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ORIGINAL ARTICLE

Epigeic harvestmen (Arachnida: Opiliones) of reforested Norway spruce forest stands in Slovakia: A case study

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Abstract. We evaluated the effect of different ecological factors on epigeic harvestmen (Opiliones) in stands of Norway spruce of different ages planted on former agricultural land in the Western Carpathians (Slovakia). In total, 15 species of harvestmen were recorded, which is 42.9% of the 35 species of harvestmen currently recorded in Slovakia. The most abundant species were *Nelima sempronii*, *Lacinius ephippiatus*, *Mitopus morio*, *Oligolophus tridens*, *Leiobunum gracile* and *Platybunus bucephalus*. Species richness and diversity was not associated with any forest characteristic. There was a negative association between the percentage of Norway spruce and abundance of harvestmen and positive association between the chemical element Ca^{2+} and harvestmen abundance. Beta diversity of harvestmen assemblages was low. Composition of harvestmen assemblages was significantly related to percentage of spruce, humus content, Ca^{2+}, C/N and soil pH. *Lacinius ephippiatus* was most abundant in pitfall traps with a low percentage of spruce, *Oligolophus tridens* plots where there was low humus content and *Leiobunum gracile* tended to be more abundant in plots with more alkaline soils.

INTRODUCTION

Significant ecological and climatic changes can occur in single aged stands of spruce due to forest management or sudden major disturbances (e.g. selective logging, clear logging, or remediation), which can subsequently affect the species composition and abundance of arthropods. For example, changes in the age structure of the remaining stand, as well as the breakup of the canopy, directly or indirectly affect the environmental conditions in forests (Canham et al., 1990). Effects of species composition and/or age of trees and the undergrowth (Heyborne et al., 2003; Samu et al., 2014; Staněk et al., 2020; Stiegel et al., 2020), quality, volume of soil and coarse woody residues (Castro & Wise, 2010; Ranius et al., 2015), degree of shading and/or degree of tree density in stands (Spitzer et al., 2008; Isaia et al., 2015; Košulič et al., 2016; Vincent et al., 2020) on invertebrate communities are already documented. For example, Čuchta et al. (2019) report that Collembola can be used as an indicator group of mesofauna in the assessment of changes in the soil environment of mountain spruce forests caused by disturbance. Lang et al. (2014) report the effect of forest type on the abundance, diversity, community structure and composition of Carabidae and Staphylinidae, which indicates that the effects of overall management are small and mainly mediated by the structure of habitats, such as canopy cover or plant diversity. Abundance and species richness of beetles is higher in old than in young stands and species richness lower in unmanaged than managed stands.

Harvestmen (Opiliones) are poorly studied despite the fact that they and spiders are very important generalist predators and/or saprophages not only in agroecosystems (e.g. García et al., 2010; Stašiov et al., 2011; Mihál et al., 2015) but also in forests (for example Spitzer et al., 2008; Mihál et al., 2010; Mihál & Astaloš, 2011; Merino-Sáinz & Anadón, 2015). Harvestmen are excellent bioindicators and used in nature conservation assessment and planning (Komposch, 2022). The effect of the forest environment on species richness, abundance and composition of harvestmen has so far only been sporadically studied (e.g Mihál & Gajdoš, 2010; Černecká et al., 2017; Mihál & Černecká, 2017). The most important ecological factors affecting assemblages of harvestmen at large scales are altitude, habitat and moisture at the landscape level (Vitosha Mt., Bulgaria; Mitov & Stoyanov, 2005) and altitude, temperature, human activity and moisture at the country level (Czech Republic; Klimeš, 1997). At a local scale, humidity and structural diversity of habitat are the main factors influencing the structure of communities of harvestmen (Curtis & Machado, 2007). Purchart et al. (2013) report that although intensively managed monocultures of spruce are viewed as species-poor habitats (as are coniferous monocultures in general, particularly with respect to deadwood-associated arthropods), structural interventions (e.g. opening up

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of stands, enhancing the mosaic character of homogenous plantations by small-scale clear-cutting, etc.) may result in greater habitat availability for many epigeic arthropods and thus enhance the biodiversity in such stands (also e.g. Fahy & Gormally, 1998; Mullen et al., 2003).

The aim of this research was to study the species richness, abundance and structure of harvestmen communities in different aged spruce plantations with different soil chararacteristics. We assumed a significant effect of these factors on communities of harvestmen because structurally complex habitats provide more niches, which are assumed to increase species diversity (Tews et al., 2004). Therefore, we assumed that patterns in the distributions of species of harvestmen would depend on within-habitat heterogenity. We predicted (i) the highest species diversity and abundance would be recorded in the oldest and most open stands, (ii) the most heliophilic and xero-thermophilic species in the oldest, most open stands and (iii) the most hygrophilous species in the youngest, most shaded stands.

MATERIAL AND METHODS

Study site

The plots studied were in stands of Norway spruce (*Picea abies* (L.) H. Karst.) planted on former farmland near the forest complex of Vrchdobroč, central Slovakia, in the western part of the Slovenské Rudohorie Mountains, Veporské Vrchy Hills, which is the source of the Ipeľ River (48°54´40˝N, 19°58´67˝E) and at an altitude in the Vrchdobroč ranges from 740 to 917 m, the rocky substrate is granodiorite crystalline and prevailing type of soil is brown forest (cambisol), sandy-loam. The average monthly temperature in the growing season (from June to October) in 2016 and 2017 was 14.3°C, the average precipitation from June to October 2016 and 2017 was 400 mm (Slovak Hydrometeorological Institute, Bratislava, Weather Station Detvianska Huta, 2 km away from the stands studied).

Spruce stands at Vrchdobroč were established in the last decades of the last century on former farmland that was converted to forest by governmental resolution enacted in 1960. The government reforestation program was in response to unsustainable regional deforestation and growing problems with flooding in the middle and lower reaches of the Ipeľ River. The deforestation of the original beech and beech-fir forests due to increasing settlement in the Vrchdobroč area at the beginning of the 20th century led to a radical transformation of the landscape and a change in hydrological conditions. Flow rate at the source of the Ipeľ River the Lučenecký brook and Rimava River declined over the last 50 ears from about 60% to 29%, the greatest decline in Czechoslovakia at that time. According to the reforestation plan, forest area was to increase from 7,648 to 15,738 ha by 1980.

The structure of the plantations in this area changed dramatically after a series of heavy snow falls and high winds during the winter 1993/1994, which decimated stands of spruce at the pole stage of growth in entire areas at high altitudes and parts of stands at low altitudes. After these disturbances, spruce forests in the locality of Vrchdobroč were considerably fragmented. This weather-induced fragmentation was compounded by the planting of other woody species that were preferred over spruce, especially *Abies alba* Mill*., Fagus sylvatica* L. and *Acer pseudoplatanus* L. (Vacek et al., 2009). Thus, at the time of this study, there were few extensive monocultures of spruce in the locality of Vrchdobroč. The research plots were mainly located in the few remaining monocultures of spruce, but in some cases the only option was to locate them in mixed species stands.

Characteristics of research plots

Harvestmen were sampled in nine plots. Each plot had an area of 416 m². Six plots had dimensions of 20.4 m × 20.4 m and three 10.0 m × 41.6 m. Tree stocking of plots ranged between 0.8–0.9. The dominant species was spruce and at the highest stocking the canopy cover was densest. In the individual plots the species of herbaceous plants in the undergrowth were: *Athyrium filix-femina* (L.) Roth, *Carex sylvatica* Huds., *Fragaria vesca* L., *Geranium robertianum* L., *Rubus hirtus* Waldst. et Kit., *R. idaeus* L., *Senecio umbrosus* Waldst et Kit. and *Urtica dioica* L. Other characteristics and photographs of the plots are listed in Table 1 and depicted in Fig. 1.

Sampling and data collection

Pitfall traps were used to study the activity of harvestmen and were set in the plots from June 2016 to April 2019. Three traps filled with 2% solution of fomaldehyde (volume 0.5 l, neck diameter 9 cm, 13.5 cm deep) were set in the centre of each plot in a line at least 5 m apart and 5 m from the edge of the forest. The distance between the plots in a stand was 300 to 500 m and the closest distance of the nearest traps from those in two neighbouring plots was at least 20 m. The pitfall traps were covered with square wooden covers (15 × 15 cm) 3 or 4 cm above the trap. In 2016, traps were changed once a month from June to November. In November 2016, the traps were filled with an antifreeze formaldehyde solution and left in the plots until April 2017. The same procedure was followed in 2017. The last collection and disposal of traps took place in April 2018. Thus, the traps were emptied 15 times during the study. The catch of each trap was processed and determined individually in the laboratory.

Harvestmen were identified using morphological keys as well as information on the Internet (Šilhavý, 1956, 1971; Martens, 1978; Hillyard, 2005; Arachnologische Gesellschaft, 2022; British Arachnological Society, 2022; Oger, 2022; van Duinen,

Table 1. Basic characteristics of the plots studied in forest stands at Vrchdobroč Mt.

Plot No.	Altitude (m a.s.l.)	Location	Spruce (%)	Age (years)	Number of trees	Exp.	pH (H_2O)
A1	870	48°32´00˝N, 19°34´44˝E	72.6	21	157	SW	4.36
A2	890	48°32´02˝N, 19°34´46˝E	55.3	21	85	SW	4.41
A3	830	48°31´52˝N, 19°33´45˝E	100	21	60	E	4.27
B1	850	48°31´58˝N, 19°34´31˝E	100	31	83	E	4.23
B2	820	48°31´46˝N, 19°34´06˝E	99.1	31	111	SW	4.19
B3	830	48°31´48˝N, 19°34´09˝E	99.1	31	111	SW	4.18
C1	820	48°31´42˝N, 19°34´16˝E	100	51	54	S	4.8
C2	800	48°31´33˝N, 19°34´05˝E	96.7	51	61	E	4.42
C3	825	48°31´38˝N, 19°33´50˝E	66	51	50	S	4.1

Notes: Age – stand age (in 2016), Exp – exposure. Other tree species at RSPs A1: *Larix decidua* 26.8%, *Populus tremula* 0.6%, A2: *Larix decidua* 44.7%, B2: *Populus tremula* 0.9%, B3: *Larix decidua* 0.9%, C2: *Abies alba* 3.3%, C3: *Abies alba* 32.0%, *Fagus sylvatica* 2.0%.

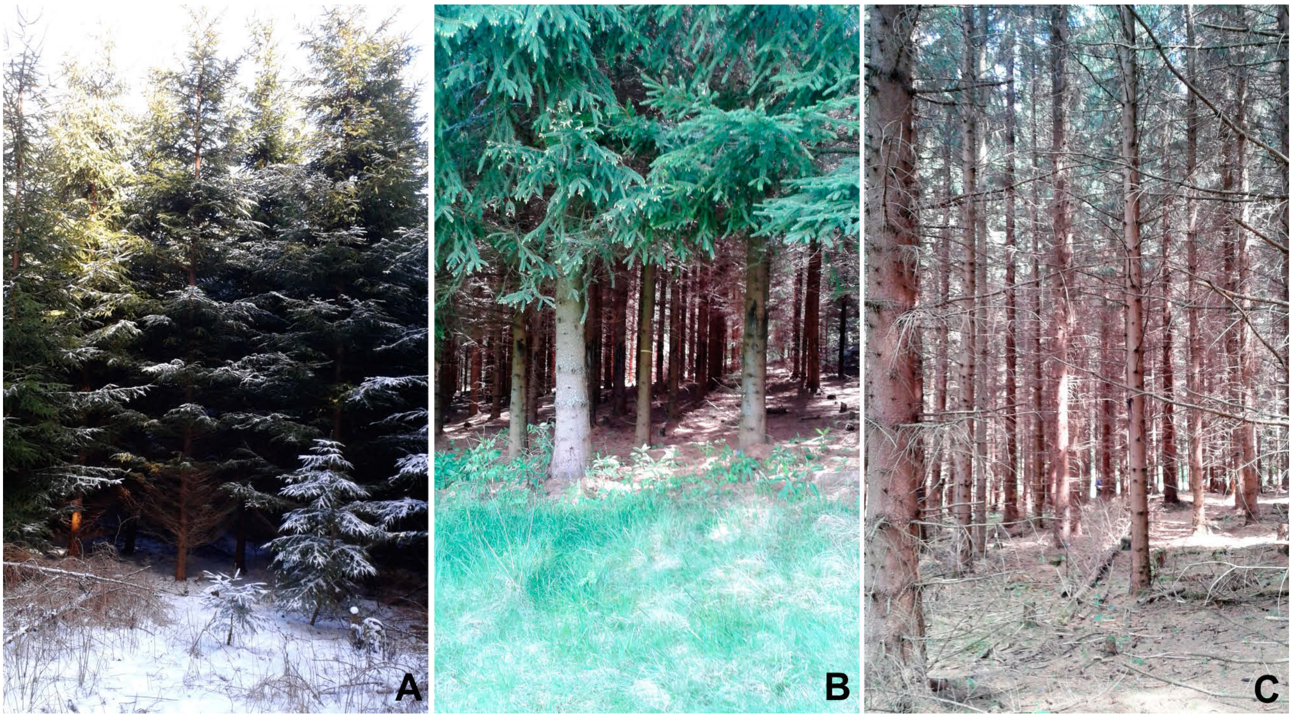

Fig. 1. A picture of plot A3 in the youngest 21-year-old stand, plot B1 in the middle aged 31-year-old stand and plot C2 in the oldest 51-years-old stand. Photographs taken by E. Luptáková and I. Mihál.

2022). Scientific nomenclature of the species follows that of Kury et al. (2021).

The dominance index (D) was calculated for the species at each locality (Losos et al., 1984). Dominance classes were arranged using the classification of Tischler (1976): (D > 10 – eudominant, 5 < D < 10 – dominant, 2 < D < 5 – subdominant, 1 < D < 2 – recedent, and 1 < D – subrecedent). The majority of the material was preserved in 70% ethanol and deposited in the collection of the Institute of Forest Ecology SAS, Zvolen, Slovakia.

Environmental characteristics

We used percentage of spruce (based on the total number of all trees in a plot) and number of trees, stand age, humus content, C/N, Ca^{2+}, soil reaction (pH) to explain characteristics of harvestmen assemblages. We included all trees with an average thickness of over 7 cm at breast height in the evaluation of the number of trees in the plots. In October 2017, samples of soil were collected from upper soil horizons in each plot in order to determine pedobiological and pedochemical characteristics. Three soil samples (0.5 kg of soil from three places in a stand were sieved to produce 0.5 kg of fine earth per stand) were collected in each plot and used to measure soil pH by potentiometric methods in H_2O and KCl solution, while chemical analyses of biogenic element contents (C, Ca^{2+}, N) and humus were done using inductively coupled plasma atomic emission spectroscopy (AES-ICP) and elemental analysis with thermal conductivity detection (EA-TCD) in a certified laboratory in the National Forestry Centre in Zvolen, in 2017.

Data analysis

All statistical analyses were done using statistical software R 3.6.0 (R Core Team, 2019) implemented in RStudio 1.2.1335 (RStudio Team, 2019). The catches of each trap were pooled for the whole sampling period. The relationships between harvestmen species richness, abundance, Shannon diversity and forest characteristics was assed using generalized linear mixed models (GLMM; by using R-package lme4 (Bates et al., 2015). Plot identity was used as random factor to account for any additional differences associated with spatial heterogeneity in species metrics. GLMMs with Poisson distribution and log-link function were used to fit abundance, and GLMMs with Gaussian distribution with log-link function were used to fit species richness and diversity data. As the number of harvestmen caught by each trap varied greatly (28–309), species richness was rarefied to the lowest number caught per trap. Due to small sample size (9 plots, 3 traps per plot) only simple GLMMs with single predictors were fitted. Type-III analysis-of-variance was computed for the models' objects by using R-package car (Fox & Weisberg, 2019); pseudo-R^2 for the analysed models was calculated (marginal R^2 representing the variance explained by fixed factors and conditional R^2 representing the variance explained by both fixed and random factors) using R-package MuMIn (Bartoń, 2019).

Detrended correspondence analysis (DCA) followed by distance-based redundancy analysis (db-RDA), from the package vegan (Oksanen et al., 2018), were used to evaluate the association of forest characteristics with the composition of the assemblages of harvestmen. In db-RDA, the Bray-Curtis dissimilarity index was calculated for individual traps and used as a response variable representing species composition of harvestmen. Species were not scaled (standardised), as this may put too much weight on rare species in the analysis. The adjusted R^2 was calculated for each explanatory variable used individually as single predictor in db-RDA as a goodness-of-fit statistic. Only statistically significant variables were used in the final model. The permutation test with 9,999 unrestricted permutations was used to test the significance of the explanatory variables.

RESULTS

The 27 pitfall traps caught 3,658 individuals of 15 species of harvestmen. There were 471 females, 1,017 males, 1,066 subadults and 1,104 juveniles. The six most abundant species (*Lacinius ephippiatus, Leiobunum gracile, Mitopus morio, Nelima sempronii, Oligolophus tridens,* *Platybunus bucephalus*) accounted for 79.4% of the harvestmen assemblages (Table 2). Most individuals were caught in the youngest 21-year old stands (1,548 ex.), followed by the oldest 51-year old stands (1,343 ex.) and the 31-year old stands (767 ex.). The average number of species caught per trap was 9.7 ± 1.4 (mean ± SD), the range 6–11 and the average number of individuals caught per trap 135.5 ± 81.1 (mean ± SD), range 28–309.

Rarefied species richness and Shannon diversity were not associated with any forest characteristic (Table 3). There was a negative association between percentage of Norway spruce and harvestmen abundance, and positive association between Ca^{2+} and harvestmen abundance (Fig. 2). The largest percentage of variability explained by plot identity (as the random effect) was associated with harvestmen abundance and less so with harvestmen diversity (Table 3).

Beta diversity of harvestmen assemblages was low (1st DCA axis length = 1.60, 2nd = 1.53 SD units). Composition of harvestmen assemblages was significantly associated with the percentage of spruce, humus, Ca^{2+}, C/N and soil pH (Table 4). The first ordination axis revealed a gradient with soil Ca^{2+}, the second a gradient with humus content of soil and percentage of spruce (Fig. 3). Species such as *Lacinius ephippiatus* was mainly associated with the lowest percentage of spruce, *Oligolophus tridens* with low humus content, *Nelima sempronii* with soil with a high content of Ca^{2+} and *Leiobunum gracile* with forest growing in more alkaline soils (Fig. 3). Other species in the middle of ordination space did not show any consistent trend.

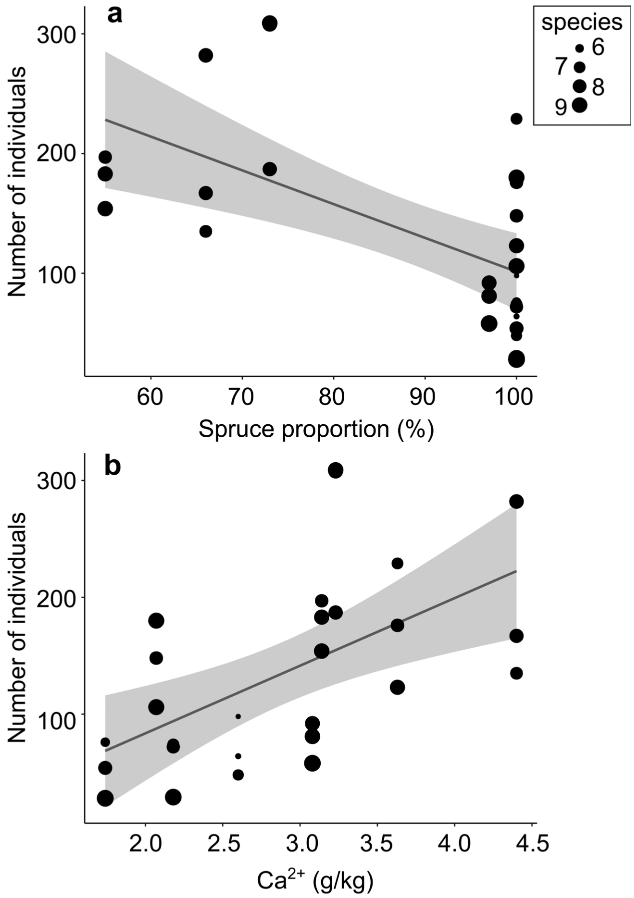

Fig. 2. Relationship between the percentage of spruce (a), soil Ca^{2+} (b) and harvestmen abundance (activity density). Point size denotes rarefied species richness; 95% confidence bands for the regression lines are shown as shaded areas.

DISCUSSION

In this study, patterns in species richness, abundance and species composition of assemblages of harvestmen in stands of Norway spruce were assessed as there are very few studies on harvestmen in this type of habitat, e.g. Klimeš (1999) in Czech Republic, Stašiov (2008), Mihál et al. (2010) and Urbanovičová et al. (2014) in Slovakia and Kataja-aho et al. (2016) in Finland. Species richness and Shannon diversity are not associated with any forest characteristic. In addition, the abundance of harvestmen is negatively associated with the percentage of Norway spruce and positively associated with the chemical element Ca^{2+}.

Table 2. Number of individuals and dominance (Σ/%) of particular species of harvestmen in stands of different ages during the period 2016–2019.

Species	Stand age			
	21-year-old	31-year-old	51-year-old	Do
Dicranolasma scabrum (Herbst, 1799)	0/0	0/0	1/0.1	+
Egaenus convexus (Koch, 1835)	4/0.3	12/1.6	28/2.1	++
Lacinius ephippiatus (Koch, 1835)	285/18.4	135/17.6	124/9.2	+++++
Leiobunum gracile (Thorell, 1876)	139/9	58/7.6	244/18.2	+++++
Lophopilio palpinalis (Herbst, 1799)	159/10.3	92 /12	25/1.9	++++
Mitopus morio (Fabricius, 1779)	234/15.1	119/15.5	181/13.5	+++++
Mitostoma chrysomelas (Hermann, 1804)	5/0.3	3/0.4	5/0.5	+
Nelima sempronii Szalay, 1951	323/20.9	30/3.9	195/14.5	+++++
Nemastoma lugubre (Müller,1776)	49/3.2	31/4	29/2	+++
Oligolophus tridens (Koch, 1836)	103/6.7	140/18.3	202/15	+++++
Platybunus bucephalus (Koch, 1835)	127/8.2	70/9.1	197/14.6	+++++
Platybunus pallidus Šilhavý, 1938	119/8	75/9.8	108/8	++++
Rilaena triangularis (Herbst, 1799)	0/0	1/0.1	0/0	+
Trogulus nepaeformis (Scopoli, 1763)	1/0.1	0/0	1/0.1	+
Trogulus tricarinatus (Linnaeus, 1767)	0/0	1/0.1	3/0.3	+
Total	1,548/100	767/100	1,343/100	

Notes: Do – dominance, +++++ eudominant, ++++ dominant, +++ subdominant, ++ recedent, + subrecedent.

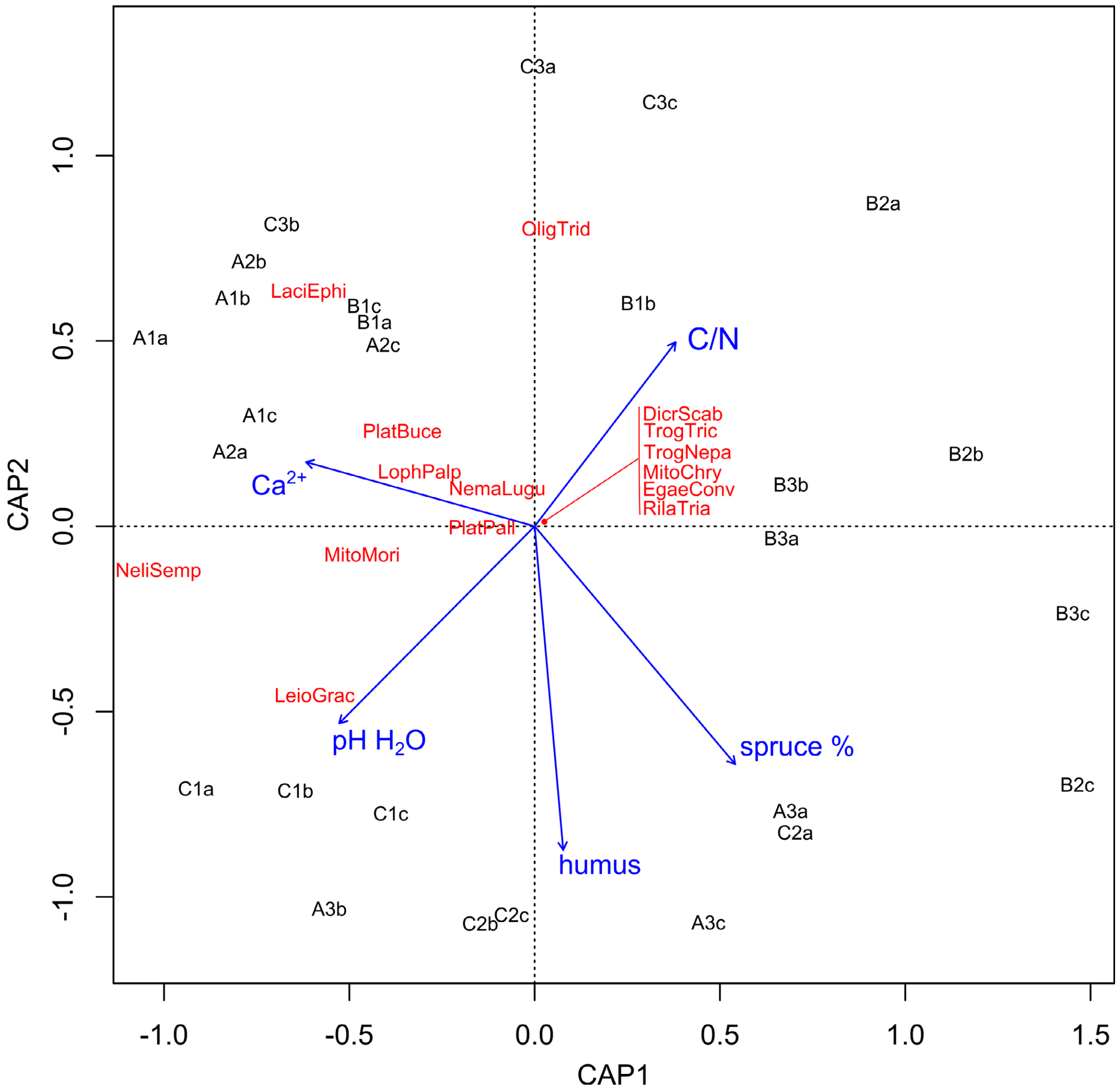

Fig. 3. Ordination plot of distance-based Redundancy Analysis (dbRDA) of the association between species composition of harvestmen communities and forest characteristics. The scale indicates the Bray-Curtis dissimilarity. The abbreviations of the species names are composed of the first four letters of the genus and the species' names. A1a–C3c denotes pitfall traps from plots A1–C3, respectively.

On the other hand, species composition of harvestmen assemblages is significantly associated with the percentage of spruce, humus content, Ca^{2+}, C/N and soil pH.

Harvestmen more or less evenly occur in forests, ecotones and open areas. In spruce stands such species include e.g. *Nemastoma lugubre, Mitostoma chrysomelas, Trogulus nepaeformis, Rilaena triangularis, Lophopilio palpinalis, Oligolophus tridens, Lacinius ephippiatus* and *Mitopus morio*, which commonly occur in forests and open and ecotonal communities (Stašiov, 2004). Generally, highly structured and diverse forest habitats contain a higher diversity of food resources and provide more ref-

Table 3. Results of GLMMs analysis of the association between particular forest characteristics and species richness, abundance and Shannon diversity of harvestmen assemblages. Likelihood-ratio test statistics (χ^2), associated probabilities (P) and goodness-of-fit measures (marginal and conditional R^2) are displayed. Results significant at P ≤ 0.05 are highlighted in bold. For explanation of forest characteristics see Table 1.

Habitat characteristics	Species richness			Abundance			Shannon diversity		
	χ^2	P	R^2m/R^2c	χ^2	P	R^2m/R^2c	χ^2	P	R^2m/R^2c
Spruce %	0.4065	0.524	<0.01/0.01	**7.1833**	**0.007**	**0.37/0.72**	1.1459	0.284	0.05/0.19
No of trees	0.6773	0.411	<0.01/0.01	0.0555	0.814	<0.01/0.72	0.1681	0.682	0.02/0.18
Stand age	0.5743	0.449	<0.01/0.01	0.0165	0.898	<0.01/0.72	0.2126	0.645	0.01/0.17
Humus	0.4740	0.491	<0.01/0.01	1.1708	0.279	0.09/0.72	0.6389	0.424	0.04/0.18
Ca^{2+}	0.0117	0.914	<0.01/0.01	**7.8750**	**0.005**	**0.39/0.72**	0.2396	0.625	0.01/0.17
C/N	0.0013	0.979	<0.01/0.01	0.1311	0.717	0.02/0.72	0.0296	0.863	<0.01/0.16
pH	0.0327	0.857	<0.01/0.01	0.9873	0.320	0.09/0.72	0.1026	0.749	<0.01/0.17

Table 4. Results of dbRDA analysis of the associations of particular forest characteristics and composition of harvestmen assemblages. Goodness-of-fit measures (adjusted R^2) and associated probabilities (P) are displayed. Results significant at P ≤ 0.05 are highlighted in bold. For explanation of forest characteristics see Table 1.

Forest characteristics	F	P	R^2
Spruce %	**4.2208**	**<0.001**	**0.12**
No. of trees	1.3572	0.201	0.02
Stand age	1.1076	0.333	<0.01
Humus	**3.5522**	**0.004**	**0.10**
Ca^{2+}	**3.7035**	**0.002**	**0.10**
C/N	**2.3113**	**0.036**	**0.05**
pH	**3.6162**	**0.005**	**0.10**

uges than areas with adverse environmental conditions and predators, and thus provide more living space, and support a greater abundance of arthropods (Denno et al., 2005; Košulič et al., 2016). Based on our results it is concluded that the abundant occurrence of eudominant species (e.g. *Lacinius ephippiatus, Leiobunum gracile, Mitopus morio, Nelima sempronii, Platybunus bucephalus*) in all of the differently aged stands (Table 2) may be a result of suitable ecological and trophic environmental conditions in the locality Vrchdobroč.

The microhabitat requirements of the species collected are well known. For example, *Lophopilio palpinalis* does not have a specific requirement for a particular level of humidity (Mihál, 1998; Stašiov & Maršalek, 2002), *Lacinius ephippiatus* commonly occurs in spruce forests in shady and humid places, *Trogulus tricarinatus* (Linnaeus, 1767) and *Nemastoma lugubre* occur mainly where the soil is slightly moist. On the other hand, *Opilio saxatilis* Koch, 1839 prefers drier habitats and *Phalagium opilio* Linnaeus, 1758 open habitats, such as meadows, where it often dominates harvestmen communities (Stašiov & Maršalek, 2002). Knowledge of the habitat and ecological demands of harvestmen can be used to assess their occurrence in forests subject to natural or anthropogenic disturbances.

Many species of harvestmen are ubiquitous and are not primarily associated with specific habitats, such as some beetles, spiders and other groups of insects that occur in ecotonal communities or open habitats in forests (Spitzer et al., 2008; Zakkak et al., 2014; Isaia et al., 2015; Stephens et al., 2016). Most Central/Eastern European species of harvestmen are inhabitants of shaded and humid forest habitats. For example, Mitov & Stoyanov (2005) state that for the ecological classification of species of harvestmen the type of habitat and moisture are the most important factors. Their data, gathered from a study carried out on a Bulgarian mountain, indicates that altitude is the main factor determining the ecological profiles of the harvestmen.

Generally, species richness of harvestmen is higher in forest habitats than in open, non-forest habitats (Curtis & Machado, 2007). The authors attribute this to less marked seasonality in temperature and humidity in forests and a greater diversity of suitable micro-habitats. Along a transect from the interior of a forest through forest/meadow edge in to a meadow, Blick & Bliss (1993) report the highest diversity of species of harvestmen in the ecotone and the highest number of individuals in the interior of the forest. Thorn et al. (2016) report the effect windstorms and logging on changes in canopy cover and microhabitats in a spruce forest in south-eastern Germany. In addition to other arthropods, the authors also report the occurrence of 8 species of harvestmen. Overall, beetle, spider and harvestmen communities were more affected by changes in canopy cover than in microhabitats. *Mitopus morio*, *Paranemastoma quadripunctatum*, *Platybunus bucephalus*, *Oligolophus tridens* and *Lacinius ephippiatus* were the most abundant harvestmen. Several of these species were also recorded at Vrchdobroč. Similarly, Tomasson et al. (2014) also report the dominant occurrence of *Lacinius ephippiatus, Leiobunum tisciae, Lophopilio palpinalis, Mitopus morio, Oligolophus tridens* and *Rilaena triangularis* in forests of pine and spruce in Estonia. There is also a report of the effect of logging on harvestmen in spruce stands in Maine in the United States (Jennings et al., 1984). These authors report that of the total number of 7 species of harvestmen, *Leiobunum calcar* (Wood, 1868) was the most frequently collected (dominance = 90%) and that the most individuals and species of harvestmen were recorded in uncut strips of the original stand between the clearings and in the original closed canopy forest. In contrast, the fewest individuals and species occurred in 1 to 6 year-old clear-felled areas. In our study, a related species *Leiobunum gracile* was recorded, which was most dominant in the oldest 51-year-old stands (dominance D = 18.2%) and belonged to the group of eudominant species with a dominance of 12.1%. Similarly, in the stands studied, *Lacinius ephippiatus, Leiobunum gracile, Mitopus morio* and *Nelima sempronii*, which are typical harvestmen for ecotones and open habitats, along with *Oligolophus tridens, Platybunus bucephalus* and *Platybunus pallidus* Šilhavý, 1938, that prefer shaded stands, where they are the most dominant species (Table 2). Likewise, in a Pannonian thermophilous forest, Spitzer et al. (2008) report significantly more arachnids, i.e., spiders and harvestmen, in sparse than dense stands, whereas the number of species did not differ in stands with different canopy covers, however, canopy cover affected species composition.

The highest occurrences of harvestmen are reported in 3-10 year-old clear-felled areas in beech forests (Mihál & Černecká, 2017) and the most dominant species are *Lophopilio palpinalis, Egaenus convexus, Nemastoma lugubre, Lacinius ephippiatus, Dicranolasma scabrum* and *Trogulus tricarinatus*. These areas are colonized by dense growths of herbaceous plants and shrubs, which provide shaded microhabitats where the temperature and humidity varies less than in open areas exposed to sun and therefore more suitable for the mesohygrophilic harvestmen *Nemastoma lugubre, Dicranolasma scabrum, Trogulus tricarinatus, Lophopilio palpinalis* and *Lacinius ephippiatus*. All of these species of harvestmen were also recorded at Vrchdobroč, but in spruce stands with a closed canopy (albeit of different ages). The effect of spruce stand age on communities of harvestmen is also reported for Germany by Sühring et al. (2006), with similar species composition in the 90-year-old and 58-year-old spruce stands. Similarly, in our study, eudominant and dominant species occured in all of the different aged spruce stands. Similarly, Purchart et al. (2013) report the population characteristics of epigeic arthropod assemblages (spiders, ground beetles, centipedes, millipedes and woodlice, suborder Oniscidea) in different aged spruce stands with different local environmental factors (litter, coarse and fine woody debris, canopy closure, moss, herbaceous plant and shrub cover). In general, litter depth, herbaceous plant cover, canopy closure and the amount of coarse woody debris are most closely associated with the compositions of assemblages of all the groups. On the other hand, appropriate intervention in spruce stands may help increase habitat availability for most epigeic arthropods, thus enhancing, or at least maintaining, biodiversity within such habitats.

We conclude that the structure of the community of harvestmen studied is significantly associated with the percentage of spruce, humus content, content of Ca^{2+}, C/N and pH of the soil. On the other hand, at the locality studied the beta diversity of harvestmen assemblages was low, due to the almost identical ecological and climatic conditions in all the stands of spruce so that the different aged stands did not have a significant effect on the species richness of harvestmen. However, composition of the harvestmen assemblages was significantly associated with the percentage of spruce, humus content, Ca^{2+}, C/N and soil pH. In general, greater differences in harvestmen communities in forest ecosystems are reported when ecotone and open habitats are included in the study in addition to those with closed canopies (Mihál & Gajdoš, 2010; Urbanovičová et al., 2014; Černecká et al., 2017).

In terms of confirming our initial predictions, (1) the highest species diversity and number of harvestmen will be recorded in the oldest stands, is partially confirmed (in the oldest 51-year-old stands, a maximum of 14 species were recorded, but only 1,343 individuals which is less than in the youngest stands (1,548 individuals), (2) the most heliophilic and xero-thermophilic species of harvestmen will be recorded in the oldest, less structured stands is not confirmed (number of species of harvestmen caught were similar in all the stands) and (3) the most hygrophilous species of harvestmen will be recorded in the youngest stands is not confirmed (the occurrence of these species of harvestmen was similar in all the stands).

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