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SPIDER COMMUNITIES OF NEAR-SUMMIT ECOSYSTEMS IN THE UZHANSKY NATIONAL NATURE PARK (UKRAINIAN CARPATHIANS): A FOCUS ON THE OVERGROWING OF GRASSLANDS

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Abstract

The study examined spider communities in the near-summit ecosystems of the Ukrainian Carpathians, focusing on transitional zones from old-growth forests to subalpine grasslands. In total, 3460 adult spiders, representing 90 species from 19 families, were recorded (29 species in forests, 51 in ecotones, and 71 in grasslands). Four species new to the Ukrainian Carpathians and seven rare species listed in the Carpathian Spider Red List were identified. A four-step analysis of Hill diversities was performed to compare the spider communities across ecosystems. Grassland communities were significantly more diverse than those in forests and ecotones in terms of Shannon and Simpson diversity indices ($q = 1, 2$), while no significant differences were observed between forests and ecotones. Non-metric multidimensional scaling revealed that ecotones serve as unique transitional ecological zones, combining elements of forest and grassland ecosystems. However, the spider communities in ecotones did not differ significantly from those in forests (pairwise perMANOVA). Both were characterized by a similar ratio of families, species composition of dominants, low activity density, and a limited number of indicator species. Consequently, the expansion of shrub-dominated ecotones may lead to shifts in spider community composition and a decline in grassland ecosystem diversity. The study highlights the importance of conserving near-summit ecosystems, particularly grasslands, which serve as habitats for both typical and rare spider species in the Carpathians.

Keywords: *Araneae*, biodiversity, mountain grasslands, old-growth forests, ecotones, shrub encroachment.

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INTRODUCTION

Mountain ecosystems are vital to regional environmental balance, economic growth, and social resilience, as they support rich biodiversity and provide essential ecosystem services. Research on these ecosystems is conducted worldwide (Körner 2004, Dainese et al. 2024, Urbach et al. 2024), focusing on understanding the causes and consequences of timberline shifts and the reduction of subalpine grasslands driven by natural and anthropogenic factors (Gartzia et al. 2014, Tokarczyk 2017, Piccinelli et al. 2020, Hagedorn & Flower 2021, Körner 2021). Such zones are sensitive indicators of global climatic change and key biodiversity hotspots, maintaining a high proportion of rare and specialist species (Hilpold et al. 2018, Mitka et al. 2022, Steinwandter & Seeber 2023).

Researching the environmental determinants of biodiversity, the drivers of biodiversity change, and the consequences of these changes is crucial for conserving vulnerable, often semi-natural mountain ecosystems. Over the past century, traditional land-use practices in the Carpathians, which involved removing woody plants followed by livestock grazing, lowered the upper forest limit by several hundred meters, thereby expanding grassland areas. However, these pastures (locally called polonyna) are now undergoing ecological succession, particularly within protected areas (Kozak et al. 2007, Kucharzyk & Augustyn 2008, Sitko & Troll 2008, Tokarczyk 2017, Mitka et al. 2022). The pattern of polonyna overgrowth depends on the type of upper forest limit. For instance, between 1930 and 2000, the area of subalpine grasslands in the Polonynian Carpathians of Ukraine decreased by 24% due to the expansion of coniferous forests, while the upper limit of beech forests remained stable or even shifted downward (Sitko & Troll 2008, Martazinova et al. 2011). Grasslands established below the potential timberline, in areas formerly occupied by beech or sycamore-beech forests, rapidly underwent ecological succession toward shrub-dominated vegetation (Kucharzyk & Augustyn 2008, Durak et al. 2014, Tokarczyk 2017, Mitka et al. 2022). The scale of this overgrowth is currently unknown.

In the East Carpathian Biosphere Reserve, particularly in the Uzhansky National Nature Park, unique subalpine deciduous shrub formations, dominated by rowan (*Sorbus aucuparia*), willows (primarily *Salix silesiaca*), and sycamore (*Acer pseudoplatanus*) have developed. Patches of thickets encroach on treeless areas, including forming an ecotone between the forest and grassland ecosystems. The expansion of beech is constrained by sod-grass communities and is limited only to a narrow zone at the upper forest limit (Stoyko 2004, Stoyko 2008, Mitka et al. 2022).

Shrub encroachment on the *polonyna* is a potential threat to this habitat and its specialist species. Therefore, to understand the impact of this process on these vulnerable ecosystems, a comprehensive study of mountain summit ecosystems, with an emphasis on vegetation and key bioindicator animal groups, is necessary. Within this study, to examine the formation of invertebrate communities on the ridge tops in Uzhansky NNP, we encompassed ecosystems ranging from old-growth forests near their upper limit to *polonynas*. Some results from this research, particularly concerning the fauna of insects, have already been published (Glotov et al. 2021, Koval & Chumak 2021, Koval et al. 2021a, Koval et al. 2021b, Koval & Dedus 2022). This paper focuses on spiders, one of the most abundant and diverse arthropod groups.

Spiders are widely recognized as effective indicators of habitat changes due to their dependence on vegetation structure and their ability to reflect successional dynamics (Uetz 1979, Maelfait 1996, Maelfait et al. 2002, Gallé et al. 2017, Gallé et al. 2021, Lyons et al. 2018, Hamřík & Košulič 2019). However, the extent of vegetation role in shaping spider assemblages is still ambiguous (Lafage et al. 2019). Furthermore, only a small proportion of arachnological literature addresses spider communities at the upper forest limit in European mountains (Frick et al. 2006, Frick et al. 2007, Muff et al. 2007, Muff et al. 2009, Blasbichler et al. 2023). A knowledge gap exists concerning the effects of land abandonment and the establishment of nature protection regimes on spiders in mountain regions (Noel & Finch 2010, Zakkak et al. 2014, Hilpold et al. 2018, Nardi & Marini 2021). Studies were not conducted on spider communities of the upper forest limit and grasslands below the potential treeline in the Ukrainian Carpathians.

The work aimed to study and compare spider communities in near-summit ecosystems (forests, ecotones, and grasslands) by analyzing their taxonomic composition, species diversity, activity density, dominance structure, and indicator species. One of the tasks was to determine whether these ecosystems serve as habitats for rare and little-known spider species in the Ukrainian Carpathians. This approach allows us to assess the current state of near-summit ecosystems, particularly mountain grasslands (*polonynas*), and identify species preferences within specific habitats. Repeated studies will help assess community changes resulting from the expansion of deciduous shrub ecotones dominated by rowan.

MATERIALS AND METHODS

Study area and study sites

The research was conducted in the Uzhansky National Nature Park, created in 1999. Its territory is located in Zakarpattia Oblast near the borders of Poland and Slovakia and is part of the international East Carpathian Biosphere Reserve. The area encompasses low and mid-altitude mountain regions, with elevations ranging from 220 to 1250 m above sea level (Herenchuk 1981). The research was conducted on two mountain ridges: Yavirnyk (maximum elevation 1017 m a.s.l.) and Stinka (1092 m a.s.l.), within the montane belt, at the boundary between the moderately cool (spruce-beech forests) and cool (spruce forests) bioclimatic zones (Fig. 1). The area belongs to the orographic ecoregion of Polonyna Ravka-Runa, which is part of the Polonynian Beskids (Kruhlov 2008).

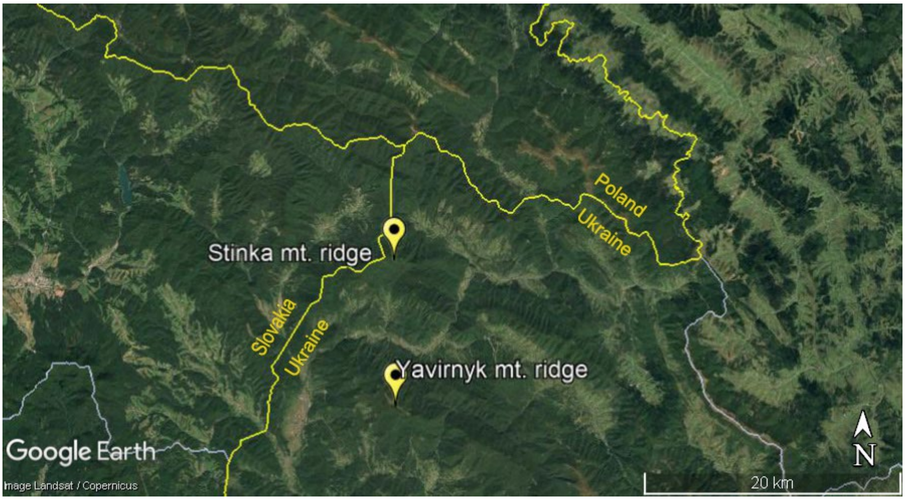

Figure 1. The location of the study area – mountain ridges Yavirnyk and Stinka (Ukraine; Uzhanskyi NNP).

Six study sites were situated: three on the Stinka (S) and three on the Yavirnyk (Ya) mountain ridges. They represent the main types of near-summit ecosystems, forming a transitional zone from forests to subalpine grasslands (‘lowered’ subalpine grasslands located below the potential upper limit of the forest).

Forests (F): Old-growth sycamore-beech forests (*Acereto pseudoplatani–Fageta*) near the upper limit, over 150 years old, in the regeneration stage with fallen, rotten, and dead-standing trees. Forest stand density is 0.6–0.7.

S [49.00361°N, 22.55364°E; 925–960 m; southwest-facing slope]: Association: *Acereto (pseudoplatani)–Fagetum (sylvaticae) lunariosum (redivivae)*. Located on rocky outcrops. Ya [48.90272°N, 22.56036°E; 970–1010 m; northeast-facing slope]: Association: *Acereto (pseudoplatani)–Fagetum (sylvaticae) dentariosum (bulbiferae)*.

Ecotones (E): A narrow diffuse treeline ecotone with ‘krummholz’ turning into deciduous shrub-dominated communities between forest and grassland.

S [49.00492°N, 22.55597°E; 940–950 m]: Thickets of *Sorbus aucuparia*, *Salix* spp., *Acer platanoides* undergrowth, with scattered *Betula pendula* and *Abies alba*. Locally transitioning into raspberry and/or blackberry thickets. Ya [48.90225°N, 22.55983°E; 990–1010 m]: Thickets of *Sorbus aucuparia* with *Salix* spp., *Acer platanoides*, and *Acer pseudoplatanus* undergrowth, transitioning into tall-grass communities.

Grasslands (*G. polonynas*): Open patches of ‘lowered’ subalpine grasslands. Treeless areas alternate with thickets of shrubs, similar in composition to ecotones.

S [49.00503°N, 22.55569°E; 945–965 m]: Tall-grass communities (the association *Achylleo strictae–Calamagrostietum arundinaceae*) with dwarf (*Vaccinium*) wind heaths. Ya [48.90519°N, 22.55355°E; 990–1017 m]: *Nardus stricta* swards (associations: *Nardetum campanulosum abietinae and Poetum Chaixii scorzonerosum*) with dwarf (*Vaccinium*) wind heaths.

The encroachment of shrub-dominated vegetation on grasslands and the expansion of ecotones are intensifying at both ridges, primarily on the Stinka, where the state border between Ukraine and Slovakia passes, and there is currently no anthropogenic impact.

Sampling methods and material processing

Three study plots, spaced more than 10 meters apart, were established within each study site, resulting in 18 plots: 6 in forests, 6 in ecotones, and 6 in grasslands. In each plot, one pitfall trap (16 cm in diameter, filled with 5% formaldehyde solution as a preservative) and one combined trap (a large yellow plastic funnel) were installed. Only spider specimens collected from the pitfall traps were analyzed, as the material from the combined traps, positioned one meter above the ground, was unrepresentative due to the high proportion of juvenile individuals. The material was removed every 17–23 days. The traps were active from 15 April to 30 October in both 2018 and 2019. All collected specimens were preserved in a 70% ethanol solution. The material is stored at the Institute of Ecology of the Carpathians, NAS of Ukraine (Lviv). The specimens were identified using Nentwig et al. (2025), and nomenclature followed the World Spider Catalog (2025).

Data analysis

The total activity density and activity density of each species were standardized to catches per 100 trap days. Dominance structure was analysed following Stöcker & Bergmann (1977), using the following dominance classes: 31.7–100% – eudominant; 10.1–31.6% – dominant; 3.2–10.0% – subdominant; 1.1–3.1% – recedent; and <1.0% – subrecedent. An analysis of similarity percentages (SIMPER, Clarke 1993) was also performed to identify the species most responsible for the observed patterns. This method disaggregates the Bray-Curtis dissimilarities between samples to determine the species contributing most to the dissimilarity between habitat types (Clarke & Warwick 2001).

A four-step analysis of Hill diversities (Chao & Hu 2023) was performed to compare the spider communities of forests, ecotones, and grasslands. Hill diversities model the influence of rare or common species through the order of the exponent q: at $q = 0$, all species are weighted equally, representing species richness; $q = 1$ (the exponential of Shannon's entropy), species are weighted by their relative abundances, reflecting the diversity of common species; $q = 2$ (the inverse of Simpson's concentration), dominant species have a greater influence (Chao et al. 2014, 2020). The four-step analysis included rarefaction to the observed diversity, extrapolation to double the sample size, and comparison of assemblages based on sample coverage and completeness. Non-asymptotic diversity curves were used to compare assemblages at the same sample completeness ($C_{\max}$) when the asymptotes were not reached, particularly for species richness ($q = 0$). Evenness was calculated at $C_{\max}$ using Pielou's index, which ranges from 0 to 1, with values closer to 1 indicating more even communities. All curves were presented with 95% confidence intervals derived via a bootstrap method. The iNEXT4.steps package (Chao & Hu 2023) was used to analyze the species diversity.

The reliability of differences in parameter values among groups (forest, ecotone, grassland) was assessed using ANOVA (one-way Analysis of Variance), the non-parametric Kruskal–Wallis test (for data where homogeneity of group variances was not maintained), and the corresponding pair-wise tests: Tukey's Honestly Significant Difference (HSD) test and Dunn's post hoc test (Quinn & Keough 2002). Permutational multivariate analysis of variance (perMANOVA, based on the Bray-Curtis similarity index; Anderson 2001) was used to test the hypothesis of differences in spider community composition and species abundance between study plots. Non-metric multidimensional scaling (NMDS, using relative activity density of species) was employed to visualize and evaluate patterns of similarity among spider communities. We used indicator species analysis (IndVal, Dufrêne & Legendre 1997) to designate spider species associated with different habitats. All statistical analyses were done using the PAST program (Hammer et al. 2001).

RESULTS

Community composition and diversity patterns

In total, 3460 adult spiders, belonging to 90 species and 19 families, were captured. Of these, 777 individuals from 29 species and 12 families were recorded in old-growth forests, 1101 individuals from 51 species and 15 families – in ecotones, and 1582 individuals from 71 species and 17 families – in grasslands. The family with the highest species richness was Linyphiidae (30 species; 33.3% of all species); other species-rich families included Agelenidae (5; 5.6%), Gnaphosidae (14; 15.6%), Lycosidae (12; 13.3%), and Thomisidae (5; 5.6%). Six species (6.7% of those recorded), namely *Coelotes terrestris* (Wider, 1834), *Inermocoelotes inermis* (L. Koch, 1855), *Callobius claustrarius* (Hahn, 1833), *Cybaeus angustiarum* L. Koch, 1868, *Trochosa terricola* Thorell, 1856, and *Ozyptila trux* (Blackwall, 1846), were found in all 18 traps that operated during the vegetation periods of two years.

Based on ANOVA and Tukey's post hoc test, grasslands have significantly lower proportions of Agelenidae ($F = 11.40$; $p<0.01$) and Linyphiidae ($F = 2.31$; $p<0.01$) compared to forests and ecotones. In contrast, in open ecosystems, the contribution of Gnaphosidae ($F = 5.40$; $p = 0.02$) was higher than in forests, and of Lycosidae ($F = 49.32$; $p<0.01$) – than both in forests and ecotones (Fig. 2).

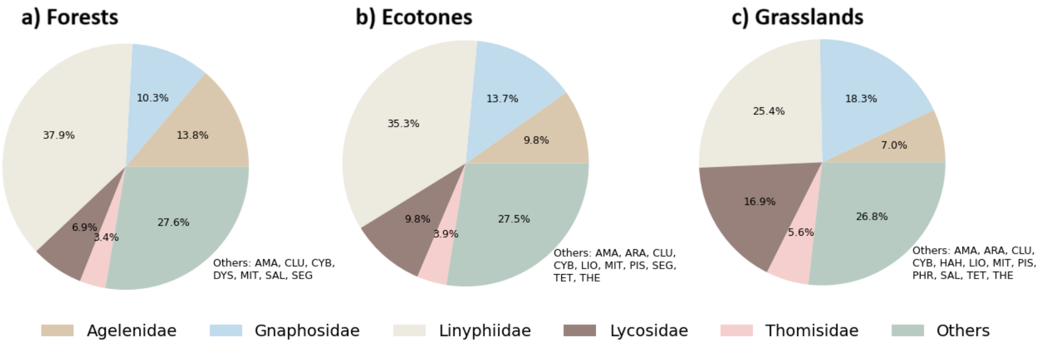

Figure 2. The spider family composition of the near-summit ecosystems: a) in forests, b) in ecotones, and c) in grasslands.

The estimated sample completeness for old-growth forests is higher than that of ecotones and grasslands when $q < 0.5$. However, confidence intervals overlap (Fig. 3a). For $q = 0$, the estimated sample completeness for forests, ecotones, and grasslands is 0.83, 0.76, and 0.68, indicating that approximately 17–32% of rare species remain undetected. For $q > 0.5$, the sample completeness across the studied ecosystems is similar. The corresponding values for $q = 1$ are 0.99, 0.98, and 0.99. All ecosystem types showed a sample completeness profile of 100% for $q = 2$ (Tab. 1: step 1).

Table 1. The numerical values for the three special cases of $q = 0$, 1, and 2 for abundance-based spider data collected from near-summit ecosystems in the Uzhansky NNP.

Step 1. Sample completeness profiles (Fig. 2a)			
	q = 0 Estimated / Undetected	**q = 1** Estimated / Undetected	**q = 2** Estimated / Undetected
Forests	0.83 / 0.17	0.99 / 0.01	1.00 / 0.00
Ecotones	0.76 / 0.24	0.98 / 0.02	1.00 / 0.00
Grasslands	0.68 / 0.32	0.99 / 0.01	1.00 / 0.00
Step 2. Asymptotic analysis (Fig 2b, c)			
	q = 0 Empirical / Asymptotic / Undetected	**q = 1** Empirical / Asymptotic / Undetected	**q = 2** Empirical / Asymptotic / Undetected
Forests	29.00 / 34.78 / 5.78	7.34 / 7.52 / 0.18	4.88 / 4.91 / 0,03
Ecotones	51.00 / 67.39 / 16.39	8.76 / 9.06 / 0.30	5.34 / 5.36 / 0,02
Grasslands	71.00 / 104.04 / 33.04	19.30 / 19.98 / 0.68	11.98 / 12.06 / 0,08
Step 3. Non-asymptotic coverage-based rarefaction and extrapolation. Maximum standardized coverage C_{max}=0.993 (Fig. 2d)			
	q = 0	**q = 1**	**q = 2**
Forests	31.16	7.39	4.89
Ecotones	60.50	8.92	5.35
Grasslands	87.57	19.69	12.02
Step 4: Evenness among species abundances (Fig. 2e)			
	q = 0	**q = 1**	**q = 2**
Forests	0.58	0.21	0.13
Ecotones	0.53	0.13	0.07
Grasslands	0.67	0.22	0.13

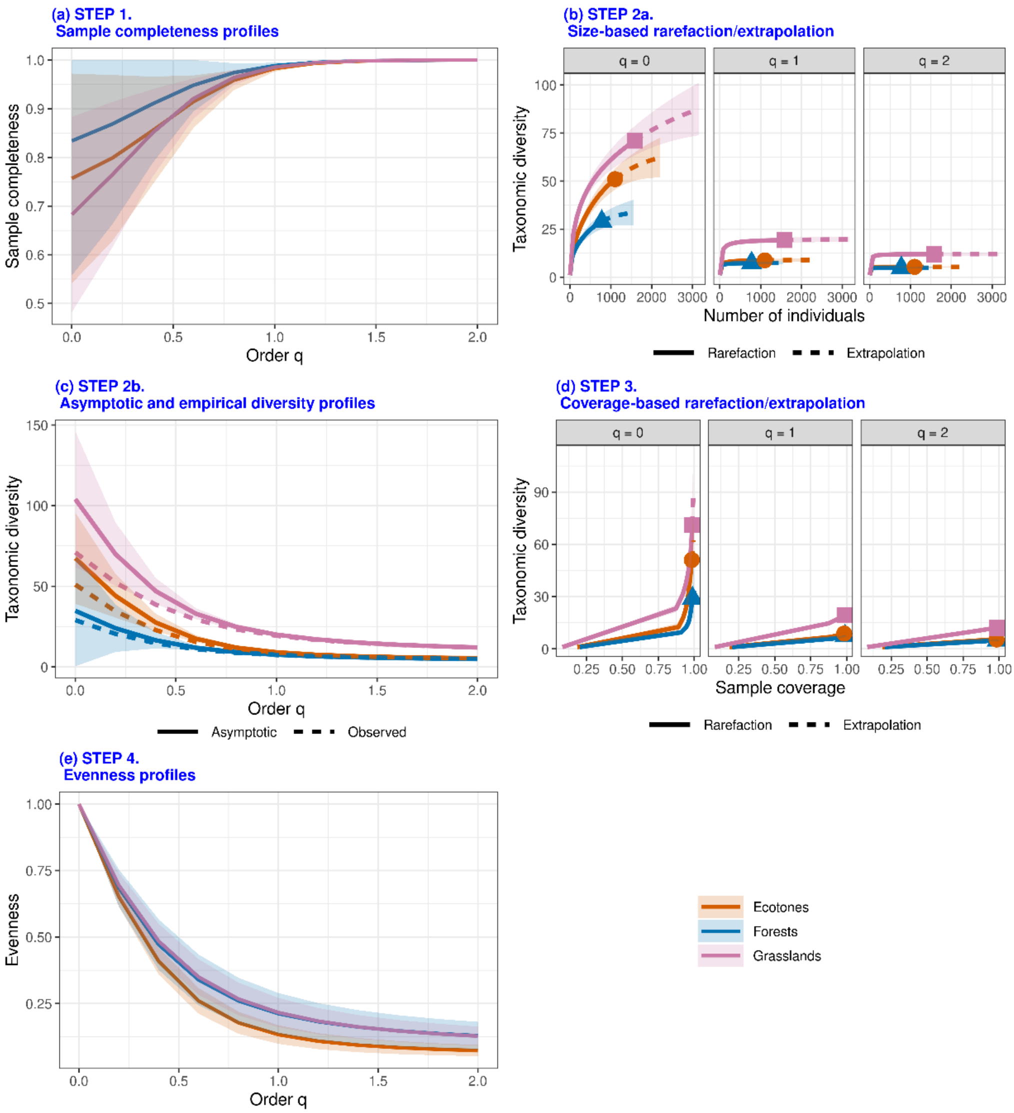

Figure 3. iNext.4steps figure for spider communities of near-summit ecosystems in the Uzhansky NNP. (a) Sample completeness. (b) Size-based rarefaction/extrapolation. (c) Asymptotic vs. empirical diversity. (d) Coverage-based rarefaction/extrapolation. (e) Evenness profiles. Solid dots/triangles: observed data. Shaded areas: 95% confidence intervals (a bootstrap method with 100 replications).

The undetected Shannon diversity (from 0.18 to 0.68) and Simpson diversity (from 0.02 to 0.08) within forests, ecotones, and grasslands suggest that nearly all abundant and highly abundant species were detected (Tab 1: step 2). Based on the asymptotic results, the analysis indicates that grassland communities are significantly more diverse than forest and ecotone communities in terms of both Shannon and Simpson diversity indices ($q = 1$, 2; non-overlapping confidence intervals in Fig. 3b, c). A moderate difference in the number of abundant species ($q = 1$) was found between grasslands and forests (12.46) and grasslands and ecotones (10.92). In contrast, the difference for highly abundant species ($q = 2$) was smaller (7.15 for grasslands vs. forests, and 6.7 for grasslands vs. ecotones). No statistically significant difference was noted between forests and ecotones. The non-stabilizing curve for $q = 0$ (Fig. 3b) indicates that the current data underestimates the actual number of species in the community, and the degree of difference in the true species richness of the entire communities cannot be precisely assessed.

The maximum coverage value ($C_{\max}$; the lower coverage of the extrapolated samples when each is extrapolated to double the reference sample size) at which all samples could be fairly compared is 0.993 (99.3%). Under standardized coverage, spider communities in grasslands are also significantly more diverse than those in forests and ecotones ($q = 1, 2, 3$; non-overlapping confidence intervals in Fig. 3d). The major difference between open and forest/ecotone ecosystems lies in rare species: particularly between grasslands and forests (56.41) and grasslands and ecotones (27.07) (Tab. 1: step 3). No statistically significant difference was observed between forests and ecotones, primarily for $q = 1$ and $q = 2$.

Under the coverage value of 99.3%, Pielou's evenness measure (Tab. 1: step 4) shows that the evenness among species abundances in grasslands and forests is higher than in ecotones. However, the profile indicates that evenness values for all ecosystems are similar for any order q between 0 and 2 (confidence intervals overlap; Fig. 3e).

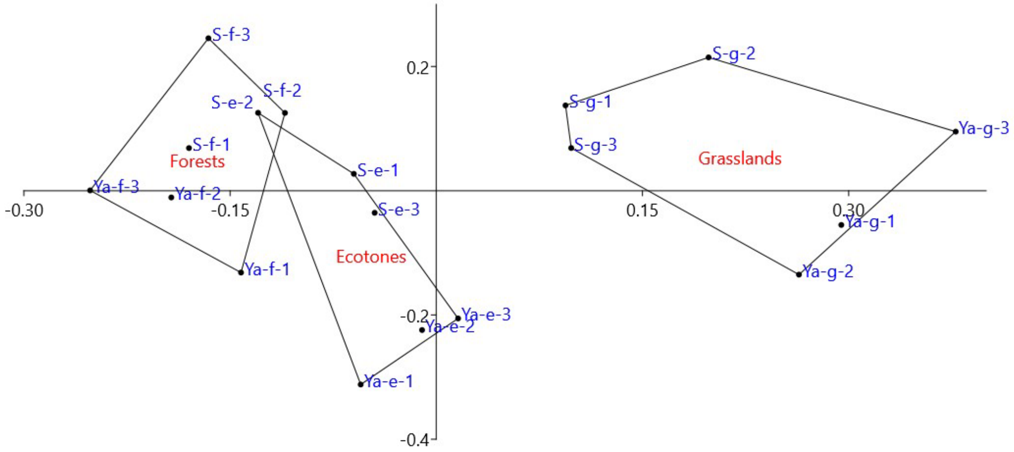

Figure 4. Non-metric multidimensional scaling (nMDS; Bray-Curtis index, stress = 0,165) of spider species communities of the near-summit ecosystems (abbreviations to the names of study plots: S – Stinka mt. ridge, Ya – Yavirnyk mt. ridge, f – forest, e – ecotone, m – grassland, 1-6 – number of study plots).

Community patterns

The spider communities of the studied ecosystems varied in species composition and relative species abundance (perMANOVA: pF = 5.074, p = 0.002, permutation N = 999). The graphical result of non-metric multidimensional scaling revealed that ecotone communities clustered with forest communities, forming a distinct group well-separated from grassland communities (Fig. 4), with intergroup differences confirmed by pairwise perMANOVA analyses.

According to the SIMPER test, the average dissimilarity between spider assemblages across all types of ecosystems was 46.8% (between forests and ecotones – 39.2%, ecotones and grasslands – 48.3%, and forests and grasslands – 53.0%).

Table 2. Contribution of dominant spider species to dissimilarities among forest, ecotone, and grassland ecosystems based on SIMPER analysis; cut off = 75%.

Taxon	Inter-group dissimilarity		Relative abundance		
	Contribution	Cumulative contribution	Forests	Ecotones	Grass-lands
Callobius claustrarius (Hahn, 1833)	19.0	19.0	12.4	29.0	10.6
Coelotes terrestris (Wider, 1834)	11.1	30.1	31.5	23.2	17.6
Inermocoelotes inermis (L. Koch, 1855)	8.5	38.6	8.4	6.8	10.0
Cybaeus angustiarum L. Koch, 1868	7.5	46.1	27.9	19.4	10.7
Trochosa terricola Thorell, 1856	6.9	53.0	4.0	4.9	8.9
Ozyptila trux (Blackwall, 1846)	5.8	58.8	2.0	1.6	7.3
Pardosa riparia (C.L. Koch, 1833)	3.5	62.3	0.0	0.1	4.1
Pardosa alacris (C.L. Koch, 1833)	3.4	65.7	0.3	2.3	3.4
Aulonia albimana (Walckenaer, 1805)	2.4	68.1	0.0	0.0	2.8
Haplodrassus signifer (C.L. Koch, 1839)	2.4	70.5	0.0	0.5	2.8
Tenuiphantes tenebricola (Wider, 1834)	2.2	72.7	4.6	1.0	0.2
Haplodrassus umbratilis (L. Koch, 1866)	1.7	74.4	0.0	0.1	2.0
Euryopis flavomaculata (C.L. Koch, 1836)	1.7	76.1	0.0	0.0	2.0

Spider activity

According to the non-parametric analysis of variance, spider communities significantly differ in activity density only between grassland and forest habitats (109.4±17.3 and 52.1±6.7 individuals per 100 trap-days, respectively; Kruskal-Wallis test for equal medians: H (χ^2) = 15,16; p < 0,01). The value of this parameter in ecotones was 80.1±5.7 individuals per 100 trap-days.

Dominance structure

Five species – *Callobius claustrarius*, *Coelotes terrestris*, *Cybaeus angustiarum*, *Inermocoelotes inermis*, and *Trochosa terricola* – exhibited high activity densities across all study sites (Tab. 2). They account for over 50% of the dissimilarities between the forest-ecotone-grassland groups, and their relative abundance exceeds 3.2% (subdominant level) in all ecosystems. None of these species qualify as eudominants (above 31.7%) in the classical sense, contributing to the diversity and evenness of the communities.

Table. 3. IndVal analysis of species associated with specific habitats. Only significant ($p \leq 0.05$) habitat associations are presented.

Ecosystems	Species	Indval, %	p
Forests	*Cybaeus angustiarum* L. Koch, 1868	45.8	0.00
	Centromerus silvicola (Kulczyński, 1887)	57.1	0.01
	Tenuiphantes tenebricola (Wider, 1834)	78.5	0.00
	Segestria senoculata (Linnaeus, 1758)	39.4	0.04
Ecotones	*Callobius claustrarius* (Hahn, 1833)	52.2	0.02
	Centromerus sylvaticus (Blackwall, 1841)	51.9	0.02
	Microneta viaria (Blackwall, 1841)	72.2	0.00
	Alopecosa trabalis (Clerck, 1757)	42.5	0.05
Grasslands	*Drassodes pubescens* (Thorell, 1856)	50.0	0.02
	Haplodrassus signifer (C.L. Koch, 1839)	89.4	0.00
	Haplodrassus umbratilis (L. Koch, 1866)	64.3	0.00
	Zelotes apricorum (L. Koch, 1876)	83.8	0.00
	Zelotes petrensis (C.L.Koch, 1839)	50.0	0.02
	Zelotes subterraneus (C.L. Koch, 1833)	33.8	0.03
	Diplostyla concolor (Wider, 1834)	42.2	0.05
	Micrargus apertus (O. P.-Cambridge, 1871)	50.0	0.02
	Pelecopsis radicicola (L. Koch, 1872)	59.0	0.01
	Agroeca brunnea (Blackwall, 1833)	75.3	0.00
	Alopecosa aculeata (Clerck, 1757)	50.0	0.02
	Alopecosa inquilina (Clerck, 1757)	100.0	0.00
	Alopecosa pulverulenta (Clerck, 1757)	44.0	0.05
	Aulonia albimana (Walckenaer, 1805)	100.0	0.00
	Pardosa alacris (C.L. Koch, 1833)	61.4	0.00
	Pardosa lugubris (Walckenaer, 1802)	83.3	0.00
	Pardosa riparia (C.L. Koch, 1833)	98.6	0.00
	Trochosa terricola Thorell, 1856	55.5	0.00
	Zora spinimana (Sundevall, 1833)	88.8	0.00
	Phrurolithus minimus C.L. Koch, 1839	83.3	0.00
	Euophrys frontalis (Walckenaer, 1802)	83.3	0.00
	Pachygnatha listeri Sundevall, 1830	53.8	0.01
	Euryopis flavomaculata (C.L. Koch, 1836)	100.0	0.00
	Ozyptila trux (Blackwall, 1846)	73.4	0.00
	Xysticus lineatus (Westring, 1851)	50.0	0.02

In old-growth forests, *Coelotes terrestris* (31.5%) and *Cybaeus angustiarum* (27.9%) contributed most to the spider communities, while in ecotones, *Callobius claustrarius* (29.0%) and *Coelotes terrestris* (23.2%) were the most abundant. *Tenuiphantes tenebricola* (Wider, 1834) also contributes to within-group similarity in forest ecosystems. Grasslands exhibit a more balanced species distribution, with notable contributions from *Callobius claustrarius* (11.6%) and *Cybaeus angustiarum* (10.7%). Compared to forests and ecotones, grasslands show higher contributions from *Inermocoelotes inermis*, *Trochosa terricola*, *Ozyptila trux*, *Pardosa riparia*, and *Pardosa alacris*, highlighting the ecological preferences of these species in the region. Among these, only *Pardosa riparia* is absent in forest ecosystems. All listed (in this paragraph) taxa explain 69.9% of the inter-group dissimilarities between spider communities.

Indicator species

IndVal analysis identified the association of species with particular ecosystem types. Table 3 illustrates that each ecosystem has a unique set of indicator species, with their number being significantly higher in grasslands. This can be explained by the greater diversity of grasslands and the different spider composition of forests and grasslands. In grasslands, many indicator species are open-habitat specialists (*Alopecosa inquilina*, *Aulonia albimana*, *Pardosa riparia*, *Euryopis flavomaculata*).

Rare species of the Carpathians

One species, *Clubiona saxatilis* L. Koch, 1866, was recorded for the first time in Ukraine (Hirna, Yanul, 2023). Three species collected in the grassland of the Yavirnyk Ridge – *Haplodrassus kulczynskii* Lohmander, 1942, *Zelotes exiguus* (Müller & Schenkel, 1895), and *Syedra gracilis* (Menge, 1869) – are reported for the first time from the Ukrainian Carpathians.

In near-summit ecosystems, rare and endemic species, included in the Red List of Carpathian spiders (Gajdoš et al., 2014), have been recorded. Specifically, in the Stinka Ridge, the following species were found: *Clubiona saxatilis* L. Koch, 1866 – NT, *Dysdera dubrovninnii* Deeleman-Reinhold, 1988 – DD, *Centromerus silvicola* (Kulczyński, 1887) – VU, *Gonatium orientale* Fage, 1931 – DD, *Palliduphantes milleri* (Staręga, 1972) – VU, endemic, *Alopecosa inquilina* (Clerck, 1757) – LC; in the Yavirnyk Ridge: *Zelotes exiguus* (Müller & Schenkel, 1895), *Centromerus silvicola* (Kulczyński, 1887) – VU, *Palliduphantes milleri* (Staręga, 1972) – VU, endemic, *Xysticus lineatus* (Westring, 1851) – NT, and *Alopecosa inquilina* (Clerck, 1757) – LC. Four of the seven identified rare species occur in the ecotones (one was shared between ecotones and forests, and another between ecotones and grasslands), three in the grasslands, and two in the forests (Fig. 5).

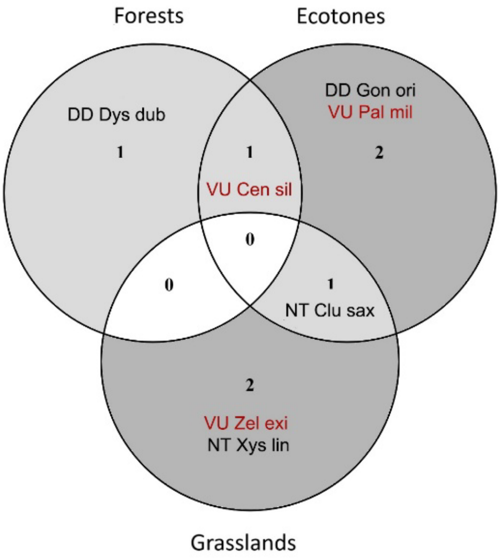

Figure 5. Venn diagram: species from the Red List of Carpathian spiders (Gajdoš et al. 2014) recorded in the near-summit ecosystems in the Uzhansky NNP.

DISCUSSION

The study comprehensively analyses spider communities in near-summit ecosystems, focusing on old-growth forests, ecotones with deciduous shrubs, and grasslands below the potential upper limit of the forests. The results highlight high species richness across these ecosystems, including four species previously not recorded in the Ukrainian Carpathians and seven species listed in the Red List of Carpathian spiders (Gajdoš et al. 2014). However, the current data likely underestimate the true species richness in the communities, particularly in grasslands. According to the iNEXT4.steps analysis, approximately 17%, 24%, and 32% of rare species remain undetected in forests, ecotones, and grasslands, respectively. Therefore, additional research is required for a more accurate assessment of spider diversity.

Two distinct spider community types were identified: one associated with forests and the other with grasslands. Spider communities in ecotones showed greater similarity to those in forests, suggesting that light availability may have a stronger influence on spider community composition than the type of ground vegetation (Muff et al. 2009). The result supports the hypothesis that shading from woody vegetation is a primary driver of spider distribution in European ecosystems (Entling et al. 2007, Muff et al. 2009).

The tall canopies of old-growth forests create stable microclimatic conditions, reducing fluctuations in temperature, humidity, and wind (Schowalter 2017). This stability limits niche diversity (Hamřík et al. 2023), leading to communities dominated by forest specialists, such as *Coelotes terrestris* and *Cybaeus angustiarum*. Consequently, forests exhibit lower species diversity, activity density, and representation of rare species compared to grasslands. Forests also contain fewer indicator species (only four, including the vulnerable species *Centromerus silvicola*).

Ecotones, with their intermediate light and vegetation conditions, provide habitats for both forest and grassland invertebrates while supporting unique ecological niches (Lloyd et al. 2000, Horváth et al. 2002, Erdős et al. 2013, Blasbichler et al. 2023, Ho et al. 2023, Klimm et al. 2024). While ecotones exhibit high species richness, their diversity does not surpass that of adjacent grasslands, consistent with findings from mountainous landscapes where grasslands are more diverse than forests (Erdős et al. 2013, Blasbichler et al. 2023). iNEXT analysis revealed significantly higher Shannon and Simpson diversity indices ($q = 1, 2$) for grassland communities compared to forests and ecotones, while forests and ecotones did not show significant differences in diversity.

Non-metric multidimensional scaling (NMDS) further demonstrated the transitional nature of ecotone spider communities, which occupy an intermediate position between forest and grassland communities. The similarity of ecotone and forest communities reflects the higher representation of shaded-habitat families such as Agelenidae and Linyphiidae. Ecotones also harbor dominant species shared with forests, such as *Callobius claustrarius* and *Coelotes terrestris*, and lack species exclusively associated with them, highlighting their role as transitional zones. Indicator species included generalist taxa such as *Callobius claustrarius* (Hahn, 1833), *Centromerus sylvaticus* (Blackwall, 1841), *Microneta viaria* (Blackwall, 1841), and *Alopecosa trabalis* (Clerck, 1757).

The results underscore the critical threat posed by shrub encroachment into grasslands due to the expansion of the ecotone. This process reduces the presence of rare species and increases "trivialization" of species composition, particularly affecting grassland-dwelling families such as Gnaphosidae and Lycosidae. These findings align with broader ecological principles, emphasizing habitat loss as a major driver of species decline (Caro et al. 2022).

Conservation efforts should focus on protecting near-summit mountain grasslands, as these areas support the greatest species diversity, including many indicators and rare (low-abundance) species. Even small, isolated grassland patches can sustain species-rich spider communities due to the high dispersal abilities of spiders (Horváth et al. 2009).

Additionally, targeted studies of ecotones between old-growth forests and grasslands can inform more effective conservation measures, supporting the long-term survival of biodiversity in these complex and dynamic ecosystems.

CONCLUSIONS

This study highlights the distinct community patterns and diversity of spiders in the near-summit ecosystems of the Polonynian Beskids (Ukrainian Carpathians), emphasizing the ecological importance of transitional zones between old-growth forests and grasslands.

Grasslands exhibit significantly higher species richness and diversity compared to forests and ecotones, as demonstrated by Shannon and Simpson indices ($q = 1, 2$). Rare (non-abundant) species, indicator species, and species adapted to open habitats, particularly from the Gnaphosidae and Lycosidae families, are also more prevalent in grasslands, underscoring their ecological uniqueness and conservation significance. The limited study of local grasslands is highlighted by the identification of three species found here for the first time in the Carpathians: *Haplodrassus kulczynskii*, *Zelotes exiguus*, and *Syedra gracilis*.

Forest spider communities are characterized by the dominance of typical Carpathian forest species, a higher representation of Agelenidae and Linyphiidae families, and relatively low diversity and activity density. The unique environmental stability of old-growth forests is crucial for supporting forest-specialist species.

While ecotones exhibit some increased species richness due to edge effects, their overall diversity remains similar to that of forests due to the influence of the forest canopy and reduced habitat variation compared to grasslands. Ecotones serve as important buffer zones, supporting both forest- and grassland-associated species. However, no species were exclusively associated with ecotones, reflecting their transitional nature. At the same time, only here was one of the three registered vulnerable species found, namely *Pallidiphantes milleri*. The encroachment of shrubs into grasslands through ecotone expansion poses a biodiversity threat by reducing habitat for rare grassland species.

This study improves the understanding of spider community formations in mountain ecosystems. Protecting near-summit ecosystems is crucial for maintaining regional biodiversity, especially for rare and vulnerable species. Conservation efforts should focus on preventing shrub encroachment into grasslands to maintain a landscape mosaic.

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