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Research Article

Microclimate and vegetation structure shape harvestman (Opiliones) assemblages in an isolated forest fragment and adjacent potential biological corridors

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Abstract

The conservation value of forest fragments is highly dependent on the internal habitat quality and functional connectivity. Biological corridors are widely used to mitigate fragmentation, but their efficacy for many arthropod groups, including harvestmen, remains understudied in fine-scale agricultural landscapes. We assessed how microclimatic and vegetation structural conditions influenced ground-living harvestman (Opiliones) assemblages in the protected floodplain forest fragment Jarovská bažantnica (Slovakia) and in adjacent linear habitats of varying width that could potentially serve as biological corridors. A total of 3,067 individuals representing 11 species were captured. Multivariate ordination revealed that surface air temperature was the sole significant predictor structuring overall assemblage composition, segregating xero-tolerant species in warmer microsites from moisture-dependent species in cooler microsites. Coverage-standardised species richness (Hill q = 0) increased significantly with higher tree-layer cover and decreased with increasing minimum surface temperature. Effective Shannon diversity (Hill q = 1) was positively associated with litter depth and negatively with increasing mean surface temperature. Activity-density, expressed as captures per trap-day, decreased with increasing soil moisture. Amongst the three linear habitats examined, the widest corridor (15 m) supported the highest coverage-standardised richness and effective diversity, whereas 5 m and 10 m elements exhibited lower values. The 15 m element also most closely resembled forest-interior conditions in terms of vegetation structure and microclimate and observed effective diversity. Overall, our results indicate that harvestman assemblages in this fragmented landscape are primarily associated with fine-scale microclimatic and vegetation-structural conditions. Wider and structurally complex linear habitats may provide more suitable conditions for forest associated harvestmen. However, because our study is limited to a single forest fragment and only one linear habitat represented each width, these findings should be interpreted as site-specific patterns rather than general evidence of corridor effectiveness or a minimum functional width.

Key words: Arachnida, assemblage composition, biodiversity conservation, floodplain forests, habitat fragmentation, Slovakia

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Introduction

Agricultural intensification leads to the destruction and fragmentation of habitats, often eliminating patches and disrupting linear elements in the landscape (Benton et al. 2003; Tscharntke et al. 2005; Kristensen et al. 2016; Jankielsohn 2023). This exerts continuous pressure on the less disturbed areas, contributing to a documented decline in arthropod diversity across both open and forested landscapes (Gossner et al. 2016; Seibold et al. 2019; Jankielsohn 2023; Langraf et al. 2024a, 2024b). In Slovakia, where monoculture fields average 12 hectares, the largest in the EU, this issue is particularly acute (Gális 2020). Consequently, functional biological corridors within agricultural landscapes are crucial for providing connectivity and suitable conditions for wild organisms to thrive.

As linear landscape elements, biological corridors are key conservation tools designed to mitigate fragmentation by facilitating species movement and gene flow between isolated habitats (Gilbert-Norton et al. 2010; Eriksson et al. 2013; Gutiérrez-Chacón et al. 2020). Consequently, landscape-scale measures, such as ecological networks and biological corridors, may support arthropod abundance and diversity in intensively used agricultural landscapes (Langraf et al. 2021; Plath et al. 2021; Horňák et al. 2023).

Harvestmen are amongst the arthropod groups that can benefit from such corridors. They are common components of terrestrial environments and appropriate subjects for ecological research (Pinto-da-Rocha et al. 2007; Muster et al. 2014).

Harvestmen serve as effective bioindicators of ecosystem stability because of their sensitivity to habitat changes (Stašiov 2001; Pinto-da-Rocha et al. 2007; Gerlach et al. 2013; Litavský et al. 2018, 2019a, 2024; Komposch 2022). This sensitivity stems from their dependence on specific microclimatic conditions, as they tolerate only narrow ranges of temperature and humidity and are highly vulnerable to desiccation (Santos 2007). Consequently, they respond negatively to anthropogenic disturbances, such as forest fragmentation, wildfires and livestock farming, with assemblages exhibiting changes in species composition and reduced species richness (Curry et al. 1985; Dennis et al. 2001; Machado et al. 2007). Their species richness itself is a key component of biodiversity that supports broader ecosystem resilience (Ferreira et al. 2019, 2020; Rubim et al. 2023).

In addition to their indicator value, harvestmen provide crucial ecosystem services. As predators, they are significant agents of biological pest control in arable land and semi-natural habitats (Todd 1949; Leathwick and Winterbourn 1984; Dixon and McKinlay 1989; Clark et al. 1994; Halaj and Cady 2000; Acosta and Machado 2007; Wolff et al. 2014; Papura et al. 2020). They serve as prey for other invertebrates and vertebrates, making them a part of the food chain.

Harvestmen (Opiliones) inhabit both open (meadows, pastures and arable land) and forest habitats, including their edges. They are primarily epigeic organisms, but can also be found in the shrub and tree layers. Amongst common European species, those with long legs, such as members of the genera *Mitopus*, *Platybunus* and *Rilaena*, are typically found in vegetation. Shorter legs in other species represent an adaptation for life in leaf litter and soil, for example, in the genera *Trogulus*, *Mitostoma* and *Nemastoma* (Zach et al. 2010). Some species have also adapted to synanthropic (human-altered) environments, such as *Opilio canestrinii*, *Opilio saxatilis*, *Opilio parietinus*, *Phalangium opilio* and, more recently, *Leiobunum limbatum*.

As hygrophilous epigeic predators and scavengers, harvestmen are strongly dependent on the microclimatic and vegetation-structural conditions of their biotope (Pinto-da-Rocha et al. 2007; Tourinho et al. 2020; Litavský et al. 2024). Therefore, our research investigates the effects of specific microclimatic variables on harvestmen assemblages, namely soil moisture at 11 cm depth, soil temperature (T1) at 6 cm depth and air temperature at ground level (T2) and 15 cm above ground (T3). We also examine the effects of vegetation-structural conditions, i.e. species richness and cover across herb, shrub and tree layers and litter layer thickness.

Given this dependence, we formulated testable hypotheses linking the measured conditions to specific harvestman community metrics. First, we hypothesised that assemblage composition would be primarily structured by the microclimatic gradient, such that assemblages in warmer and drier conditions would be dominated by xero-tolerant species, whereas those in cooler and more humid environments would be dominated by moisture-dependent species. Second, we expected that species richness, diversity and evenness would increase with greater vegetation structural complexity, because this factor provides stable microhabitats and greater resource heterogeneity. Finally, we expected that overall activity density would be associated with microclimatic conditions, particularly temperature and humidity, given the strong physiological sensitivity of harvestmen to desiccation (Santos 2007).

This study aimed to investigate the dynamics and determinants of harvestman (Opiliones) assemblages within the protected area of Jarovská bažantnica (Slovakia) and its immediate surroundings. The study area included the core of the biocentre (an isolated 80-ha forest fragment designated as a 'biocentre' under Slovak landscape planning), ecotones and adjacent linear vegetation elements. These elements have been designated as biological corridors in local landscape planning. Such corridors are linear, often tree-dominated vegetation elements that are structurally similar to forests and enhance landscape connectivity by facilitating organism movement and ecological flows. It is important to note, however, that these linear elements do not establish a continuous connection to the main Danube floodplain forest complex; rather, they connect the biocentre to small habitat patches within the agricultural matrix. We, therefore, assess their quality as potential corridor habitats rather than confirming their effectiveness as landscape-scale connectors. Using extensive field data and statistical analyses, we sought to elucidate the impact of microclimatic variables and vegetation structural conditions on the spatial distribution and species composition of harvestmen. By examining these complex interactions, we aimed to gain a better understanding of how spatial, environmental and microclimatic factors influence harvestman assemblages within an isolated biocentre representing a hardwood floodplain forest surrounded by agricultural land.

Material and methods

Study sites

The research was conducted within the protected area of Jarovská bažantnica (Slovakia), which is located southwest of the centre of Bratislava, on the right bank of the Danube River, in the cadastral area of Jarovce, next to the Austrian

border. It represents a biocentre with an area of approximately 80 hectares, consisting of hardwood floodplain forests and is surrounded by agricultural land. The Jarovská bažantnica biocentre is isolated from the main Danube floodplain forest complex by the D2 highway and a railway line, both of which lack eco-ducts or other crossing structures. The straight-line distance from the biocentre to the nearest continuous floodplain forests is approximately 2 km, but no functional corridor network connects them (Fig. 1).

In the Jarovská bažantnica protected area and its surroundings, nine study sites were established: three sites located at least 100 m deep into the forest, representing forest biotopes (1F-3F), three study sites that form field-forest ecotones (1E-3E) and three sites representing various biological corridors of different widths (1C-3C) (Fig. 1). The linear vegetation elements included in this study — designated as biological corridors in local planning — extend from the biocentre edge into the agricultural matrix, providing connectivity to small habitat patches. Corridor 1C (0.6 km in length) connects the biocentre to a 2.7 ha forest fragment. Corridors 2C and 3C originate from the biocentre and merge after 1.8 km and 0.6 km, respectively, at a junction point, from which a single corridor continues for an additional 2.5 km to a 5.9 ha orchard. Approximately 100 m beyond the orchard, there is a 4.5 ha fragment of floodplain forest, currently represented largely by garden areas. Thus, the total length of corridor 2C is 4.3 km, while corridor 3C totals 3.1 km. However, none of these corridors establishes a continuous connection to the main floodplain forests.

It should be emphasised that the distance of the individual study plots that form the biological corridors from the edges of the biocentre was approximately the same, while the width of the biological corridors varied (1C had a width of 5 m, 3C – 10 m, while the study plot 2C was 15 m wide) (Table 1).

Sampling

During the research on epigeic macrofauna, we employed the pitfall trap method, described by Brown and Matthews (2016). At each study site, five traps were placed in a straight line at approximately 5-metre intervals. At study sites

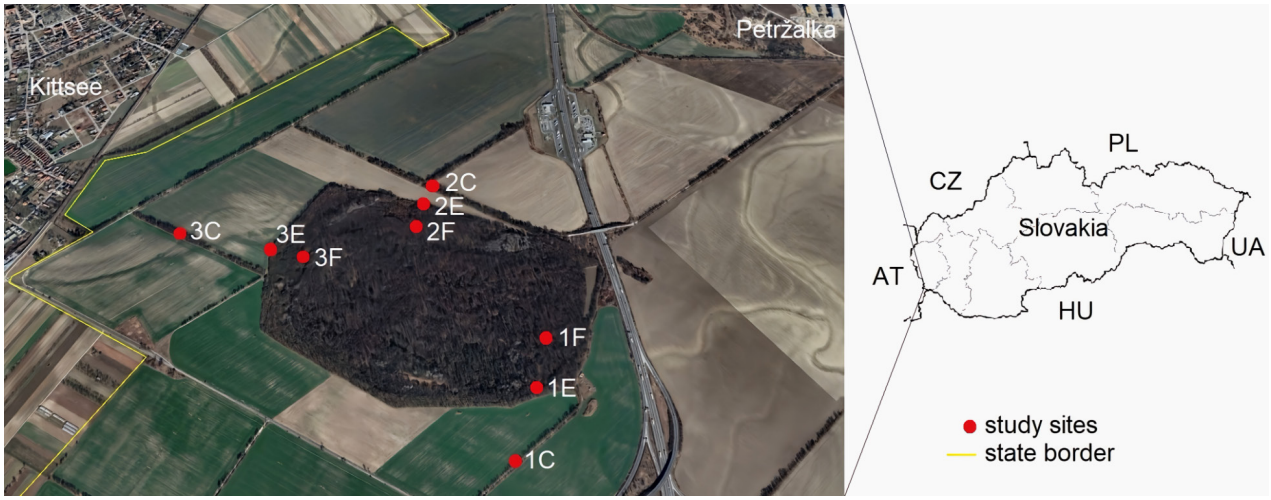

Figure 1. Distribution of study sites: 1F–3F (forest biotopes), 1E–3E (field-forest ecotones) and 1C–3C (biological corridors) within the Jarovská bažantnica protected area and its vicinity. AT–Austria, CZ–Czechia, HU– Hungary, PL– Poland, UA– Ukraine

Table 1. Description of the study plots within the Jarovská bažantnica biocentre and its surroundings with recorded plant dominance: 1 denoting less than 1% dominance, 2 denoting 1–50% dominance and 3 denoting more than 50% dominance.

Plot ID	Habitat Type	Coordinates (N, E)	Alt. m a.s.l.	Tree Layer (E_3)	Shrub Layer (E_2)
1C	Biological Corridor 5 m	48°04'28.21"N, 17°05'42.80"E	137	*Fraxinus excelsior* (2) *Robinia pseudoacacia* (2)	*Robinia pseudoacacia* (2) *Sambucus nigra* (2)
1E	Field-Forest Ecotone	48°04'36.00"N, 17°05'47.00"E	135	*Fraxinus excelsior* (3) *Acer campestre* (2)	*Acer campestre* (2) *Sambucus nigra* (2) *Euonymus europaeus* (1) *Fraxinus excelsior* (1) *Ulmus minor* (1) *Viburnum lantana* (1)
1F	Forest Stand	48°04'42.00"N, 17°05'49.00"E	135	*Acer pseudoplatanus* (2) *Fraxinus excelsior* (2)	*Staphylea pinnata* (3) *Acer pseudoplatanus* (2) *Sambucus nigra* (2)
2C	Biological Corridor 15 m	48°05'3.36"N, 17°05'30.55"E	135	*Prunus cerasifera* (2) *Prunus padus* (2) *Robinia pseudoacacia* (2)	*Sambucus nigra* (2) *Prunus padus* (2) *Prunus cerasifera* (1)
2E	Field-Forest Ecotone	48°05'0.71"N, 17°05'28.85"E	135	*Acer campestre* (2) *Fraxinus angustifolia* (2) *Prunus padus* (2) *Ailanthus altissima* (1) *Robinia pseudoacacia* (1)	*Cornus sanguinea* (2) *Corylus avellana* (2) *Acer campestre* (1) *Ailanthus altissima* (1) *Prunus cerasifera* (1) *Prunus padus* (1) *Sambucus nigra* (1) *Staphylea pinnata* (1)
2F	Forest Stand	48°04'57.00"N, 17°05'28.00"E	134	*Fraxinus angustifolia* (2) *Ulmus glabra* (2) *Acer campestre* (1) *Ailanthus altissima* (1)	*Corylus avellana* (2) *Sambucus nigra* (2) *Staphylea pinnata* (2) *Ailanthus altissima* (1)
3C	Biological Corridor 10 m	48°04'57.06"N, 17°04'45.67"E	136	*Prunus cerasifera* (2) *Robinia pseudoacacia* (2)	*Sambucus nigra* (2) *Euonymus europaeus* (1) *Prunus cerasifera* (1) *Rosa canina* agg. (1)
3E	Field-Forest Ecotone	48°04'54.18"N, 17°05'2.22"E	139	*Acer campestre* (2) *Prunus cerasifera* (2) *Robinia pseudoacacia* (2) *Juglans regia* (1) *Ulmus glabra* (1)	*Prunus cerasifera* (2) *Prunus spinosa* (2) *Acer campestre* (1) *Ulmus glabra* (1)
3F	Forest Stand	48°04'53.00"N, 17°05'8.00"E	149	*Fraxinus angustifolia* (3) *Acer campestre* (1)	*Acer campestre* (2) *Prunus cerasifera* (2) *Ailanthus altissima* (1) *Sambucus nigra* (1)

1E–3E and 1F–3F, trap lines were placed parallel to the edge of the arable land, whereas in the biological corridors (1C–3C), traps were placed along their midline. Each trap consisted of a collection container inserted into the soil, with the rim level with the surface of the ground to ensure that the animals fell into the container. The traps were constructed using 0.5-litre plastic cups with an internal diameter of 9 cm. Two nested cups per trap were used: the outer cup stabilised the hole in the ground, whereas the inner cup functioned as the actual trap.

The traps were filled halfway with a 4% formaldehyde solution, supplemented with ethylene glycol-based antifreeze (FRIDEX G48 READY) and a few drops of detergent to reduce surface tension.

The traps were equipped with covers to prevent flooding from rainwater and to reduce evaporation. The study was conducted from 30 March 2022 to 29 March 2023 with monthly sampling (13 sampling events). For each study plot and sampling date, the material from the five traps was pooled to create a representative sample. In the laboratory, samples were processed through sorting, identification and preservation in 75% ethanol. Harvestmen (Opiliones) were identified according to Martens (1978) and Litavský (2025). Specimens were deposited at the Faculty of Natural Sciences of the Comenius University in Bratislava in the Department of Environmental Ecology and Landscape Management.

At each study site, we conducted a phytosociological survey within a 150 m^2 sample area (30 m × 5 m). Within this area, we estimated the percentage cover for the tree, shrub and herb layers and recorded the species present in each. Pitfall traps were placed in the central part of these 30 m sections, where phytosociological surveys were conducted. For each plant species, we assigned indices (1–3), based on Tansley and Chipp (1926): 1 denotes less than 1% dominance, 2 denotes 1–50% dominance and 3 denotes more than 50% dominance. The phytosociological survey was conducted from May to June 2022, with a spring aspect supplemented in March 2023. The nomenclature of vascular plants was interpreted following Govaerts (2024). We also recorded the average thickness of the litter layer across all study sites by taking three measurements per site in both autumn and spring (Table 2).

Temperature and humidity were recorded every 15 min from 30 March 2022 to 29 March 2023 using TMS-4 data loggers (Wild et al. 2019) placed near the third trap at each study site. In total, we used nine TMS-4 data loggers, which measured soil temperature at a depth of 6 cm (T1), air temperature at ground level +2 cm (T2) and 15 cm above the ground (T3) were recorded. In addition, soil moisture was recorded at a depth of approximately 11 cm using the same TMS-4 data loggers, which measure volumetric water content via a capacitive sensor (Frequency Domain Reflectometry). From the collected data, we included the maximum, minimum and average values of temperature and humidity recorded between the intervals when the entomological material was sampled in our analyses.

Table 2. Coverage (E_1 – E_3 [%]) and species richness (E_1_spe – E_3_spe) of plants within the herbaceous (E_1), shrub (E_2) and tree (E_3) layers and the thickness of the litter layer at the individual study sites (litter).

Environmental parameters	Study sites								
	1C	1E	1F	2C	2E	2F	3C	3E	3F
E_1 [%]	100	95	80	75	35	85	95	85	100
E_2 [%]	7	12	80	40	65	40	35	35	20
E_3 [%]	45	85	40	60	75	75	50	75	80
E_1_spe	21	27	24	21	29	34	17	25	22
E_2_spe	2	6	3	3	8	4	4	4	4
E_3_spe	2	2	2	3	5	4	2	5	2
Litter [cm]	2	2.5	3.5	1	1.5	2	1.5	1	3

Data analyses

The attributes of the Opiliones assemblage, such as species composition, abundance, dominance, observed species richness, diversity, evenness and effective diversity (Hill numbers) were evaluated (Table 5). Evenness was expressed as Pielou's evenness index (J), derived from the Shannon–Wiener index (Spellerberg and Fedor 2003; Fedor and Zvaríková 2019). Species diversity was quantified using effective diversity (Hill numbers), which express diversity as the effective number of equally abundant species and provide a unified framework for comparing diversity across different orders of q (Chao et al. 2014). Hill numbers were calculated in R using the iNEXT package (Hsieh et al. 2016).

Environmental covariation among predictors was explored using principal component analysis (PCA; "*vegan*" package in R) as an unconstrained ordination of plot-level mean values. All variables were centred and scaled prior to the analysis to place the predictors on a common scale. PCA loadings were used to interpret the dominant environmental gradients and identify potentially redundant predictors. PCA was supplemented by pairwise correlation analyses to guide the selection of non-collinear predictors for subsequent constrained ordination (see Suppl. material 1).

Community-environment relationships were analysed using partial redundancy analysis (pRDA) in the "*vegan*" package, using Hellinger-transformed species abundance data and untransformed environmental predictors. To justify the use of linear constrained ordination, detrended correspondence analysis (DCA) on raw species abundances was used to estimate the gradient length (first axis length = 2.36 SD units), indicating a short to moderate compositional gradient. Candidate predictors were chosen, based on ecological hypotheses and refined using forward selection. The statistical significance of terms was evaluated using the Monte Carlo permutation test (999 permutations) and non-significant predictors were excluded. Finally, the significant environmental predictor (T2_ave) was fitted as a vector on to the ordination diagram.

To account for the potential design/spatial structure, the final model was fitted as pRDA conditioned on the Block (individual transects forest – ecotone – biological corridor). We additionally tested for residual spatial autocorrelation in the full (unconditioned) RDA model using Moran's I ("*spdep*" package in R) and found no evidence of residual autocorrelation (Moran's I, $p > 0.05$). Assemblage composition was additionally summarised using hierarchical cluster analysis on Hellinger-transformed species data (Euclidean distance, Ward's linkage); the resulting dendrogram and cluster assignments are provided in Suppl. material 1: fig. S2).

Harvestman pitfall-trap catches were interpreted as activity-density rather than absolute abundance because capture rates depend on both the density and surface activity of individuals. As the number of functional traps and exposure duration varied amongst sampling events, sampling effort was quantified as effective trap-days, calculated as the sum of the exposure days of all functional traps within each sample. Activity-density was expressed descriptively as individuals $trap^{-1}$ day^{-1}.

For inferential analysis, raw integer capture counts were modelled using a generalised linear mixed-effects model fitted with the glmmTMB package in R. The natural logarithm of effective trap-days was included as an offset, so the model estimated environmental effects on the expected number of captured

individuals per trap-day. As the capture counts were overdispersed, a negative-binomial distribution (nbinom2) with a log link was used. Plot was included as a random intercept to account for repeated sampling within plots.

Average volumetric soil water content (H_ave) was recorded as a proportion ranging from 0 to 1 and rescaled so that one unit represented a 10 percentage-point increase in soil moisture (H_ave_10 = H_ave/0.10). The significance of soil moisture was evaluated using a likelihood-ratio test comparing the model containing soil moisture with the corresponding model without this predictor. A nested random-effects structure with Plot nested within Block was also evaluated. The nested structure did not improve model fit; therefore, the simpler Plot random-intercept structure was retained. Model adequacy was evaluated using simulated residuals in the DHARMa package, including tests of residual uniformity, dispersion, zero inflation and outliers (see Suppl. material 1).

Differences in the total numbers of captured individuals amongst plots may result in unequal sample completeness and consequently affect direct comparisons of observed diversity. We, therefore, standardised harvestman diversity using coverage-based rarefaction and extrapolation with Hill numbers, implemented in the R package iNEXT. Raw integer species capture counts aggregated by plot were used as input for the abundance-data analysis. In this context, "abundance-based" refers to the count-data format required by iNEXT and does not imply that pitfall-trap catches represent absolute population abundance. We calculated Hill diversity, representing coverage-standardised species richness (q = 0), effective Shannon diversity (q = 1) and effective Simpson diversity (q = 2), respectively. All plots were compared at a common sample coverage of 0.98 and 95% confidence intervals were estimated using 500 bootstrap replications (see Suppl. material 1: figs S3, S4, S6, S7).

Environmental relationships of coverage-standardised Hill diversity were analysed at the plot level. As one annual diversity estimate was available for each of the nine plots, Plot was the observational unit and was not included as a random effect. Hill-number estimates are positive continuous variables and were, therefore, log-transformed before analysis. Approximate standard errors on the log scale were derived from the iNEXT 95% confidence intervals using the delta method. Models were fitted using inverse-variance weighted linear regression, giving greater weight to more precisely estimated Hill numbers.

Candidate environmental predictors, listed in Table 3, were initially examined using Spearman correlations. Strongly correlated predictors, defined as $|\rho| \geq 0.70$, were not included in the same candidate model. The correlation matrix is provided in the Suppl. material 1: fig. S1. Variance-inflation factors were subsequently used to verify that the retained models did not exhibit problematic multi-collinearity. As only nine independent plots were available, candidate models were restricted to a maximum of two environmental predictors.

Candidate models were compared using the small-sample corrected Akaike Information Criterion (AICc), AICc weights, adjusted R^2 and leave-one-plot-out prediction error. Model selection also considered residual normality, homoscedasticity, multi-collinearity, ecological interpretability and coefficient stability in leave-one-plot-out sensitivity analyses. The best-supported model for coverage-standardised species richness was log(q0) ~ T2_min + E_3_10, where E_3_10 represents tree-layer cover expressed per 10 percentage-point increase. The best-supported model for effective Shannon diversity was log(q1) ~ T2_ave + Litter. The significance of individual predictors in the selected models

Table 3. Description of the analysed variables.

Variable	Description
T1_max [°C]	maximum soil temperature at 6 cm depth
T1_min [°C]	minimum soil temperature at 6 cm depth
T1_ave [°C]	average soil temperature at 6 cm depth
T2_max [°C]	maximum surface temperature at 2 cm above the ground
T2_min [°C]	minimum surface temperature at 2 cm above the ground
T2_ave [°C]	average surface temperature at 2 cm above the ground
T3_max [°C]	maximum temperature 15 cm above the ground
T3_min [°C]	minimum temperature 15 cm above the ground
T3_ave [°C]	average temperature 15 cm above the ground
H_max [m^3/m^3]	Θ – maximum of volumetric soil water content (soil humidity)
H_min [m^3/m^3]	Θ – minimum of volumetric soil water content (soil humidity)
H_ave [m^3/m^3]	Θ – average of volumetric soil water content (soil humidity)
E_3 [%]	cover of the tree layer
E_2 [%]	cover of the shrub layer
E_1 [%]	cover of the herb layer
E_3_spe	species richness of tree layer
E_2_spe	species richness of shrub layer
E_1_spe	species richness of herb layer
Litter [cm]	thickness of the litter layer

was evaluated using Type II F-tests. As model selection did not identify a robust environmental relationship for effective Simpson diversity (q = 2), it was reported descriptively with 95% confidence intervals, but was not subjected to further inferential interpretation (see Suppl. material 1).

Model assumptions were evaluated using residual-versus-fitted plots, normal quantile–quantile plots, the Shapiro–Wilk test and the Breusch–Pagan test for heteroscedasticity. The robustness of the selected models was examined by sequentially omitting each plot and refitting the model. Due to the limited number of independent plots, the environmental models of Hill diversity were interpreted as exploratory, site-specific relationships rather than definitive causal effects.

All analyses were conducted in R (R Core Team 2023). Community-composition analyses were performed using the vegan package. Negative-binomial mixed-effects models were fitted using glmmTMB and their diagnostics were evaluated using DHARMa. Rarefaction, extrapolation and sample-coverage analyses were performed using iNEXT. Type II tests and variance-inflation factors were obtained using car and the Breusch–Pagan test was performed using lmtest. Figures were produced using ggplot2 and ragg.

Results

A total of 3067 harvestman individuals belonging to 11 species from four families were captured. The most dominant species were *Nelima sempronii* (24.49%), *Egaenus convexus* (23.15%), *Nemastoma bidentatum sparsum* (19.27%), *Oligolophus tridens* (11.35%) and *Astrobunus laevipes* (10.89%). The abundance and dominance of individual harvestman species differed amongst the study plots (Table 4).

Table 4. Harvestman species composition (abundance and dominance) recorded in the individual forest (1F, 2F, 3F), ecotonal (1E, 2E, 3E) and biological corridor (1C, 2C, 3C) study plots in the Jarovská bažantnica protected area.

Abundance										
Family/species	**1C**	**1E**	**1F**	**2C**	**2E**	**2F**	**3C**	**3E**	**3F**	**∑**
Trogulidae Sundevall, 1833										
Trogulus agg. *tricarinatus* (Linnaeus, 1767)	17	7	8	5	12	18	8	16	9	100
Nemastomatidae Simon, 1872										
Nemastoma bidentatum sparsum (Gruber & Martens, 1968)	0	125	59	110	81	106	3	53	54	591
Phalangiidae Latreille, 1802										
Egaenus convexus (Koch, 1835)	5	33	50	192	204	110	22	27	67	710
Lacinius ephippiatus (Koch, 1835)	0	4	46	0	0	1	0	1	1	53
Oligolophus tridens (Koch, 1836)	0	21	211	6	39	69	0	1	1	348
Phalangium opilio Linnaeus, 1758	0	0	0	4	2	0	1	6	0	13
Rilaena triangularis (Herbst, 1799)	0	9	62	0	4	19	0	1	23	118
Opilio saxatilis Koch, 1839	27	0	0	5	8	1	0	4	0	45
Sclerosomatidae Simon, 1879										
Astrobunus laevipes (Canestrini, 1872)	0	86	7	77	7	0	0	2	155	334
Leiobunum rotundum (Latreille, 1798)	0	0	0	0	0	0	0	0	4	4
Nelima sempronii Szalay, 1951	19	223	103	84	69	56	18	76	103	751
Dominance										
Family/species	**1C**	**1E**	**1F**	**2C**	**2E**	**2F**	**3C**	**3E**	**3F**	**D [%]**
Trogulidae Sundevall, 1833										
Trogulus agg. *tricarinatus* (Linnaeus, 1767)	25.00	1.38	1.47	1.04	2.82	4.74	15.39	8.56	2.16	3.26
Nemastomatidae Simon, 1872										
Nemastoma bidentatum sparsum (Gruber & Martens, 1968)	0.00	24.61	10.81	22.77	19.01	27.90	5.77	28.34	12.95	19.27
Phalangiidae Latreille, 1802										
Egaenus convexus (Koch, 1835)	7.35	6.50	9.16	39.75	47.89	28.95	42.31	14.44	16.07	23.15
Lacinius ephippiatus (Koch, 1835)	0.00	0.79	8.43	0.00	0.00	0.26	0.00	0.54	0.24	1.73
Oligolophus tridens (Koch, 1836)	0.00	4.13	38.65	1.24	9.16	18.16	0.00	0.54	0.24	11.35
Phalangium opilio Linnaeus, 1758	0.00	0.00	0.00	0.83	0.47	0.00	1.92	3.21	0.00	0.42
Rilaena triangularis (Herbst, 1799)	0.00	1.77	11.36	0.00	0.94	5.00	0.00	0.54	5.52	3.85
Opilio saxatilis Koch, 1839	39.71	0.00	0.00	1.04	1.88	0.26	0.00	2.14	0.00	1.47
Sclerosomatidae Simon, 1879										
Astrobunus laevipes (Canestrini, 1872)	0.00	16.93	1.28	15.94	1.64	0.00	0.00	1.07	37.17	10.89
Leiobunum rotundum (Latreille, 1798)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.96	0.13
Nelima sempronii Szalay, 1951	27.94	43.90	18.86	17.39	16.20	14.74	34.62	40.64	24.70	24.49

Environmental gradients and multi-collinearity amongst predictors

PCA identified two dominant gradients in the environmental dataset. The first axis (PC1) explained 51.7% of the standardised variance and primarily represented a microclimatic gradient, with all temperature metrics loading strongly in one direction and humidity metrics loading in the opposite direction. Vegetation structure co-varied with this gradient, with herb-layer cover (E_1) loaded negatively and shrub-layer cover (E_2) loaded positively, indicating that the microclimate gradient was associated with a shift in understorey structure. The second axis (PC2) explained 13.5% of the variance and reflected a woody cover

and plant-layer richness gradient, with canopy cover (E_3) and plant species richness in shrub and tree layers (E_2_spe, E_3_spe) loading positively, in contrast to greater litter depth and herb-layer cover (negative loadings). Together, PC1 and PC2 accounted for 65.3% of the total standardised variation (Fig. 2).

PCA results were complemented by pairwise correlation screening to guide selection of non-collinear predictors for subsequent pRDA. Pairwise correlations (Spearman's ρ) amongst vegetation structure, litter and microclimate predictors are presented in Suppl. material 1; this was used to identify strongly collinear predictor pairs (e.g. herb vs. shrub cover; humidity metrics) and to define a reduced set of constraints for pRDA.

Harvestmen assemblage composition across the microclimatic gradient

DCA indicated relatively short compositional gradients (DCA1 axis length = 2.36 SD), supporting the use of a linear approach (pRDA) for subsequent constrained ordination analyses.

Therefore, we applied pRDA on the Hellinger-transformed harvestmen community data, while controlling for spatial structure by conditioning on transects (Block; Fig. 1.). After accounting for Block, the average surface temperature at 2 cm above ground (T2_ave; Fig. 3) was the only significant environmental

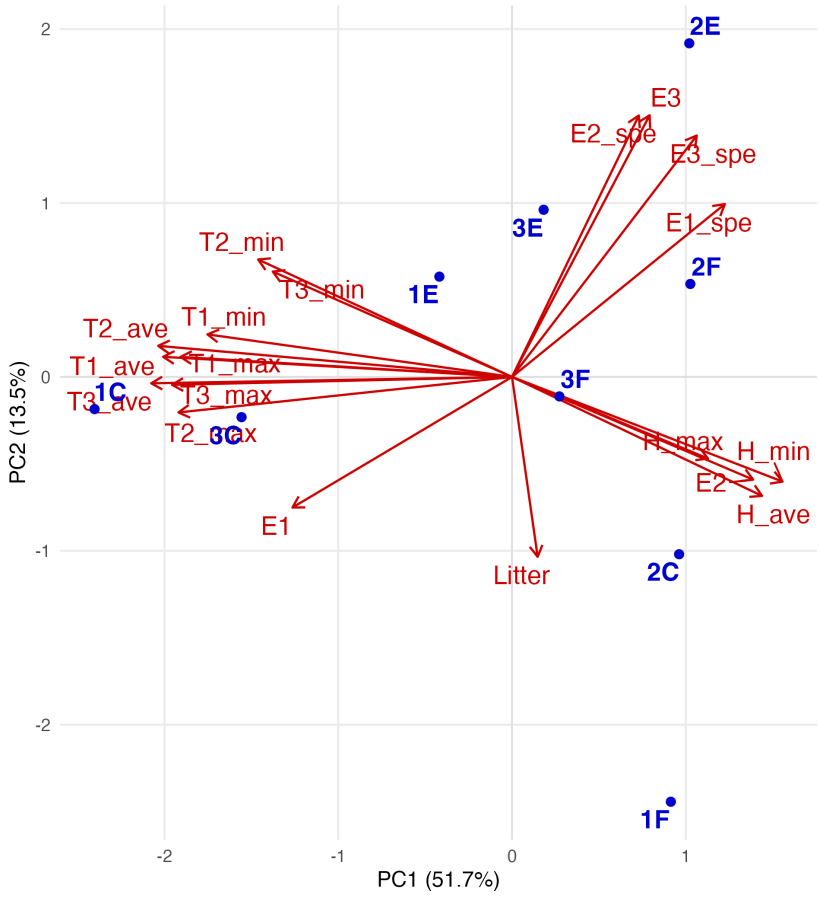

Figure 2. Principal component analysis of environmental variables at studied area (vegetation cover in the herb (E_1), shrub (E_2) and canopy (E_3) layers; plant species richness within each layer (E_1_spe, E_2_spe, E_3_spe); litter depth; and microclimate metrics (for details, see Table 3). Study plots: 1C, 1E, 1F, 2C, 2E, 2F, 3C, 3E, 3F.

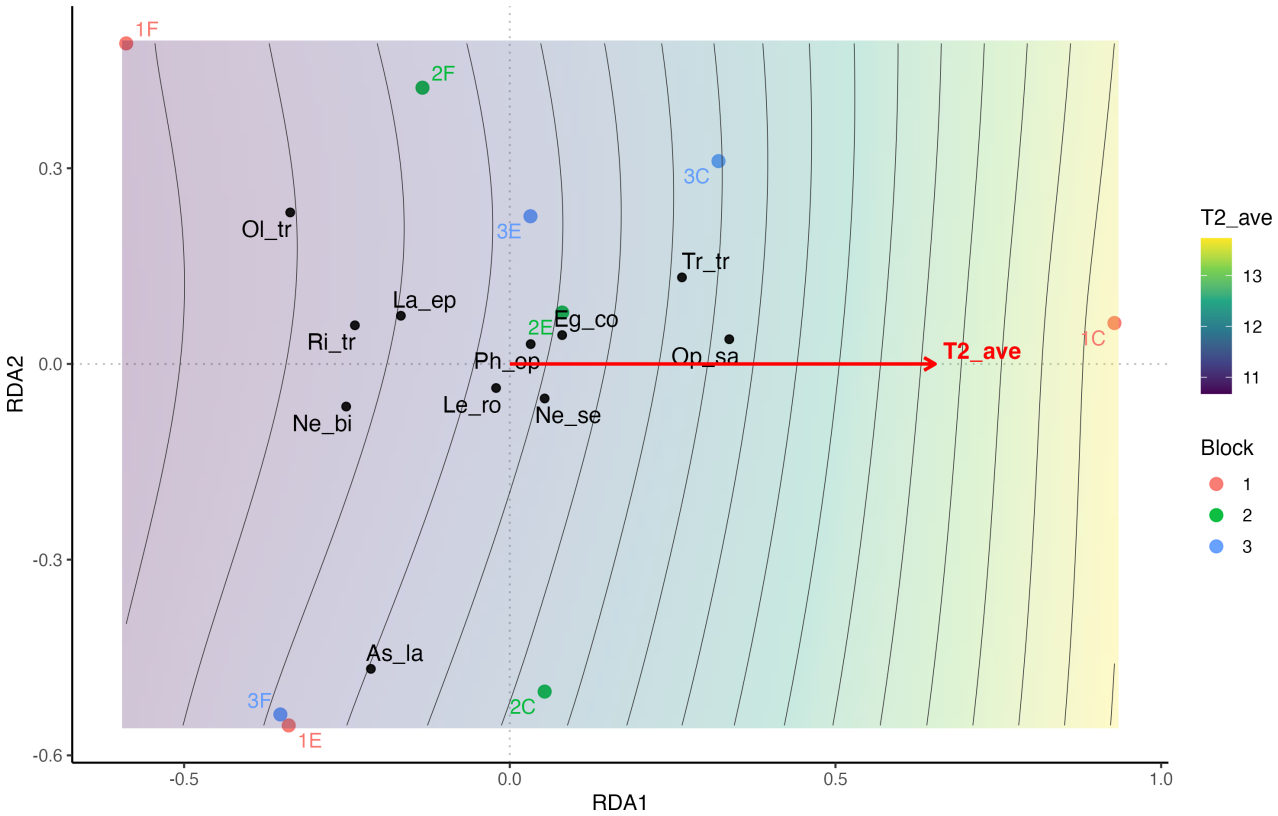

Figure 3. Partial Redundancy Analysis ordination diagram showing the relatedness of the harvestman assemblages between the different samples and study plots (1C, 1E, 1F, 2C, 2E, 2F, 3C, 3E, 3F) and average surface temperature at 2 cm (T2_ave) with GAM surface fit for temperature. Tr_tr – *Trogulus* agg. *tricarinatus*; Ne bi – *Nemastoma bidentatum sparsum*; Ph_op – *Phalangium opilio*; Op_sa – *Opilio saxatilis*; Eg_co – *Egaenus convexus*; La_ep – *Lacinius ephippiatus*; As_la – *Astrobunus laevipes*; Le_ro – *Leiobunum rotundum*; Ne_se – *Nelima sempronii*; Ri_tr – *Rilaena triangularis*; Ol_tr - *Oligolophus tridens*.

predictor of harvestmen community distribution (pseudo-F = 4.46; p = 0.007). Temperature was associated with 35.10% of total inertia (constrained inertia = 0.08933 of total inertia = 0.25250), while Block explained an additional 25.53% (conditioned inertia = 0.06498). Hierarchical cluster analysis (Euclidean distance on Hellinger-transformed data; Ward.D2 linkage) supported three main plot groups and one solitary plot: (3F, 1E, 2C), (3E, 3C) and (2F, 2E, 1F), with plot 1C forming a single-plot branch (Suppl. material 1). A GAM smooth of T2_ave was overlaid on the pRDA ordination to facilitate visual interpretation of the temperature gradient. Conditions with higher temperature were occupied primarily by the species *Opilio saxatilis*, *Trogulus* agg. *tricarinatus*, *Egaenus convexus* and *Nelima sempronii*. In comparison, conditions with lower temperature were preferred by harvestman species *Oligolophus tridens*, *Rilaena triangularis*, *Nemastoma bidentatum sparsum*, *Lacinius ephippiatus* and *Astrobunus laevipes*.

Species richness and diversity of harvestman assemblages

The number of harvestmen captured varied substantially amongst plots, ranging from 52 individuals at plot 3C and 68 at plot 1C to 508 at plot 1E and 546 at plot 1F (Table 5). Coverage-standardised species richness (q = 0) was

Table 5. Numbers of harvestmen captured and diversity attributes of harvestman assemblages at individual study plots.

Plot	1C	1E	1F	2C	2E	2F	3C	3E	3F
N	68	508	546	483	426	380	52	187	417
Species richness	4	8	8	8	9	8	5	10	9
Evenness (J)	0.91	0.71	0.83	0.72	0.68	0.79	0.78	0.67	0.72
Standardised q = 0	3.81	6.71	6.89	6.35	7.77	5.79	4.86	8.96	6.40
Standardised q = 1	3.31	4.20	5.13	4.25	4.35	4.65	3.50	4.59	4.61
Standardised q = 2	3.02	3.36	4.14	3.65	3.33	4.08	3.05	3.61	3.89

N represents the raw number of individuals captured, Unstandardised descriptive indices: species richness: number of harvestman species at individual study plots; Evenness (J): Pielou's evenness index, based on the Shannon–Wiener index; Hill numbers standardised at a common sample coverage of 0.98: q = 0 represents coverage-standardised species richness, q = 1 represents effective Shannon diversity and q = 2 represents effective Simpson diversity; study plots: 1C, 1E, 1F, 2C, 2E, 2F, 3C, 3E, 3F.

lowest at corridor plots 1C and 3C and highest at ecotone plots 3E and 2E. Effective Shannon diversity (q = 1) was highest at forest plot 1F, followed by forest plots 2F and 3F, whereas effective Simpson diversity (q = 2) was also highest in these three forest plots. Corridor plots 1C and 3C had the lowest q = 1 and q = 2 values. Observed species richness and Pielou evenness (J) are retained in Table 5 for comparison. Notably, plot 1C had high evenness despite low Hill diversity, indicating an even distribution amongst a small number of species, whereas plot 3E had high standardised richness, but lower effective diversity, reflecting the presence of uncommon species alongside a few dominant taxa.

Harvestman activity-density decreased significantly with increasing average soil moisture after accounting for variation in effective trap-days and repeated sampling within plots (β = −0.663 ± 0.121 SE, z = −5.91, p < 0.001; Table 6). Each 10 percentage-point increase in volumetric soil water content was associated with an estimated 48.5% reduction in the expected number of individuals captured per trap-day (IRR = 0.515, 95% CI: 0.414–0.642; Table 6). This model was supported by the likelihood ratio test (χ^2 = 28.31, df = 1, p < 0.001), reducing AIC from 931.69 to 905.36.

Table 6. Negative-binomial generalised linear mixed-effects model of harvestman activity-density. Raw capture counts were modelled with the logarithm of effective trap-days included as an offset.

Predictor	Estimate	Std. Error	z value	*p* value	IRR	95% CI for IRR
(Intercept)	−0.388	0.461	−0.842	0.400	—	—
H_ave_10	−0.663	0.112	−5.914	< 0.001	0.515	0.414–0.642
Likelihood-ratio model comparison						
Model	**df**	**AIC**	**logLik**	**LRT χ^2**	***p* value**	
Null model	3	931.69	−462.84	—	—	
Soil-moisture model	4	905.36	−448.68	28.323	< 0.001	

H_ave_10 represents a 10 percentage-point increase in average volumetric soil water content. IRR denotes the incidence-rate ratio. Plot was included as a random intercept and log effective trap-days were included as an offset. The estimated random-intercept variance was 1.225 (SD = 1.107) and the negative-binomial dispersion parameter was 1.94. The full model AIC was 905.36.

Coverage-standardised species richness (q = 0) was significantly associated with minimum surface temperature and tree-layer cover (Table 7). Minimum surface temperature had a negative relationship with standardised richness (β = −0.251 ± 0.024 SE on the log scale, t = −10.41, p < 0.001). Each 1 °C increase in minimum surface temperature was associated with an estimated 22.2% reduction in standardised richness (95% CI: 17.5–26.7% reduction), holding tree-layer cover constant. Conversely, tree-layer cover had a positive relationship with standardised richness (E_3_10: β = 0.058 ± 0.011 SE, t = 5.07, p = 0.002). Each additional 10 percentage points of tree-layer cover was associated with an estimated 5.9% increase in standardised richness (95% CI of 3.0–8.9% increase), holding minimum temperature constant. The model explained 95.3% of the variation in standardised richness (R^2 = 0.953; adjusted R^2 = 0.938) and received the strongest support amongst the candidate models (AICc = −12.32).

Coverage-standardised effective Shannon diversity (q = 1) was significantly associated with mean surface temperature and litter depth (Table 8). Mean surface temperature had a negative relationship with effective diversity (β = −0.106 ± 0.020 SE on the log scale, t = −5.22, p = 0.002). Each 1 °C increase in mean surface temperature was associated with an estimated 10.1% reduction in effective Shannon diversity (95% CI: 5.5–14.5% reduction), holding

Table 7. Inverse-variance weighted linear model of coverage-standardised species richness, Hill q = 0. The dependent variable was log-transformed before analysis.

Predictor	Estimate	Std. Error	t value	*p* value
(Intercept)	2.7264	0.1393	19.569	< 0.001
T2_min	−0.2513	0.0241	−10.410	< 0.001
E_3_10	0.0575	0.0113	5.074	0.002
Type II ANOVA				
Predictor	**df**	**F value**	***p* value**	
T2_min	1	108.366	< 0.001	
E_3_10	1	25.746	0.002	

Overall model: F(2, 6) = 61.270, p < 0.001, R^2 = 0.953, adjusted R^2 = 0.938, AICc = −12.32. T2_min represents annual mean minimum surface temperature; E_3_10 represents tree-layer cover expressed per 10 percentage-point increase. Estimates are presented on the log scale. The model was weighted by the inverse variance of the iNEXT estimates.

Table 8. Inverse-variance weighted linear model of coverage-standardised effective Shannon diversity, Hill q = 1. The dependent variable was log-transformed before analysis.

Predictor	Estimate	Std. Error	t value	p value
(Intercept)	2.5644	0.2438	10.517	< 0.001
T2_ave	−0.1063	0.0204	−5.219	0.002
Litter	0.0610	0.0223	2.742	0.034
Type II ANOVA				
Predictor	**df**	**F value**	**p value**	
T2_ave	1	27.234	0.002	
Litter	1	7.519	0.034	

Overall model: F(2, 6) = 19.091, p = 0.003, R^2 = 0.864, adjusted R^2 = 0.819, AICc = −17.82. T2_ave represents annual mean surface temperature; Litter represents litter depth in centimetres. Estimates are presented on the log scale. The model was weighted by the inverse variance of the iNEXT estimates.

litter depth constant. Litter depth had a positive relationship with effective diversity (β = 0.061 ± 0.022 SE, t = 2.74, *p* = 0.034). Each additional centimetre of litter depth was associated with an estimated 6.3% increase in effective Shannon diversity (95% CI: 0.7–12.2% increase), holding mean temperature constant. The model explained 86.4% of the variation in effective Shannon diversity (R^2 = 0.864, adjusted R^2 = 0.819) and was the best-supported candidate model (AICc = −17.82). Residual diagnostics indicated no significant departure from normality or homoscedasticity. However, the litter-depth effect was less stable than the temperature effect in leave-one-plot-out sensitivity analyses and should, therefore, be interpreted cautiously.

Discussion

Our study confirms that the structure of harvestmen (Opiliones) in an isolated floodplain forest fragment is primarily associated with microclimatic conditions and vegetation structure, while the potential role of corridors remains uncertain due to the lack of landscape-level replication.

In other countries, many authors, such as Komposch (2000), Šejnohová (2005), Marx and Schönhofer (2005) and Komposch et al. (2015), have focused on the study of harvestman assemblages (Opiliones) in floodplain forests. However, these studies did not investigate their occurrence in relation to such a broad spectrum of parameters as microclimatic and vegetation-structural environmental conditions.

Research on harvestmen in western Slovakia provides valuable context for our findings. Studies on non-isolated floodplain forests near Bratislava have identified microclimatic gradients and vegetation structure as key determinants of Opiliones assemblage composition and diversity (e.g. Litavský et al. (2019a, 2022, 2024)), mirroring the primary drivers we identified (temperature and canopy cover). However, a critical difference emerged in community outcomes. These extensive, well-connected forests typically support a richer harvestman fauna (12–14 species in comparable studies) with more balanced assemblages (Litavský et al. 2019a, 2019b, 2022, 2024). In contrast, our isolated 80-ha fragment hosted only 11 species, but had a remarkably high total number of captured individuals (n = 3,067). This pattern of reduced species richness coupled with the high activity of a few dominant species (*Nelima sempronii* and *Egaenus convexus*) indicates a community shaped by strong environmental filtering. We posit that the conditions within our isolated fragment represent a biotically simplified and compositionally shifted state. While the proximate drivers (microclimate and habitat structure) remain the same as in continuous forests, their intensity and combined biocenotic effects are greatly exacerbated. Isolation amplifies microclimatic edge effects and limits dispersal, intensifying filtering pressure. This results in an assemblage in which generalist species with broad tolerances thrive, whereas more sensitive forest specialists (such as *Zachaeus crista*, *Lophopilio palpinalis* and *Mitostoma chrysomelas*) are absent. This aligns with Thienemann's biocenotic principles, in which harsh or restricted conditions lead to low diversity, but high individual numbers of tolerant taxa (Thienemann 1918, 1920). A consequential finding is that the invasive harvestman *Opilio canestrinii* has not colonised this highly filtered environment.

Community composition: filtered by a temperature gradient

The most significant finding was that the surface air temperature (T2_ave) was the sole statistically significant predictor of the overall harvestman assemblage composition. This aligns strongly with the fundamental physiology of Opiliones, which, as hygrophilous arthropods with high susceptibility to desiccation, possess a narrow thermal and humidity tolerance (Santos 2007). Our results corroborate the hypothesis that microclimate acts as a primary environmental filter (Kraft et al. 2015), sorting species, based on their climatic niches. The segregation of species along this gradient was clear, with warmer, presumably drier microsites associated with species, such as *Opilio saxatilis* and *Trogulus* agg. *tricarinatus*, which are often considered more tolerant of disturbed or open habitats (Stašiov 2004; Pinto-da-Rocha et al. 2007; Litavský et al. 2025). In contrast, cooler microhabitats supported species, such as *Oligolophus tridens*, *Nemastoma bidentatum sparsum*, *Rilaena triangularis* and *Lacinius ephippiatus*, which are typically linked to stable, humid forest interiors (Stašiov 2004; Muster et al. 2014; Tomasson et al. 2014; Litavský et al. 2024). Similar patterns of species segregation along a canopy-cover gradient were observed by Černecká et al. (2017), who found that open habitats favoured xero-tolerant species, such as *Egaenus convexus* and *Oligolophus tridens*, whereas forest cover supported hygrophilic species. This pattern mirrors the distribution of other ground-dwelling arthropods along microclimatic gradients created by forest edges or management practices (Balázs et al. 2024; König et al. 2024), highlighting the universal importance of thermal and hydric niches.

Determinants of species richness and diversity: the role of vegetation structure and temperature

Contrary to the potential expectation that moisture would uniformly benefit all community parameters, effective diversity (Hill numbers) characterised as standardised species richness (q = 0) and standardised Shannon diversity (q = 1) were primarily influenced by temperature and vegetation structure, not directly by humidity. Standardised richness increased with higher tree-layer cover (E_3) and decreased with minimal surface temperature (T2_min) (see Suppl. material 1: fig. S5). This suggests that the positive effect of canopy cover on standardised species richness may be partially mediated by its modification of the understorey microclimate (e.g. reduced extreme temperatures and higher humidity), thereby creating more niches for different species (Davis et al. 2019; Rodrigues et al. 2025). Furthermore, increased litter depth and reduction in average surface temperature (T2_ave) contributed to higher standardised Shannon diversity (q = 1). This strongly supports our hypothesis and existing literature indicating that structural complexity (from vegetation to litter attributes) provides a greater variety of microhabitats for shelter, reproduction and foraging, thereby supporting a more diverse assemblage (Lassau et al. 2005; Litavský et al. 2021, 2024; Tobisch et al. 2023).

Our finding that the forest interior supported the most diverse communities align with Bragagnolo et al. (2007), who reported that continuous mature forests harbour higher richness of rare Opiliones species compared to fragmented habitats. The litter layer offers a stable and humid microenvironment that

is crucial for the survival of many litter-dwelling species (Bogyó et al. 2015; Litavský et al. 2018, 2024; Gongalsky 2021). In contrast, the presence of generalist species in areas with high tree cover, but varying shrub and litter density highlights species-specific niche partitioning within the forest interior. The ecotone effect observed in our study, where species from both forest and open habitats co-occur, parallels the findings of Silva et al. (2024) in the Atlantic Forest-Cerrado transition zone.

Activity-density and soil moisture: a counterintuitive negative relationship

The most counterintuitive result was the significant negative relationship between harvestman activity density and average soil humidity (H_ave). This contradicts the classical view of Opiliones as strictly moisture-dependent and also contradicts our initial hypothesis. However, this pattern may be explained by several non-exclusive mechanisms. First, high soil moisture in our study system, particularly in the forest core and lower-lying corridors, may correlate with prolonged seasonal waterlogging or cooler soil temperatures, conditions that can be suboptimal for epigeic activity and may limit prey availability (Mackay et al. 1986; Hayes et al. 2025). Second, the highest activity-density of individuals was recorded in plots with intermediate vegetation structure (e.g. forest edges and certain corridors), where slightly warmer and drier conditions might increase activity — even if absolute species richness is lower (De Sassi et al. 2012; Robinson et al. 2018). Third, it is possible that the dominant species in our study, *Nelima sempronii* and *Egaenus convexus*, exhibit broader moisture tolerances or even a preference for less saturated soils compared to rarer, more specialist species (Stašiov 2004; Litavský et al. 2019a). This finding highlights that overall activity-density and species-level responses can be decoupled and that a simple "more moisture equals more harvestmen" rule does not hold in complex, semi-natural landscapes. However, we cannot exclude the possibility that biotic interactions, such as prey availability or predation, also contribute to the observed patterns.

Conservation implications and the role of biological corridors

Our results suggest that the value of biological corridors for harvestmen may be associated with their internal environmental heterogeneity and habitat quality, which could, in turn, be influenced by corridor width. Amongst the three corridors examined, the narrower corridors (5 m and 10 m) supported lower observed and coverage-standardised diversity than 15 m corridor, indicated that they can be ineffective for several forest specialists. These patterns may reflect differences in temperature, humidity, vegetation structure and litter accumulation, which can influence habitat suitability for species adapted to forest interiors (Mestre et al. 2018). Such environmental filtering may reduce effective diversity and result in assemblages dominated by a relatively small number of generalist species with similar tolerance to edge-associated conditions (Passy et al. 2017). However, because each corridor width was represented by only one study plot, the effect of width cannot be separated conclusively from local environmental conditions,

spatial position and Block identity. The narrower corridors should, therefore, not be considered categorically ineffective for forest specialists, based on the present data.

The 15 m corridor supported standardised species richness and effective diversity values that were more similar to those of some forest and ecotone plots. This observation suggests that wider corridors may have greater potential to develop buffered microclimatic conditions and forest-like vegetation structure (Haddad and Tewksbury 2005; Haddad et al. 2015). This pattern was consistent for both observed and coverage-standardised diversity metrics, confirming that the difference is not merely an artefact of sampling intensity, but they do not by themselves establish a causal effect of corridor width. Replicated studies across a broader and continuous range of corridor widths would be required to identify such a threshold.

This finding contributes to a taxon-specific understanding of functional corridor dimensions. Literature reveals a broad spectrum of width requirements: studies on grassland butterflies recommend widths up to 250 m for effective connectivity (Pryke and Samways 2001), while for some Orthoptera in forest clearings, corridors of 10–40 m can support species richness comparable to much larger patches (Theuerkauf and Rouys 2006). Conversely, research on a boreal butterfly shows that even 4 m wide corridors can channel insect movement (Riva et al. 2018), highlighting that thresholds for basic movement can be far lower than those required for sustaining resident populations. Our study contributes a site-specific observation suggesting that both corridor dimensions and internal habitat quality should be considered when evaluating corridor suitability for harvestmen.

The D2 highway and railway may represent additional barriers limiting connectivity between Jarovská bažantnica and other remnants of the Danube floodplain. The absence of eco-ducts (wildlife-crossing structures) exacerbates isolation, although movement and connectivity were not measured directly in our study. Future landscape-level research should assess the permeability of these transport corridors before specific mitigation measures are proposed. If substantial barrier effects are confirmed, appropriately designed crossing structures and habitat connections could be considered as potential measures to improve connectivity (Van Der Ree et al. 2011).

The high coverage-standardised species richness observed in ecotones can be attributed to the edge effect, where species from both the forest interior and adjacent open habitat (corridors or agricultural land) occur together, increasing overall diversity (Ries and Sisk 2004; Ries et al. 2004; Rischen et al. 2023). However, the core forest plots maintained the highest effective Shannon and Simpson diversity, emphasising their irreplaceable value.

While our results provide valuable insights into the environmental filters shaping harvestman assemblages, it is important to acknowledge that Opiliones are a relatively species-poor group compared to other arthropod taxa and their overall abundance and influence on ecosystem functioning may be limited. Consequently, generalisations from our findings to other taxonomic groups — particularly those with different ecological requirements or dispersal abilities — should be made with caution. The patterns observed here are likely specific to harvestmen and may not fully represent the responses of other arthropod communities to habitat fragmentation and corridor design.

Limitations and future research

This study has limitations that point to future research directions. As all sites are embedded within a single fragment and only three spatial blocks were available, some of the observed differences — particularly in activity-density of harvestmen — may reflect block-level spatial structure rather than habitat position; we, therefore, emphasise relationships with measured microclimate and vegetation structure and interpret habitat contrasts cautiously.

A key limitation of this study is the low level of true replication at the landscape scale. Sampling was necessarily restricted to a single forest fragment and, although we collected multiple samples per plot, the number of independent replicates was limited to spatial blocks. As a result, repeated sampling within a plot should not be interpreted as additional independent replication and treating such repeated measures as independent would constitute pseudo-replication. To minimise this issue, we revised the multivariate analyses by aggregating species-composition data to the plot level and using permutation schemes constrained within blocks. Nevertheless, the small number of independent replicates limits statistical power. Our results should, therefore, be interpreted as site-specific patterns that are consistent with effects of microclimate and vegetation structure, rather than as definitive, broadly generalisable estimates of fragmentation effects. Replication across additional fragments and landscapes will be necessary to test the robustness of these relationships and strengthen inference beyond the studied system.

Conclusions

Our findings indicate that harvestman assemblages in the isolated Jarovská bažantnica forest fragment are strongly filtered by fine-scale environmental conditions, confirming their role as sensitive bioindicators. Assemblage composition was primarily structured by surface temperature, while coverage-standardised species richness and effective Shannon diversity were driven by a combination of vegetation structural complexity (tree canopy cover, litter depth) and temperature (minimum and mean surface temperature). A key observational finding was that, amongst the three corridors examined, the widest corridor most closely resembled forest-interior conditions in terms of vegetation structure and microclimate and supported the highest coverage-standardised richness and effective diversity. This pattern suggests that corridor dimensions, sufficient to buffer edge effects and allow the development of complex vegetation, may contribute to habitat quality for forest-associated fauna.

Therefore, conservation management must adopt a dual focus: first, on preserving high-quality habitat structure within core fragments and, second, on ensuring that connecting landscape elements are designed with adequate width and management to achieve and maintain the necessary structural and microclimatic quality. For the agricultural landscapes of Slovakia and similar regions, investing in such well-designed ecological infrastructure is not an enhancement, but a necessity to mitigate fragmentation and safeguard invertebrate biodiversity. However, because our study is limited to a single forest fragment, these recommendations remain conditional; further research across multiple fragments and landscapes is necessary to confirm the generality of our findings and to develop robust guidelines for corridor design in agricultural landscapes.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following: DeepSeek
Used for: Literature discovery and brainstorming

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Author contributions

J.L., D.B. and O.M. conceived and designed the study, conducted fieldwork and processed biological samples. J.L. and R.M. interpreted the data and wrote the first draft. R.M. performed statistical analyses and interpreted the data. H.Ž. identified the plants and interpreted the data. All authors read and approved the final manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Microclimate and vegetation structure shape harvestman (Opiliones) assemblages in an isolated forest fragment and adjacent potential biological corridors

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