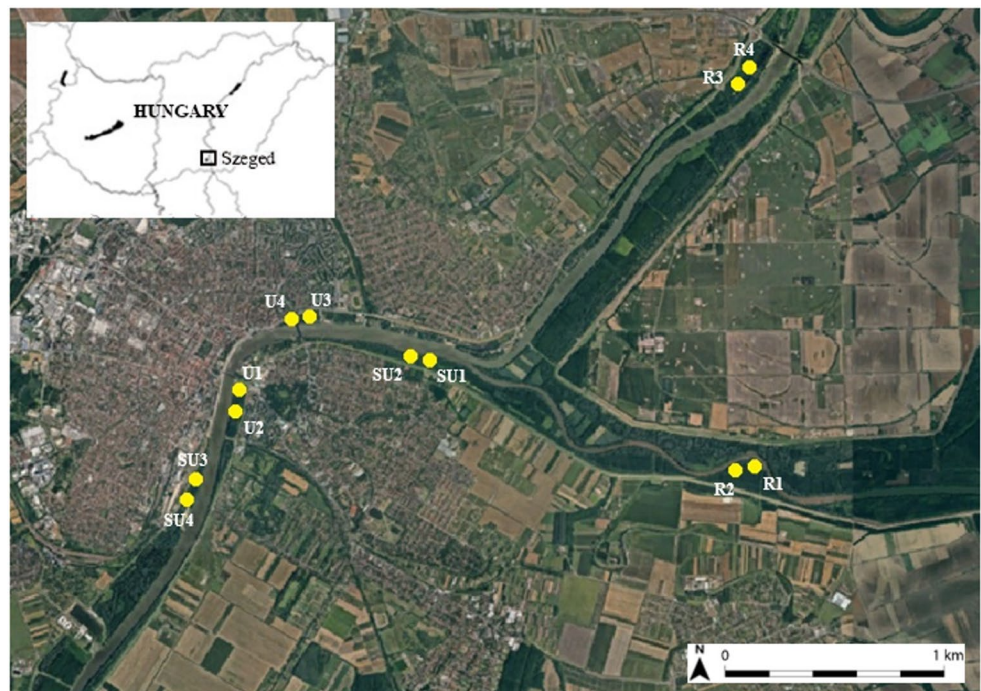
1. Increasing disturbance hypothesis: the number of species decreases from rural sites to heavily disturbed urban ones (Gray 1989);
2. Habitat specialist species hypothesis: the number of forest specialist species decreases towards strongly disturbed urban areas due to higher levels of disturbance (Magura et al. 2004);
3. Opportunistic species hypothesis: opportunistic species can take advantage of high levels of disturbance, and their dominance increases in heavily disturbed habitats (Gray 1989);
4. Matrix species hypothesis: urban forest patches become artificial park-like areas with open patches, allowing species to enter the forest patches from surrounding matrices (open habitats in our study). Therefore, the number of species associated with open habitats in urban areas is higher compared to suburban and rural areas (Tóthmérész et al. 2011);
5. Hygrophilous species hypothesis: rural areas provide higher humidity; thus, the number of hygrophilous species decreases from rural areas to urban habitats (Magura et al. 2013);
6. Xerophilous species hypothesis: urbanization leads to decreased humidity in forests, resulting in the highest number of xerophilous species in urban habitats (Horváth et al. 2012);
7. Photophilous species hypothesis: urban forest patches become more open and clearer due to urbanization, leading to an increase in the number of photophilous species from rural areas to urban areas (Horváth et al. 2012);
8. Disturbance-sensitive species hypothesis: the number of disturbance-sensitive species decreases from rural habitats to urban ones (Tajthi et al. 2017);
9. Web-building species hypothesis: the number of species of web-building spiders decreases from rural sampling areas to urban sampling areas due to intensified forest management (Lövei et al. 2018).

## Materials and methods

### Study area and sampling

To evaluate the impacts of urbanization, the sampling design followed the standardized framework of the international GlobeNet protocol (Niemelä et al. 2000), which establishes hierarchical spatial criteria to monitor biodiversity along human disturbance gradients. An urbanization gradient, consisting of rural, suburban, and urban habitat areas, was chosen for spider collection in Szeged city and the surrounding semi-natural separated floodplain forest patches in the Tisza floodplain (Fig. 1). In accordance with the macro-spatial requirements of the GlobeNet protocol, these primary urban-gradient zones were located at least one kilometer apart from each other. These study areas were characterized by forest patches dominated by white poplar (*Populus alba*), white willow (*Salix alba*), European white elm (*Ulmus laevis*), European ash (*Fraxinus excelsior*), and London plane tree (*Platanus x acerifolia*). All study sites consisted of urban woodland habitats.

**Fig. 1** Map of the study area. The study area is in and around Szeged City (46° 15' N, 20° 10' E). The dotted areas indicate the forested areas. Circles indicate the locations of the twelve sampling sites. Letters indicate the habitat types: *R* rural, *SU* suburban, *U* urban



The rural habitat was characterized by low-intensity forest management without any on-site buildings. Intensive forestry operations such as clear-cutting were absent during the study period. In the suburban areas, there were walking and hiking trails, moderately visited by tourists and dog walkers. Here, the undergrowth was not thinned, while fallen trees and broken branches were regularly removed. The urban sampling areas were near a frequently visited riverbank and a campsite. Fallen trees and branches were periodically removed, and shrubs were heavily thinned, resulting in a park-like environment. The lawn was also frequently mowed in the urban areas, and the cut phytomass was removed.

Four spatially distinct forest patches (hereafter referred to as sampling sites) were selected within each macro-habitat type (rural, suburban, urban). While these four sites shared the same overarching habitat type, and dominant tree composition to serve as valid statistical replicates for that gradient level, they represented physically separated and spatially independent units. Each site was larger than 2,500 m<sup>2</sup> and separated from the nearest adjacent patch by a minimum distance of 100 m. Ten pitfall traps were randomly placed at least 10 m apart within each sampling area to capture spiders. During each sampling period, 120 samples were collected (three habitat types  $\times$  four sampling areas  $\times$  ten pitfall traps). The pitfall traps contained 100 milliliters of 75% ethylene glycol as a killing and preservative fluid. Traps were emptied every four weeks from early June to early October 2014. Thus, there were four sampling periods during this time. The collected samples were sorted in the laboratory, and the spiders were stored in 70% ethyl alcohol until further processing. The identification of species was carried out using the standard key of Nentwig et al. (2024). To characterize the local habitat structure and provide a robust empirical foundation for testing our environmental demand hypotheses (specifically the hygrophilous, xerophilous, photophilous, and web-building species hypotheses), we assessed six microenvironmental variables at all 12 sampling sites. These specific variables were chosen because ground-dwelling spider assemblages are highly sensitive to microclimatic shifts and the structural complexity of the forests.

**Table 1** Mean values ( $\pm$ SE) of the six assessed environmental variables along the urbanization gradient

| Environmental variable              | Rural           | Suburban        | Urban           |
|-------------------------------------|-----------------|-----------------|-----------------|
| Relative humidity (%)               | 76.3 $\pm$ 0.86 | 70.4 $\pm$ 0.97 | 58.3 $\pm$ 1.05 |
| Cover of leaf litter (%)            | 24.3 $\pm$ 2.25 | 22.6 $\pm$ 2.42 | 15.2 $\pm$ 1.75 |
| Cover of decaying wood material (%) | 16.1 $\pm$ 1.13 | 15.3 $\pm$ 1.22 | 5.2 $\pm$ 0.23  |
| Cover of herbs (%)                  | 24.1 $\pm$ 2.83 | 25.3 $\pm$ 3.09 | 37.2 $\pm$ 1.13 |
| Cover of shrubs (%)                 | 47.6 $\pm$ 1.24 | 53.4 $\pm$ 1.13 | 5.3 $\pm$ 1.82  |
| Canopy cover (%)                    | 94.2 $\pm$ 1.12 | 82.4 $\pm$ 1.52 | 64.7 $\pm$ 2.64 |

Environmental data collection was synchronized with the monthly pitfall trap emptying schedule across the four sampling periods from early June to early October 2014 to capture temporal variations. At each sampling site, microclimatic and structural parameters were recorded as follows:

- **Relative Air Humidity (%):** Measured monthly at the soil surface level (approx. 5 cm above ground) at the center of each site using a calibrated digital thermo-hygrometer during standardized midday hours (11:00–14:00) to minimize diurnal fluctuation bias.
- **Vegetation and Floor Cover (%):** The percentage cover of leaf litter, decaying wood material, herbs, and shrubs was visually estimated monthly within a 2  $\times$  2 m quadrat centered around each of the ten pitfall traps per site.
- **Canopy Cover (%):** Evaluated monthly above each pitfall trap using a spherical densiometer to quantify forest openness.

To match the temporal scale of the spider capture data, which were pooled across the collection periods for robust assemblage-level analysis, the monthly environmental measurements were averaged to generate a representative seasonal mean ( $\pm$ SE) for each gradient zone (Table 1). These environmental variables served a dual purpose: first, they empirically validated that our designated rural-suburban-urban gradient successfully captured a shifting environmental disturbance continuum (i.e., confirming that urban sites exhibited significantly lower humidity and canopy cover); second, they provided the essential ecological context required to interpret the community separation observed in our multidimensional scaling (MDS) ordination and Indicator Value (IndVal) analyses (Table 1; Fig. 3).

## Data processing

The collected species were categorized based on their habitat affinity (forest, generalist, open habitat), ecological demands (hygrophilous, xerophilous, shade-preferring, and photophilous), hunting strategy (web-builder and hunter), and sensitivity to disturbance (insensitive to disturbance and sensitive to disturbance), using the works of Buchar and Ruzicka (2002) and Nentwig et al. (2024). For statistical analysis, the captures from each trap were pooled for each collection period.

A generalized linear model (GLM) was used to assess the differences among the three habitat types regarding the number of spiders, species with different habitat affinity and ecological demands, web-building species, and disturbance-sensitive species. The distribution of the dependent variables was taken as Poisson distribution with the *log link* function. This distribution assumes that the mean and variance of the

data are equal. Actual data deviates from this assumption, as the variance is much larger than the mean (O'Hara and Kotze 2010). This biological condition (overdispersion) was also incorporated into the model using Pearson  $\chi^2$  (Zuur et al. 2009). Therefore, GLMs based on quasi-Poisson distribution were used. For multiple comparisons among means, an LSD test was carried out if GLM indicated a significant difference between the means (StatSoft Inc. 2010).

We compared the composition of ground-dwelling spider assemblages along the urbanization gradient by sites using multidimensional scaling (MDS). For the MDS ordination, we utilized the Hellinger distance (Legendre and Legendre 2012). This metric was specifically chosen because pitfall trap datasets are typically characterized by a high frequency of zeros and highly skewed species dominance; the Hellinger distance effectively down-weights hyper-abundant species by square-rooting relative abundances, avoiding the "species abundance paradox" during metric ordination.

We used the Indicator Value (IndVal) method (Dufrêne and Legendre 1997) to identify species that were characteristics of various stages of urbanization. This method derives indicator species based on habitat classification. We acquired the habitat classification through hierarchical cluster analysis at the habitat level, using Bray-Curtis dissimilarity to assess activity-density.

## Results

### Faunistic findings

There were 4409 individuals trapped belonging to 43 species. The most abundant species was *Ozyptila praticola*, with 1734 individuals, followed by *Piratula hygrophila*, with 842 specimens. These two species accounted for over 58% of the total individuals. In terms of raw sample counts across the gradient, the highest number of individuals was captured within the rural sites (1,814 individuals), followed by the suburban sites (1,479 individuals), while the lowest catch was recorded in the urban habitats (1,116 individuals; Table 2). The distribution of species among the three habitat types is presented in Table 2.

### Analysis of spider distribution along the urbanization gradient

The result of the generalized linear model (GLM; Fig. 2) revealed that overall spider species richness did not differ significantly among the three habitat types along the urbanization gradient ( $\chi^2=1.34$ ; df=2, 9;  $p=0.512$ ; Fig. 2A). No significant differences were found in the number of forest species among the three habitat types ( $\chi^2=3.06$ ; d.f.

= 2, 9;  $p=0.216$ ; Fig. 2B). The number of generalist species was significantly higher in rural and suburban areas compared to urban ones ( $\chi^2=17.52$ ; d.f. = 2, 9;  $p<0.001$ ; Fig. 2C). Contrarily, the number of species associated with open habitat was significantly lower in rural and suburban sites than in urban ones ( $\chi^2=18.18$ ; d.f. = 2, 9;  $p<0.001$ ; Fig. 2D). The number of hygrophilous species was significantly highest in suburban areas, with significant differences observed between rural and urban areas ( $\chi^2=42.64$ ; d.f. = 2, 9;  $p<0.001$ ; Fig. 3A). Additionally, a significantly higher number of xerophilous and photophilous species were collected from urban habitats than from rural and suburban habitats (xerophilous species:  $\chi^2=11.98$ ; df=2, 9;  $p<0.01$ ; Fig. 3B, photophilous species:  $\chi^2=24.99$ ; df=2, 9;  $p<0.001$ ; Fig. 3C). The number of disturbance-sensitive species was significantly higher in rural and suburban habitats than in urban ones ( $\chi^2=12.29$ ; d.f. = 2, 9;  $p<0.01$ ; Fig. 4A). The number of web-building species was significantly lower in rural and suburban habitats than in urban areas ( $\chi^2=8.30$ ; d.f. = 2, 9;  $p<0.05$ ; Fig. 4B).

The ordination (MDS) based on the abundances revealed that the ground-dwelling spider assemblages of rural and suburban habitats were different (separated) from the urban habitat assemblage (Fig. 5), and the four urban sampling sites formed a separate group.

The collected spider species were categorized into four affinity groups based on their Indicator Value (Table 3): (1) species showing no preference for any habitat (e.g., *O. praticola*, *Diplostyla concolor*, *Trochosa ruricola*, *Diplocephalus picinus*), (2) species associated with rural and suburban habitats (*P. hygrophila*, *Liocranoeca striata*), (3) species characteristic of rural habitats (*Ceratinella brevipes*, *Walckenaeria nudipalpis*), and (4) species found in urban habitats (*Tenuiphantes tenuis*, *Drassyllus praeficus*, *Pardosa agrestis*, *Zelotes apricorum*).

## Discussion

This study investigated nine research hypotheses. Four of the hypotheses were supported (matrix species, xerophilous species, photophilous species, and disturbance-sensitive species), while five of our hypotheses were not supported (increasing disturbance, habitat specialist species, opportunist species, hygrophilous and web-building species).

In this paper, the increasing disturbance hypothesis was not supported. The generalized linear model (GLM) revealed no significant difference in species richness among the three habitat types, indicating that the overall number of co-existing species remained statistically stable across the urban-rural continuum. While the number of captured individuals was numerically lower in the urban sites compared

**Table 2** List of collected species with individual numbers and their ecological traits in the three habitat types. Notations: “shade” marks shade-preferring species, “light” marks light-preferring species

| Species                        | Habitat preference | Disturbance sensitivity | Humidity preference | Light preference | Rural | Suburban | Urban |
|--------------------------------|--------------------|-------------------------|---------------------|------------------|-------|----------|-------|
| <i>Agyneta rurestris</i>       | Open habitat       | Non-sensitive           | Eurytopic           | Eurytopic        | 0     | 1        | 2     |
| <i>Alopecosa pulverulenta</i>  | Open habitat       | Non-sensitive           | Eurytopic           | Eurytopic        | 0     | 0        | 1     |
| <i>Anyphaena accentuata</i>    | Forest             | Moderately-sensitive    | Eurytopic           | Shade            | 2     | 1        | 2     |
| <i>Ceratinella brevipes</i>    | Generalist         | Moderately-sensitive    | Eurytopic           | Shade            | 6     | 0        | 0     |
| <i>Cheiracanthium mildei</i>   | Generalist         | Non-sensitive           | Eurytopic           | Eurytopic        | 0     | 0        | 2     |
| <i>Civizelotes pygmaeus</i>    | Open habitat       | Sensitive               | xerophilous         | Light            | 0     | 0        | 1     |
| <i>Clubiona lutescens</i>      | Generalist         | Non-sensitive           | Eurytopic           | Eurytopic        | 0     | 1        | 1     |
| <i>Diplocephalus picinus</i>   | Forest             | Moderately-sensitive    | Hygrophilous        | Shade            | 28    | 75       | 64    |
| <i>Diplostyla concolor</i>     | Forest             | Non-sensitive           | Hygrophilous        | Eurytopic        | 173   | 141      | 253   |
| <i>Drassyllus praeficus</i>    | Generalist         | Moderately-Sensitive    | xerophilous         | Eurytopic        | 0     | 0        | 4     |
| <i>Drassyllus pusillus</i>     | Open habitat       | Non-sensitive           | Eurytopic           | Light            | 9     | 3        | 29    |
| <i>Enoplognatha ovata</i>      | Generalist         | Non-sensitive           | Eurytopic           | Eurytopic        | 1     | 0        | 0     |
| <i>Enoplognatha thoracica</i>  | Generalist         | Non-sensitive           | Eurytopic           | Eurytopic        | 0     | 1        | 0     |
| <i>Erigone dentipalpis</i>     | Generalist         | Non-sensitive           | Hygrophilous        | Eurytopic        | 0     | 0        | 1     |
| <i>Euryopis flavomaculata</i>  | Generalist         | Moderately-sensitive    | Eurytopic           | Eurytopic        | 0     | 1        | 0     |
| <i>Gongylidium rufipes</i>     | Forest             | Moderately-sensitive    | Hygrophilous        | Eurytopic        | 0     | 0        | 1     |
| <i>Haplodrassus minor</i>      | Open habitat       | Sensitive               | Eurytopic           | Eurytopic        | 0     | 0        | 1     |
| <i>Liocranoeca striata</i>     | Generalist         | Sensitive               | Hygrophilous        | Eurytopic        | 379   | 124      | 25    |
| <i>Neon reticulatus</i>        | Generalist         | Moderately-sensitive    | Hygrophilous        | Eurytopic        | 0     | 2        | 0     |
| <i>Nerienne clathrata</i>      | Generalist         | Moderately-sensitive    | Hygrophilous        | Eurytopic        | 1     | 2        | 0     |
| <i>Ozyptila praticola</i>      | Generalist         | Moderately-sensitive    | Hygrophilous        | Eurytopic        | 814   | 388      | 532   |
| <i>Palliduphantes insignis</i> | Open habitat       | Non-sensitive           | Xerophilous         | Light            | 0     | 1        | 3     |
| <i>Pardosa agrestis</i>        | Open Habitat       | Non-sensitive           | Xerophilous         | Light            | 0     | 0        | 5     |
| <i>Pardosa alacris</i>         | forest             | Moderately-sensitive    | Xerophilous         | Shade            | 4     | 4        | 5     |
| <i>Phrurolithus festinus</i>   | Generalist         | Moderately-sensitive    | Eurytopic           | Eurytopic        | 5     | 27       | 16    |
| <i>Piratula hygrophila</i>     | Open habitat       | Moderately-sensitive    | Hygrophilous        | Eurytopic        | 295   | 535      | 12    |
| <i>Robertus arundineti</i>     | Open habitat       | Non-sensitive           | Eurytopic           | Light            | 0     | 0        | 1     |
| <i>Robertus lividus</i>        | forest             | Moderately-sensitive    | Hygrophilous        | Eurytopic        | 0     | 1        | 4     |
| <i>Steatoda albomaculata</i>   | Open habitat       | Sensitive               | Xerophilous         | Light            | 1     | 0        | 0     |
| <i>Steatoda triangulosa</i>    | Generalist         | Non-sensitive           | Eurytopic           | Eurytopic        | 0     | 0        | 1     |
| <i>Tenuiphantes flavipes</i>   | Generalist         | Moderately-sensitive    | Eurytopic           | Eurytopic        | 0     | 1        | 0     |
| <i>Tenuiphantes tenuis</i>     | Generalist         | Moderately-sensitive    | Eurytopic           | Eurytopic        | 9     | 2        | 26    |
| <i>Trachyzelotes pedestris</i> | Open habitat       | Moderately-sensitive    | Eurytopic           | Light            | 40    | 8        | 38    |
| <i>Trochosa ruricola</i>       | Generalist         | Non-sensitive           | Eurytopic           | Shade            | 38    | 153      | 70    |
| <i>Trochosa terricola</i>      | Generalist         | Non-sensitive           | Eurytopic           | Shade            | 0     | 1        | 0     |
| <i>Walckenaeria alticeps</i>   | Forest             | Sensitive               | Hygrophilous        | Shade            | 1     | 3        | 0     |
| <i>Walckenaeria nudipalpis</i> | Forest             | Moderately-sensitive    | Hygrophilous        | Eurytopic        | 6     | 0        | 0     |
| <i>Xysticus kochi</i>          | Open habitat       | Non-sensitive           | Eurytopic           | Light            | 0     | 0        | 3     |
| <i>Zelotes aeneus</i>          | Open habitat       | Non-sensitive           | Xerophilous         | Light            | 0     | 0        | 2     |
| <i>Zelotes apricorum</i>       | Generalist         | Moderately-sensitive    | Eurytopic           | Eurytopic        | 2     | 3        | 6     |
| <i>Zelotes electus</i>         | Open habitat       | Sensitive               | Xerophilous         | Light            | 0     | 0        | 3     |
| <i>Zelotes erebeus</i>         | Generalist         | Sensitive               | Eurytopic           | Eurytopic        | 0     | 0        | 1     |
| <i>Zelotes latreillei</i>      | Generalist         | Non-sensitive           | Eurytopic           | Eurytopic        | 0     | 0        | 1     |
| Total                          |                    |                         |                     |                  | 1814  | 1479     | 1116  |

to the rural ones (Table 2). This descriptive difference was not formally modeled for significance. Consequently, our findings demonstrate that urbanization primarily rearranges the composition and functional traits of the spider assemblages (as shown by the MDS and IndVal analyses) rather than inducing a statistically verifiable collapse in overall community wealth or total capture rates. This finding is consistent with previous studies on spiders in Finland

(Alaruikka et al. 2002) and Hungary (Magura et al. 2010b; Horváth et al. 2012). Alaruikka et al. (2002) investigated ground-dwelling spiders in southern Finland along a rural-suburban-urban habitat gradient, finding no differences in overall species richness between the studied habitats. At the same time, Hungarian studies (Magura et al. 2010b; Horváth et al. 2012) demonstrated that the total number of species was highest in urban habitats. One possible explanation

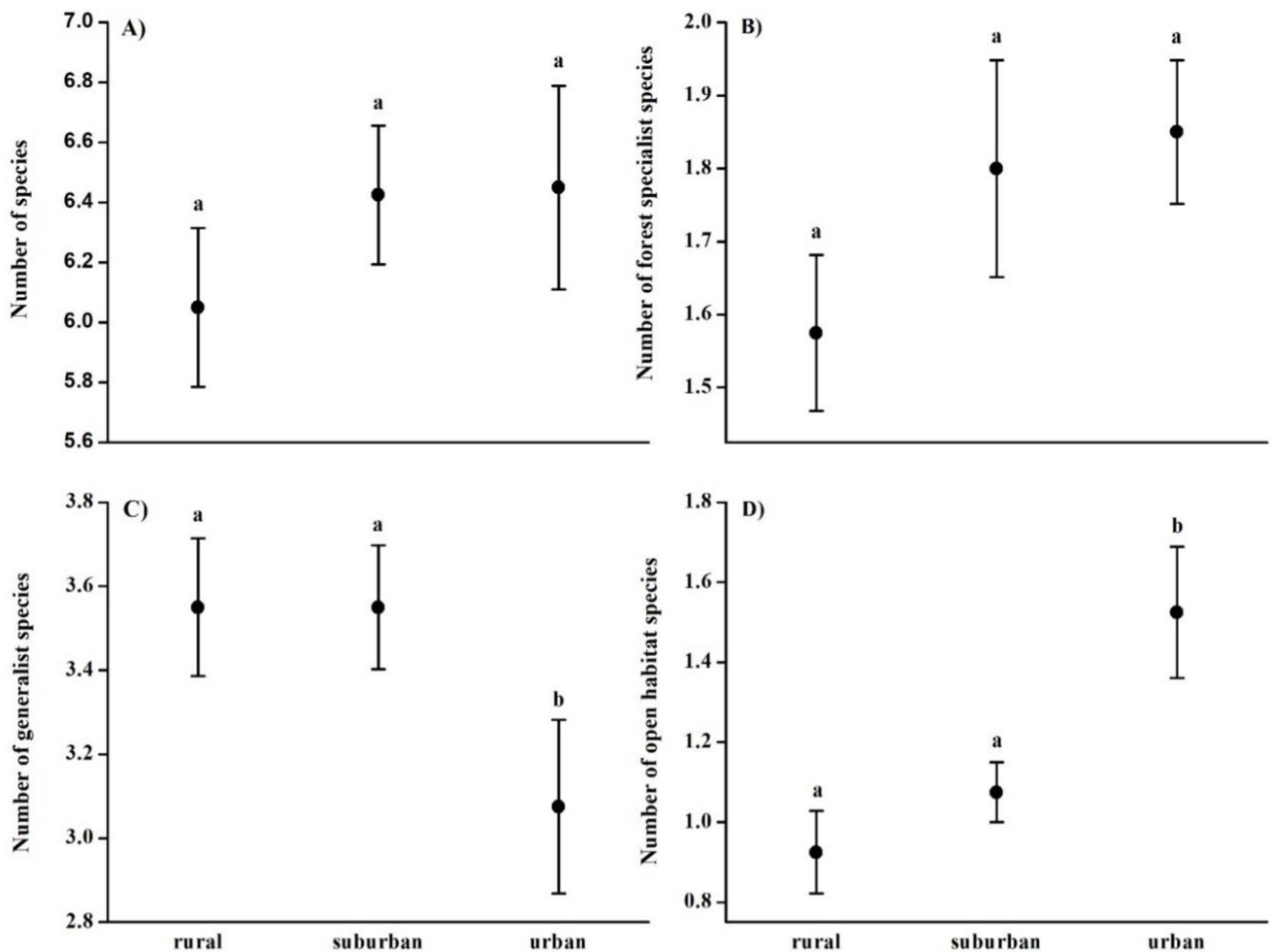


**Fig. 2** Total number of species (A), forest specialist species (B), generalist species (C), and open habitat species (D) along the rural-suburban-urban gradient ( $\pm$ SE). Different letters represent significant differences ( $p < 0.05$ ) based on the LSD test

for this difference is that urbanization results in more open patches in urban areas than in suburban and rural ones due to the landscape-transforming activities. As a result, open-habitat species from the surrounding areas may have settled in these urban forest patches, significantly increasing the number of species. Additionally, urban forest patches may be characterized by forest edge and/or transitional habitats that can significantly influence species occurrences (Lövei et al. 2006). Other studies on spiders in forests with varying levels of disturbance have also shown that species richness did not differ significantly among study areas, but the species composition varied along the disturbance gradient (Chen and Tso 2004; Hsieh et al. 2003; Ulrich et al. 2010). In previous studies based on ground beetles (Magura et al. 2004) and terrestrial isopods (Hornung et al. 2007) different findings were reported. In case of terrestrial isopods, there was no significant difference in the total number of species along the urbanization gradient (Hornung et al. 2007), while Magura et al. (2004) reported that the total number of

ground beetle species was significantly higher in the suburban and urban habitats than in the rural one. These findings suggest that various arthropod taxa may respond differently to the effects of urbanization, even within the same areas. Overall, these findings emphasize the complexity of species' responses to urbanization and emphasize the importance of considering multiple taxa and habitat types when studying the impact of urbanization on biodiversity.

Our findings did not support the habitat specialist species hypothesis, as overall species richness of forest-associated spiders remained statistically uniform across the urbanization gradient. This pattern of resilience among forest specialists in fragmented landscapes is highly consistent with previous urban-rural gradient studies conducted on macro-invertebrates in Finland (Alarukka et al. 2002) and Hungary (Horváth et al. 2012). These observations suggest that in those cases when canopy cover, and micro-habitat structure are partially preserved within urban forest remnants (Table 1) the core specialist assemblages can maintain

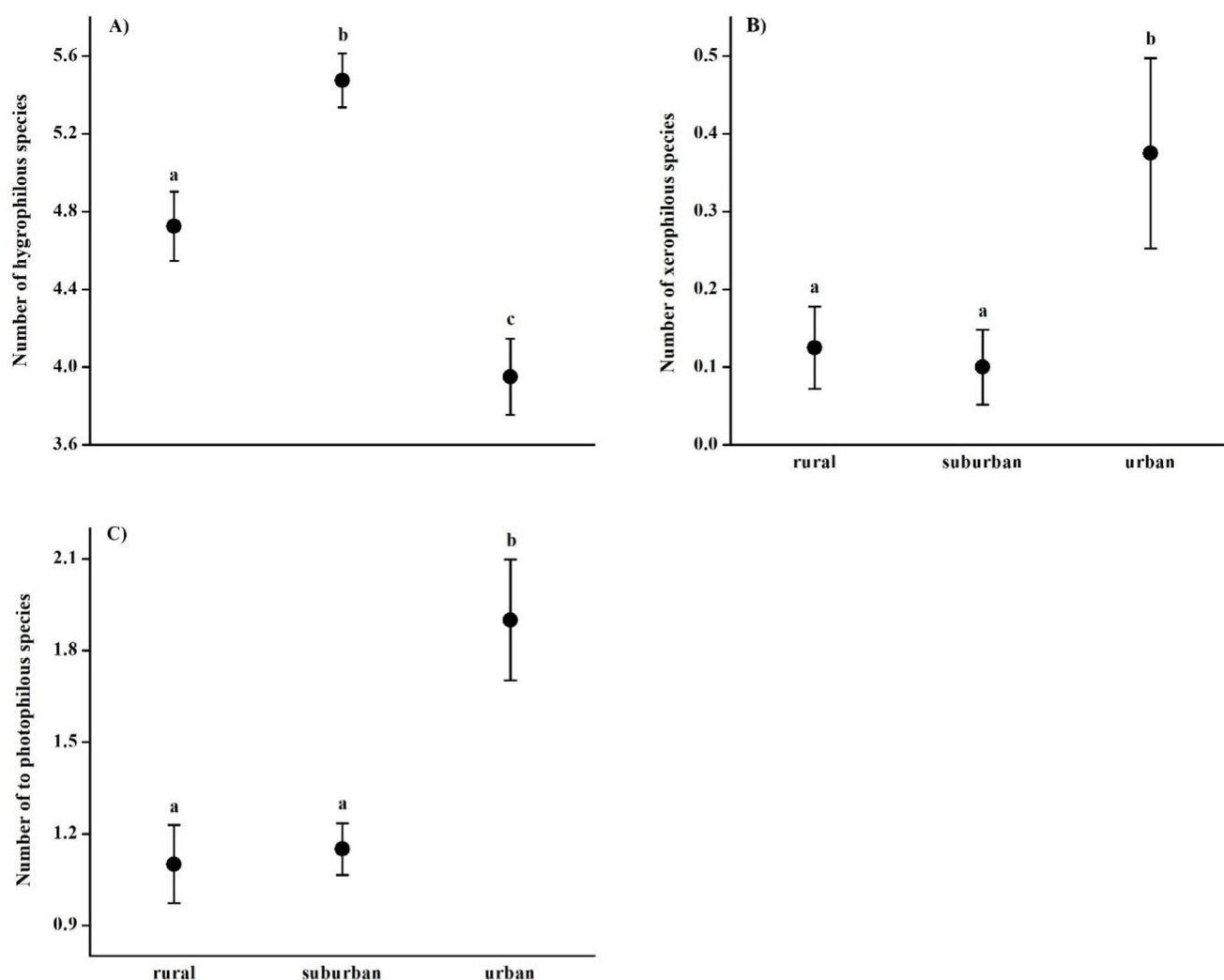


**Fig. 3** The average number of the hygrophilous species (A), xerophilous species (B), and photophilous species (C) along the rural-suburban-urban habitat gradient ( $\pm$  SE). Different letters represent significant differences ( $p < 0.05$ ) based on the LSD test

stable populations despite surrounding matrix degradation. On the other hand, numerous studies (Magura et al. 2010b; Tajthi et al. 2017; Lövei et al. 2018) supported this hypothesis. Generally, most forest species prefer shady and humid environments (Horváth et al. 2012). In our study 60% of the forest species showed a broad tolerance for shade demand. Urban habitats were characterized by lower relative humidity, reduced canopy cover, lower shrub cover, and smaller amounts of leaf litter and decaying wood compared with rural and suburban sites (Table 1). The reduction of these forest-associated habitat features may have contributed to the decline of forest species toward urban areas.

The opportunistic species hypothesis was not confirmed as generalist (less sensitive to environmental disturbance) species were predominantly collected from rural and suburban sampling areas. This finding is in accordance with the conclusion of previous studies conducted in Finland

(Alarukka et al. 2002), Hungary (Magura et al. 2010b), and Denmark (Lövei et al. 2018). In two of these studies (Alarukka et al. 2002; Magura et al. 2010b) no significant difference was observed among the individual habitat types similar to the studies on Hungarian carabids (Magura et al. 2008b). However, in the Danish study by Lövei et al. (2018) the rural sampling site had the highest number of generalist spider species. On the contrary, the study by Horváth et al. (2012) supported this hypothesis. Since almost half of the generalist species are sensitive to disturbance and one-third specifically favor higher humidity, these species prefer the more humid and less disturbed outside urban environments.

Our results supported the matrix species hypothesis which is consistent with previous research conducted in areas from Hungary (Magura et al. 2010b; Horváth et al. 2012). However, studies performed in other European countries did not find a difference in the number of open-habitat species along

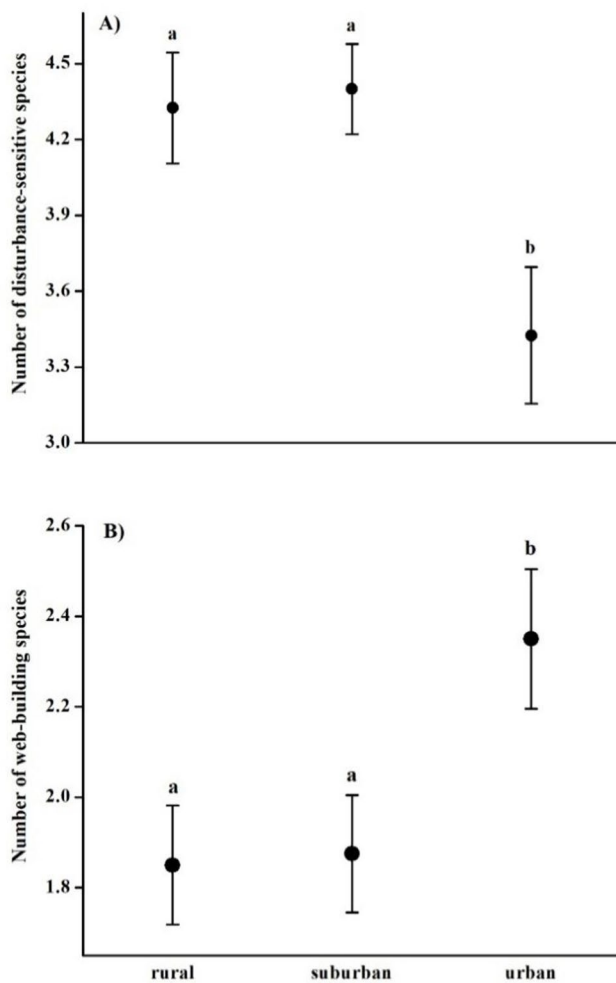


**Fig. 4** The average number of disturbance-sensitive species (A) and web-building species (B) along the rural-suburban-urban habitat gradient ( $\pm$  SE). The letters represent significant differences ( $p < 0.05$ ) based on the LSD test

the urbanization gradient (Finland: Alaruikka et al. 2002; Denmark: Lövei et al. 2018). The city park differed significantly from the suburban and other habitats, as these fragmented areas were more open and warmer. Moreover, many species associated with open habitats could penetrate urban areas from the surrounding matrices. The heavily disturbed urban habitat had higher air and soil temperatures, creating various microhabitats where these species could find suitable living conditions.

Our findings did not support the hygrophilous species hypothesis as these spiders were predominantly found in suburban areas with the highest species number. In the suburban habitat the canopy closure was higher than in the rural habitat, resulting in higher relative humidity. This higher humidity contributed to more hygrophilous species in the suburban habitat than in rural and urban ones. The decline of hygrophilous species in urban habitats may be

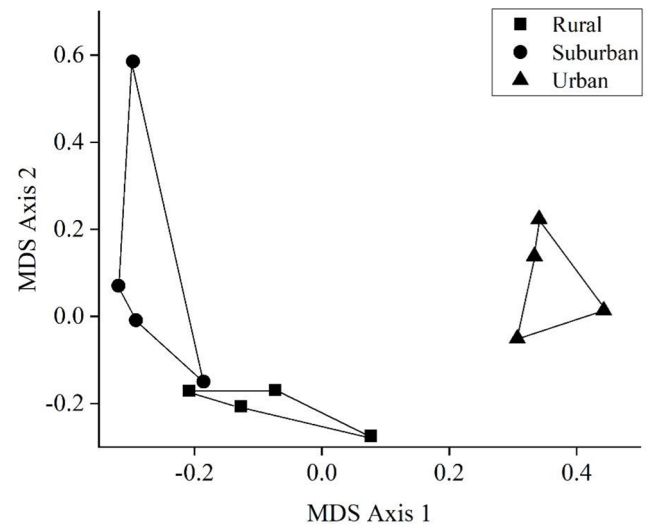


**Fig. 5** Multidimensional scaling (MDS) based on Hellinger distance of species compositions of ground-dwelling spider assemblages in flood-plain forest patches along an urbanization gradient

**Table 3** Two-way indicator table of the indicator power of species within the habitat clustering hierarchy, focusing on those species represented by more than five individuals

| Number of individuals/samples in areas |          |        |          |        |
|----------------------------------------|----------|--------|----------|--------|
| Habitat/Species                        | IndVal   | Rural  | Suburban | Urban  |
| All habitats                           |          |        |          |        |
| <i>Ozyptila praticola</i>              | 95.83 ns | 814/40 | 388/39   | 532/36 |
| <i>Diplostyla concolor</i>             | 92.50 ns | 173/36 | 141/35   | 253/40 |
| <i>Trochosa ruricola</i>               | 67.50 ns | 38/17  | 153/36   | 70/28  |
| <i>Diplocephalus picinus</i>           | 54.17 ns | 28/15  | 75/27    | 64/23  |
| <i>Trachyzelotes pedestris</i>         | 34.17 ns | 40/19  | 8/7      | 38/15  |
| <i>Phrurolithus festinus</i>           | 25.00 ns | 5/5    | 27/14    | 16/11  |
| <i>Pardosa alacris</i>                 | 9.17 ns  | 4/4    | 4/3      | 5/4    |
| Rural and suburban habitats            |          |        |          |        |
| <i>Piratula hygrophila</i>             | 92.33*   | 295/36 | 535/40   | 12/9   |
| <i>Liocranoeca striata</i>             | 83.00*   | 379/38 | 124/35   | 25/17  |
| Rural habitat                          |          |        |          |        |
| <i>Ceratinella brevipes</i>            | 12.50*   | 6/5    | 0/0      | 0/0    |
| <i>Walckenaeria nudipalpis</i>         | 12.50*   | 6/5    | 0/0      | 0/0    |
| Urban habitat                          |          |        |          |        |
| <i>Tenuiphantes tenuis</i>             | 35.08*   | 9/7    | 2/2      | 26/17  |
| <i>Drassyllus pusillus</i>             | 33.14*   | 9/7    | 3/2      | 29/16  |
| <i>Pardosa agrestis</i>                | 12.50*   | 0/0    | 0/0      | 5/5    |
| <i>Zelotes apricorum</i>               | 10.59*   | 2/2    | 3/2      | 6/6    |

In the row for all species, the first number shows the number of individuals present, and the second number indicates the number of samples where the species is present, in this sample group. The IndVal column shows the species indicator value for the corresponding clustering level, the maximum indicator value observed in all the clustering hierarchies. ns: not significant

\* $p < 0.05$

linked to the drier microclimatic conditions associated with urbanization. Relative humidity decreased markedly along the urbanization gradient in our study (Table 1), potentially reducing habitat suitability for moisture-dependent species. Previous studies have demonstrated the importance of humidity for forest arthropod communities although these studies were not conducted in urban environments. For example, Huber et al. (2007) showed that reductions in canopy closure decreased the abundance of hygrophilous spider species through microclimatic drying, while Jakus (1998) and Da Silva et al. (2011) reported higher frequencies of hygrophilous beetle species in more shaded and humid habitats. Together, these findings support the interpretation that urban-associated drying may contribute to the decline of hygrophilous spiders.

Our results supported the xerophilous species hypothesis, as the number of xerophilous species was significantly higher in the urban habitat compared to the other two habitat types. The urban sampling areas were more open than suburban and rural ones, leading to high soil surface and air temperatures in the city center. This temperature surplus indicates the prevalence of xerophilous species in urban habitats. Magura et al. (2013) pointed out that the species richness of thermophilous rove beetle species was the highest in the urban forested sites. Hoffmann and Andersen (2003) demonstrated that warm-preferring ant species occur in the highest number in open habitats where the temperature is the highest. Additionally, Menke et al. (2011) found that native ant species, which prefer warmer and drier environments, were most abundant in open habitats.

The number of photophilous species was significantly higher in urban areas than in suburban and rural ones, confirming the photophilous species hypothesis. Urbanization leads to more open sampling areas, allowing more light to reach the ground level compared to suburban and rural habitats. This increased light availability in urban habitats provides optimal living conditions for photophilous species, enabling them to establish permanent populations. A study by Lütolf et al. (2009) investigating diurnal butterflies revealed that species in dry grasslands preferred more open forest patches, and their activity-density decreased as canopy closure increased.

Our findings supported the disturbance-sensitive species hypothesis, as the number of disturbance-sensitive species was lowest in the urban habitat. Most spider species are moderately or severely susceptible to both natural and human disturbances, as evidenced by the significant decrease in their activity-density or even their complete disappearance from highly disturbed areas (Miyashita et al. 1998; Horváth et al. 2001, 2009; Tajthi et al. 2017). In the suburban area, where the minimal amount of forest management indicates low overall disturbance, we observed no

significant difference in the number of disturbance-sensitive species compared to the rural area. The urban habitat is subjected to intensive forest management, resulting in a park-like environment where microhabitats have been significantly transformed compared to natural floodplain forests. The strong disturbance in the urban habitat led to a reduction in the number of disturbance-sensitive species. This highlights the significance of disturbance-sensitive spider species as indicators of changes caused by urbanization. A study by Hogsden and Hutchinson (2004) examining butterfly communities along a disturbance gradient created by human activities found that disturbance-sensitive butterfly species were most abundant in undisturbed locations.

Contrary to our initial expectation, urban habitats contained the highest number of web-building species. This finding should be interpreted with caution because pitfall traps primarily sample ground-active individuals and may underrepresent sedentary web-building species occupying vegetation strata. Notably, most captured individuals of web-building species were males, which are generally more mobile than females and frequently move across the ground while searching for mates. Consequently, the observed pattern may partly reflect differences in male activity and detectability rather than true differences in the abundance of web-building populations among habitat types. In contrast, Miyashita et al. (1998) found that web-building spiders were most abundant in rural areas, where they had access to prey of adequate amount and size, whereas, in urban environments, the presence of larger prey and increased disturbance might have resulted in a lower number of orb-weaver species.

The clear separation of urban assemblages from rural and suburban ones suggests that urbanization acts as a strong environmental filter shaping spider's community composition. Species associated with moist, less disturbed forest habitats were largely restricted to rural and suburban sites, whereas urban habitats favored open-habitat and disturbance-tolerant species. Although urban forest patches exhibited considerable habitat heterogeneity, this did not compensate for the loss of key forest characteristics such as high humidity, continuous canopy cover, and abundant litter and woody debris. Consequently, urban habitats supported fewer hygrophilous and disturbance-sensitive species, indicating that urbanization reduces the availability of suitable microhabitats for forest specialists.

When our findings are evaluated holistically, it becomes clear that the urbanization of the Tisza River floodplain does not merely cause a neutral turnover of species, but functions as a systemic, trait-driven ecological filter. Riparian floodplain forest patches are naturally buffered, high-humidity corridors dominated by specialized, hygrophilous, and shade-preferring ground-dwelling spiders. With urban

intensification human management practices structurally transform the structure of habitats. The thinning of the canopy, and the systematic removal of leaf litter and decaying wood strip the forest floor of its natural microclimatic insulation.

This induces a severe environmental filter: the local microclimate desiccates, driving a significant reduction in relative humidity and an increase in temperature extremes. This filter proves toxic to native, specialized forest taxa, such as the hygrophilous indicator species identified in our rural and suburban sites, which lack the physiological adaptations to survive prolonged desiccation. Concurrently, the removal of structural complexity opens the environmental sieve, allowing xerophilous, photophilous, and opportunistic matrix species to actively colonize the urban forest interior from surrounding built environments.

Ultimately, this structural and microclimatic filtering explains why overall species richness remained statistically stable across our gradient despite profound compositional divergence. The urban forest patches do not experience an immediate collapse in species wealth; instead, they undergo a functional substitution where unique, vulnerable riverine specialists are effectively filtered out and replaced by ubiquitous, open-habitat generalists. These specific filtering vectors are vital for urban riparian management, demonstrating that maintaining the ecological integrity of floodplain remnants depend entirely on preserving the structural habitat features that buffer against microclimatic desiccation.

## Conclusion

Our study demonstrates that evaluating the ecological impacts of urbanization requires a shift from simple macro-level metrics, such as overall species richness, toward nuanced, trait-based community analyses. While the uniform species richness observed across our rural-suburban-urban continuum suggests a superficial community resilience, the underlying functional composition of the spider assemblages underwent a profound restructuring.

The physical modifications associated with urban forest patch management, specifically canopy thinning and the removal of leaf litter, fundamentally drove local microclimatic desiccation, resulting in higher temperatures and lower relative humidity. This environmental shift created a clear ecological filtering effect: it suppressed specialized, humidity-dependent, and disturbance-sensitive forest taxa, while simultaneously facilitating the colonization of dry-adapted (xerophilous), light-associated (photophilous), and matrix-derived open-habitat species.

From a conservation and urban planning perspective, these findings emphasize that urban forest remnants are far

from ecological dead-ends; rather, they serve as complex dynamic matrices capable of supporting diverse functional groups. However, to maintain the integrity of native forest specialist fauna within expanding urban landscapes, management strategies must actively prioritize the preservation of core microhabitats. Retaining dense canopy cover, maintaining natural understory vegetation, and leaving decaying wood and leaf litter intact are critical actions needed to buffer forest-floor microclimates against the degrading effects of human disturbance.

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**Data availability** Data will be made available upon request.

## Declarations

**Competing interests** The authors declare no competing interests.

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