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Changes within collembolan communities in windthrown European montane spruce forests 2 years after disturbance by fire

Peter Čuchta · Dana Miklisová · Ľubomír Kováč

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Abstract

• *Context* In July 2005, a wildfire occurred in windthrown spruce forests in High Tatra Mountains and damaged roughly 229 ha of previously clear-cut area.

• *Aims* The present study focuses on assessing the influence of fire disturbance upon collembolan communities and compares the subsequent development of the model communities at burnt and unburnt stands 2 years after fire disturbance.

• *Methods* Three different treatments were selected for the study: REF stands—intact forest stands; EXT stands—clear-cut windthrown stands; and FIR stands—clear-cut windthrown stands subsequently damaged by wildfire. The study of soil microarthropods was carried out in three stands of each treatment, from soil samples taken in April and September of 2007. For statistical evaluation of results repeated measure analysis of variance and cluster analysis with indicator values were used.

• *Results* Total material comprised of 3,632 specimens with 56 collembolan species identified. The highest Collembola abundance means were recorded in FIR stands, with the same parameter being significantly lower in REF and EXT stands. The mathematical methods demonstrated clear

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D. Miklisová Parasitological Institute, Slovak Academy of Sciences, Hlinkova 3, Košice 04001, Slovak Republic differences in the collembolan communities between the different treatments studied.

• *Conclusion* The present study showed that natural wildfire may increase abundance and species richness of soil Collembola in mountain spruce forests previously damaged by windthrow.

Keywords Fire disturbance · Collembola · Spruce forest · Windthrow · High Tatra Mountains

1 Introduction

Forest fire can drastically change the structure of the forest ecosystem. The overall effects of fire are complex, ranging from the removal of aboveground biomass to affecting the physical, chemical and biological components of soil ecosystems. Fire produces a broad spectrum of effects that depend on duration, fuel load and combustion, vegetation type, climate, topography, soil and area burnt (Mabuhay et al. 2006). Forest fire could influence the soil microarthropods assemblages; direct killing by the blaze and indirect impacts by altering their habitats by changing the composition of forest vegetation or by disturbing the balance of soil chemicals, water levels and pH. In addition, burning out of litter and other organic matter may cause the depletion of food source for soil microarthropods since most of them are decomposers of organic materials in forest floor and their associates (Kim and Jung 2008).

Fires are often major features of forest disruption and renovation. Widely investigated is their role in altering floristic composition, promoting tree regeneration, enhancing timber production and conditioning human ecology. Prescribed fires are increasingly employed as a management strategy in the conservation of fire-dependent species



by controlling the proliferation of native and non-native invasive plants (Coleman and Rieske 2006). Burning makes conditions more favourable for the development of tree seedlings, but, at the same time, heavily alters the environment of soil decomposer organisms (Haimi et al. 2000). On the other side, prescribed burning become more common for conservational reasons in order to allow pyrophilous species to persist. These species are dependent on fire for their long-term survival either directly or indirectly by being favoured by the disturbance. As in natural fires, the biological outcome of such burning operations can vary widely but can partly be controlled by choice of burning technique and by timing of the burning in relation to certain weather conditions (Wikars and Schimmel 2001).

There are numerous findings on the effects of fire on soil properties. The extent and duration of these effects depend firstly upon fire severity, which, in turn, is controlled by several environmental factors, that affect the combustion process, such as amount, nature and moisture of live and dead fuel, air temperature and humidity, wind speed and topography of the site (Certini 2005). Fire severity, or the amount of organic material consumed by a fire, is a key component of the fire regime that influences patterns of post-fire regeneration. Soil burn severity influences both the availability of plant propagules and the physical properties of the post-fire soil (Johnstone and Stuart Chapin 2006). Depth of burn determines patterns of survival, colonisation and regrowth of plants after fire (Wikars and Schimmel 2001). According to Malmström et al. (2009), fire severity (depth of burn) is more decisive than fire intensity (heat release) for the long-term recovery of soil fauna, whereas fire intensity determines the acute mortality of animals.

The effects of burning on the physico-chemical properties of soil are well documented. During burning, temperature and moisture conditions change drastically. Soil pH increases thereby increasing the cation exchange capacity and reducing solubility of ions. Fire modifies the levels of soil nutrients, resulting mainly in the loss of total nitrogen (Kutiel and Naveh 1987). During a fire, nutrients are abruptly mineralised and the decrease in food source may affect soil invertebrates. The effects of fire may include large flux of nutrients leaving the ecosystem through volatilisation and rapid mineralization of nutrients, losses of nutrients through accelerated erosion and leaching, adverse changes in hydrology degradation of soil physical properties and losses in microbial populations and associated processes (Sileshi and Mafongoya 2006).

Generally, the direct effects of fire on soil-dwelling invertebrates are less marked than those on microorganisms, due to the higher mobility that enables invertebrates a greater potential to escape heating by burrowing deep into the soil. However, the indirect effects of fire, particularly

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litter mass reduction, are effective at decreasing drastically both total mass and number of species of soil-dwelling invertebrates (Certini 2005). Arthropods suffer exposure to greater extremes of temperature, light and moisture, resulting in subsequent habitat loss. Those lacking adaptations to these fire-induced changes are eliminated. However, arthropods protected from fire disturbance either by life history traits, location during fire, or behavioural characteristics that prevent mortality, can benefit following fire because of potential reductions in competitors and predators, increases in dead prey for scavengers, and more nutritional plant hosts (Coleman and Rieske 2006).

In November 2004, severe wind struck the spruce forest stands of the High Tatras National Park and damaged an area of roughly 12,600 ha (about 50%) of the local spruce forests (Falt'an et al. 2008). At the majority of the damaged spruce stands in the High Tatra Mts., clear-cut management was performed and fallen trunks were harvested; whereas only a small area of the damaged spruce forest was left to natural succession. In July 2005, a wildfire occurred in windthrown stands previously clear-cut and harvested with roughly 229 ha of the damaged area (Kunca and Zúbrik 2006). The present paper is associated with the broader study focused on the initial succession of soil Arthropoda communities with the special reference to Collembola. The investigation was carried out at three differently managed forest stands mentioned above: unharmed (reference) forest stand, windthrown forest stand subsequently clear-cut and unmanaged windthrown forest stand left to the natural succession. The goal of this study was to assess the effect of wildfire on collembolan assemblages at area burnt 2 years after disturbance in comparison with areas of forest stands under different treatment. Based on literature data, we hypothesised the decrease in abundance and diversity of collembolan communities at burnt stands with potential recovery of soil microarthropods after the fire.

2 Material and methods

Three different treatments were selected in the High Tatras National Park for the study (Table 1):

REF stands (reference, control stands)—intact forest stands undamaged by severe wind, locality Smrekovec near the Vyšné Hágy village (49°7'22.3"N, 20°6'5.6"E, 1,268 m above sea level (asl); 49°7'19.1"N, 20°6'12.1" E, 1,241 m asl; 49°7'16.5"N, 20°6'12.6"E, 1,237 m asl). Forest floor covered with patches of *Polytrichum* sp. moss cushions, coniferous litter (spruce needles), *Vaccinium myrtillus*, grasses (*Calamagrostis villosa*, *Avenella flexuosa*) and *Oxalis acetosella* patches; soil profile: 0–2 cm litter (spruce needles), 2–6 cm humus

Table 1Characteristics of studystands (Gömöryová et al. 2008)

	REF	EXT	FIR
Altitude (m asl)	1,100-1,250	1,040-1,260	1,000–1,200
Aspect	SE	S	SE
Slope (%)	10-20	10	5-10
Tree species composition (%)	Spruce 80, larch 20	Spruce 90, larch 10	Spruce 70, larch 30
Stand age	120/25	80	80
Soil type	Dystric Cambisol	Dystric Cambisol	Dystric Cambisol
Dominant humus form	Mor	Mor	Mor
Parental rock	Moraine	Moraine	Stone-centred polygons

S south, *E* east; for abbreviations of study stands, see text

layer, 6–10 (15)cm dark brown mineral layer, under 15 cm and lower transition to paler mineral layer with stones.

EXT stands—windthrown forest stands subsequently clear-cut and tree stumps harvested, locality Danielov dom near the Nová Polianka village ($49^{\circ}7'17.4''N, 20^{\circ}9'45.6''E, 1,066 \text{ m asl}; 49^{\circ}7'19.6''N, 20^{\circ}9'46.3''E, 1,070 \text{ m asl}; 49^{\circ}7'22''N, 20^{\circ}9'48.2''E, 1,074 \text{ m asl}$). Dense growths of grass and herbs covered the stand with dominating *C. villosa and A. flexuosa*; soil profile: 0–2 cm litter (spruce needles), 2–6 cm humus layer, 6–10 (15)cm dark brown mineral layer, 10–15 cm transition to grey or pale brown mineral layer with stones.

FIR stands—windthrown forest stands clear-cut and subsequently damaged by wildfire, locality Tatranské Zruby village (49°8'11.58"N, 20°11'55.26"E, 1,080 m asl; 49°8'10.92"N, 20°11'52.38"E, 1,084 m asl; 49°8' 10.98"N, 20°11'50.7"E, 1,088 m asl).

The area was covered by thin layer of ash remnants and by dense growths of rosebay willowherb (*Chamaenerium angustifolium*) and grasses (*C. villosa*, *A. flexuosa*); soil profile: 0–6 cm remnants of burnt litter and upper humus layer, 6–10 (15)cm dark brown mineral layer, 10–15 cm transition to grey or pale brown mineral layer with stones.

Soil samples were taken in April and September 2007. Within each treatment, three stands were selected in reciprocal distance of roughly 100 m. Sampling plots were about 25×25 m in area; during sampling, six replicate soil cores were taken randomly with a steel corer from each individual plot. The samples represented soil cores of 3.6 cm in diameter (10 cm^2 in area) to a maximum depth of 7-12 cm (depending on the soil depth). The microarthropods were subsequently extracted in a modified high-gradient apparatus (Crossley and Blair 1991) in the laboratory for 7 days. Collembola were selected and determined to species level using key for Symphypleona (Bretfeld 1999), Poduromorpha (Fjellberg 1998), Hypogastruridae (Thibaud et al. 2004), Isotomidae (Potapov 2001), Onychiurinae (Pomorski 1998) and Tullbergiinae (Zimdars and Dunger 1994).

Community parameters were calculated for comparison of the collembolan assemblages at the stands under study: abundance (A), mean species richness (S), mean Shannon index of diversity (H') and mean Pielou index of evenness (J'). Since the samples were taken repeatedly from the same study stands during two samplings, two factorial repeated measure analysis of variance (ANOVA; stand and sampling date) was used to test differences between Collembola abundance, mean diversity indices and soil characteristics. A Box-Cox transformation was performed to normalise abundance data and number of species prior to statistical testing, other data were normally distributed. Post hoc comparison testing (Fisher's least significant difference test) was used to determine the significant differences between stands and stands×dates. Kruskal-Wallis non-parametric test was used to determine the significant differences between mean abundance values of dominant collembolan species in particular study stands. STATISTICA 9.0 software package (StatSoft, Inc. 2009) was used for both aforementioned analyses.

Similarity of the Collembola communities of particular stands was evaluated by cluster analysis (Ward's method, Euclidean distance) of logarithmically $\ln (x+1)$ transformed quantitative data using STATISTICA 9.0 (StatSoft, Inc. 2009). The cluster diagram obtained was used for typology of stands in subsequent indicator values (IndVal) analysis (Dufréne and Legendre 1997). Indicator species were defined as the most characteristic species of each group, found mostly in a single group of the typology (specificity) and present in the majority of the stands or samples belonging to that group (fidelity). The indicator value of a given species for a given group of stands is a multiple of specificity and fidelity, and is expressed as a percentage. The indicator value of a given species for a typology of stands is defined as the maximum over all groups of the typology (IndVal). A maximum value in the IndVal index is reached if all individuals of a species are found in a single group of stands and when the species occurs in all stands for that group. A threshold level of 25% for the index was accepted by Dufréne and Legendre (1997), which assumes that theoretically an important assemblage species is





present in at least 50% of one stand cluster and that its relative abundance for that cluster reaches at least 50%. Afterward, a significance test of observed maximal indicator values for a given species was applied with 1,000 permutations. A FORTRAN programme (2004) was used to compute the indicator value index and perform the randomization testing procedure.

Soil pH was measured potentiometrically using glass electrode and reference calomel electrode as active pH in water (pH/H₂O) and replacement pH in 1 M water solution of potassium chloride (pH/KCl). Soil/water ratio was 1:2.5 (Kubíková 1970). Soil carbon content was measured according to Králová et al. (1991). Dry soil was modified to have maximal size of soil particles 0.25 mm. Soil organic matter was oxidised by chrome-sulphuric mixture under increased temperature and surplus dichromate was determined by reversal titration through Mohr's salt to diphenylalanine indicator. Total N content was measured in dried (60°C) and finely milled soil samples using a NC elemental analyser (ThermoQuest, Germany; Tahovská et al. 2010). Soil phosphorus content was measured by mineralizing of dry soil with modified soil particles of maximal size 0.25 mm with perchloric acid (Sommers and Nelson 1972) and orthophosphate ions were subsequently allocated by ammonium molybdate and ascorbic acid (Murphy and Riley 1962; Watanabe and Olsen 1965). Soil sodium, potassium and calcium were measured according Kubíková (1970) by ionselective electrodes during wiggling dry fine soil with 1% solution of citric acid (ratio 1:5) and using accessory methods (Nedoma 1990). Soil moisture was analysed gravimetrically.

3 Results

Recorded soil-chemical characteristics of the studied spruce forest stands showed differences in content of

Table 2 Soil characteristics of study stands in the High Tatra Mts.

soil carbon and nitrogen as well as in average soil moisture and soil acidity (Table 2). In REF stands, we recorded significantly higher values of both carbon (p < 0.005) and nitrogen (p < 0.005) content than in FIR stands or EXT stands. We observed the highest values of soil moisture and the lowest pH in REF stands. Differences of soil pH between stands (p < 0.005 for REF–EXT stands and p < 0.005 for REF–FIR stands) were statistically significant. The highest values of total phosphorus content were recorded in FIR stands followed by REF stands and the lowest values were found in EXT stands. Difference in total phosphorus content between FIR and EXT stands was statistically significant (p < 0.05). There were no significant differences recorded between study stands in content of soil sodium, potassium or calcium.

The material comprised of 3,632 specimens of Collembola with totally 56 species identified. The highest total abundance mean $(54,500 \text{ ind.m}^{-2})$ was recorded in windthrown stands clear-cut and subsequently damaged by wildfire (FIR stands), much lower values of the parameter (24,000 ind.m⁻²) were observed in intact control forest stands (REF), and the lowest (22,872 ind. m^{-2}) in windthrown stands subsequently clear-cut and tree stumps harvested (EXT). FIR1 (p < 0.05) and FIR3 (p <0.005) stands in April were significantly different in abundance from almost all other stands (REF, EXT and FIR). Species richness recorded in individual study stands was 43 species in FIR, 38 in REF and 32 in EXT stands, respectively (Table 3). Repeated ANOVA measure of number of species confirmed significant influence of sampling date (F(1, 45)=17.20, p<0.001). Highest average value of Shannon index was observed in REF stands (1.56 ± 0.22) , followed by FIR stands (1.42 ± 0.20) and lowest average value was recorded in EXT stands (1.35 \pm 0.31). Repeated ANOVA measure of Shannon index confirmed significant influence of sampling date (F(1,

	REF1	REF2	REF3	EXT1	EXT2	EXT3	FIR1	FIR2	FIR3
W [%]	42.78	40.92	42.78	44.75	37.01	33.90	39.53	35.37	31.84
SD (W)	±5.21	±13.41	±8.35	±8.43	±4.09	±10.23	±9.63	±4.77	±5.20
pН	3.38	3.26	3.43	4.06	4.17	4.14	3.72	4.03	4.06
C [%]	13.57	17.29	17.26	9.29	10.06	9.16	11.03	8.05	8.06
N [%]	0.71	0.79	0.82	0.51	0.58	0.53	0.62	0.52	0.49
Ptot [mg.kg ⁻¹]	842	793	859	739	762	731	1,002	780	955
Na [mg.kg ⁻¹]	92	48	20	44	32	56	36	28	28
K [mg.kg ⁻¹]	148	64	60	94	142	72	88	92	68
Ca [mg.kg ⁻¹]	36	100	30	32	56	24	68	42	148

Waverage gravimetric soil moisture (% of initial weight), SD (W) standard deviation of moisture values, pH soil acidity, C soil carbon content (% of initial weight), N soil nitrogen content (% of initial weight), P_{tot} total phosphorus content in the soil, Na soil sodium content, K soil potassium content, Ca soil calcium content; for abbreviations of study stands, see text



Table 3 Ecological parameters of Collembola communities in study stands in the High Tatra Mts.

	Apr	Sep	Apr	Sep	Apr	Sep	SD Average
	EXT1	EXT1	EXT2	EXT2	EXT3	EXT3	
A [ind.m ⁻²]	25,000 ^a	21,000 ^a	14,167 ^a	25,833 ^a	17,400 ^a	33,833 ^a	22,872±6,360
S	20	23	17	19	14	13	17.67±3.78
S total	32						
Η′	1.60	1.64	1.10	1.71	0.92	1.09	1.35 ± 0.31
J′	0.89	0.83	0.86	0.91	0.53	0.68	$0.78 {\pm} 0.14$
	FIR1	FIR1	FIR2	FIR2	FIR3	FIR3	Average
A [ind.m ⁻²]	57,000 ^{ac}	38,167 ^b	36,500 ^{bc}	27,167 ^b	132,667 ^a	35,500 ^b	54,500±36,091
S	16	17	21	25	19	11	18.17±4.75
S total	43						
Η′	1.50	1.41	1.22	1.82	1.36	1.24	1.42 ± 0.20
J′	0.81	0.77	0.76	0.85	0.68	0.81	$0.78 {\pm} 0.05$
	REF1	REF1	REF2	REF2	REF3	REF3	Average
A [ind.m ⁻²]	27,167 ^a	35,167 ^a	14,667 ^a	26,833 ^a	21,500 ^a	18,667 ^a	$24,000\pm 6,640$
S	22	23	18	25	14	18	20.00 ± 4.05
S total	38						
Η′	1.46	1.80	1.29	1.78	1.28	1.72	1.56 ± 0.22
J′	0.78	0.81	0.77	0.82	0.78	0.87	$0.81 {\pm} 0.03$

A mean abundance, S average species richness, S total total species richness, H' Shannon's diversity, J' Pielou's evenness, significant differences of abundance (p<0.05) between individual stands within particular treatment are indicated by different lowercase letters in every row separately; for abbreviations of study stands, see text

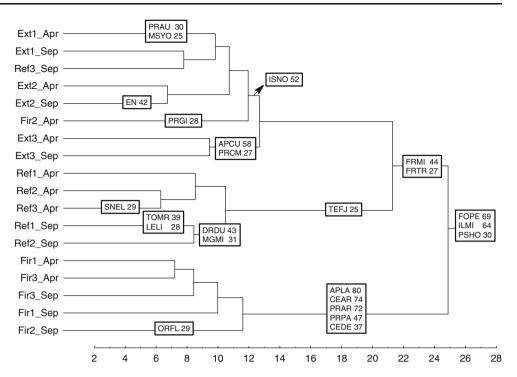
45)=7.592, p < 0.01). The same trend was observed also in Pielou index with the highest average value in REF stands (0.81±0.03) and lower average value recorded in FIR stands (0.78±0.05) and EXT stands (0.78±0.14). Repeated ANOVA of Pielou index confirmed significant influence of microsite (F (8, 45)=3.596, p < 0.01). The most abundant species at all study stands were *Folsomia penicula* (A=6,969 ind.m⁻²), *Isotomiella minor* (A=5,678 ind.m⁻²), *Anurophorus laricis* (A=5,004 ind.m⁻²) and *Protaphorura armata* (A=3,602 ind.m⁻²). Futhermore, IndVal analysis showed first two mentioned species, together with *Pseudosinella horaki*, to be characteristic for all study stands (Fig. 1).

We observed considerable differences within collembolan communities of individual study forest stands, especially in presence of individual species and mean abundance values of dominant ones. In FIR, *A. laricis* (A=12,250 ind. m⁻²), *I. minor* (A=11,861 ind.m⁻²), *F. penicula* (A= 9,111 ind.m⁻²) and *P. armata* (A=8,556 ind.m⁻²) were the most abundant. Comparing to other two forest stands we recorded, there are significantly higher mean abundance values of *Ceratophysella armata* (A=2,833 ind.m⁻², p< 0.0005) and *Ceratophysella denticulata* (A=2,639 ind.m⁻², p<0.0005). *Protaphorura pannonica* was abundant in FIR stands (A=2,611 ind.m⁻²) with noteworthy decrease of its abundance in EXT (A=1,328 ind.m⁻²), as well as in REF $(A=361 \text{ ind.m}^{-2})$. Several species were limited to FIR stands, e.g. *C. denticulata, Desoria violacea, Endonura tatricola, Hymenaphorura dentifera, Mesaphorura florae, Mesaphorura tenuisensillata, Micranurida granulata, Orchesella flavescens, Protaphorura fimata and Archaphorura sp., however, except <i>C. denticulata* their abundances were very low. On the other hand, *Friesea mirabilis, Lepidocyrtus lignorum* and *Tetracanthella fjellbergi* had notably lower mean abundance in FIR stands and *Lepidocyrtus* cf. *cyaneus, Pogonognathelus* sp. and *Tomocerus minor* totally absented there.

In unburnt EXT, Anurophorus cuspidatus (A= 4,989 ind.m⁻²) was the most abundant, followed by A. laricis (A= 2,761 ind.m⁻²) and I. minor (A= 2,533 ind.m⁻²), respectively. Folsomia manolachei, Micranurida pygmaea, Orchesella bifasciata, Parisotoma notabilis and Protaphorura campata were considerably more abundant there than in both REF and FIR stands. Lepidocyrtus serbicus, Mesaphorura yosii and Pseudachorutes laricis were limited in their occurrence to EXT stands. On the other side, significantly less abundant in EXT stands was F. penicula (p<0.01). Notably, but not significantly less abundant was also P. armata. Folsomia inoculata, Megalothorax minimus, Mesaphorura macrochaeta, Protaphorura gisini, Willemia anophthalma and Willemia denisi totally absented there.



Fig. 1 Cluster analysis of quantitative community data of Collembola in study stands in April and September 2007 in the High Tatra Mts. (Ward's method, relative Euclidean distance. $\ln (x+1)$ transformation) with the associated indicator species and indicator values (IndVal). All species with statistically significant (p <0.05, except species at first level) indicator value >25% are mentioned for stand cluster where they reached their maximum indicator value; for abbreviations of species, see Appendix



In REF, the most abundant species were F. penicula $(A=9.889 \text{ ind.m}^{-2})$ and *I. minor* $(A=2.639 \text{ ind.m}^{-2})$. Similarly with FIR stands *P. armata* (A=1,417 ind.m⁻²) was abundant there too. Comparing to both FIR and EXT stands, considerably higher abundance was observed in Desoria duodecemoculata, F. mirabilis, Friesea truncata, Pseudanurophorus binoculatus, P. horaki, Sminthurinus elegans, T. fjellbergi and T. minor. Several species were limited to REF stands, e.g. Allacma fusca, Ceratophysella sigillata, Neanura pseudoparva, Protaphorura subarmata, Pseudachorutes corticicolus and Thaumanura carolii. On the other hand, A. cuspidatus, M. pygmaea, Protaphorura aurantiaca, P. pannonica were notably less abundant in REF stands than in both EXT and FIR stands. A. laricis, Mesaphorura hylophila and O. bifasciata totally absented there.

The cluster analysis diagram of Collembola quantitative community data with the associated indicator species (IndVal) showed two main branches (Fig. 1). All species with statistically significant (p<0.05, except species at first level) indicator value >25% are mentioned for stand cluster, where they reached their maximum indicator value. First, well-separated branch represents all three windthrown forest stands damaged by wildfire (FIR1, FIR2 and FIR3) from September and stands (FIR1 and FIR3) from April with *A. laricis, C. armata, C. denticulata, P. armata* and *P. pannonica* being specific in these stands. A second branch has two characteristic species, e.g. *F. mirabilis* and *F. truncata*, and it is divided into two



marked sub-branches: (1) represented by all three reference forest stands (REF1, REF2 and REF3) from April and two stands (REF1 and REF2) from September with *T. fjellbergi* as specific species for these stands and (2) consists of all three windthrown stands with harvested wood (EXT1, EXT2 and EXT3) from both April and September together with one reference forest stand (REF3) from September and last of burnt stands (FIR2) from April. There were also some characteristic species of particular stands in lower levels of clustering distance. Observed differences between particular stands of the same treatment are caused by differences in total mean abundance values recorded for individual sampling seasons.

Significant positive correlations were found between abundance of several species and soil-chemical parameters. Abundance of *A. laricis* correlated with total phosphorus (r=0.74, p<0.05) and calcium (r=0.69, p<0.05) content in the soil. Similarly, there were correlations found between total phosphorus (r=0.86, p<0.005) and calcium (r=0.72, p<0.05) content in the soil and abundance of *C. armata*. Another correlations between total soil phosphorus and abundance of *P. armata* (r=0.75, p<0.05) and *F. penicula* (r=0.70, p<0.05) was observed. *I. minor* correlated with soil calcium (r=0.80, p<0.01). Finally, correlations were recorded between content of soil carbon (r=0.73, p<0.05), soil nitrogen (r=0.70, p<0.05), as well as soil moisture (r=0.67, p<0.05) and abundance of *F. mirabilis*.

4 Discussion

According to many studies of fire disturbance effect upon soil microarthropods (Henig-Sever et al. 2001; Wikars and Schimmel 2001; Dress and Boerner 2004; Coleman and Rieske 2006; Kim and Jung 2008; Malmström et al. 2009), the fire (prescribed or natural) negatively affected both abundance and species richness of soil microarthropods. One of the direct effects of the fire disturbance is considerable reduction of surface litter mass. There were found significant relationships between microarthropod abundance and litter mass, strongest for Collembola (Dress and Boerner 2004).

Furthermore, the abundance of microarthropods has been observed to increase over time following a disturbance by fire, indicating a recovery effect (Wikars and Schimmel 2001; Coleman and Rieske 2006). Contrary to the literature data, the present study showed an enormous increase of abundance within collembolan communities 2 years after a fire disturbance. Additionally, we found some species restricted to windthrown stands damaged by wildfire, however usually in a low abundance. In contrast to our results, Malmström et al. (2009) observed no recovery effect in their 5-year study of soil meso- and macrofauna dynamics after prescribed clear-cut burning in a boreal forest in central Sweden upon the soil meso- and macrofauna. Moreover, they found no species exclusive to the burnt area within these groups. In our study, however, we had different stand conditions, especially soil type and type of humus that are crucial for development of soil fauna communities (Ponge 2003). The study of Malmström et al. (2009) was conducted on orthic podzol with mor humus, organic profile being usually shallow, thus more sensitive to the fire. In our case we had dystric cambisol with thick organo-mineral layer determining better vertical distribution of soil fauna with less sensitivity to fire and better possibility to recover in situ after the disturbance. Our results are supported by Gömöryová et al. (2008) and Čerevková and Renčo (2009) who carried out the soilbiological observations in forest stands identical with our study in the High Tatra Mts in 2006, i.e. 1 year after the fire. The highest microbial activity in burnt stands was explained by high organic matter and water contents and by changed temperature regime as compared to the reference stand (Gömöryová et al. 2008). The FIR stands showed also the highest abundance of the free-living soil nematodes with bacterial feeders prevailing (Čerevková and Renčo 2009).

In the matter of collembolan abundance, we observed variability between particular stands of the same treatment, the most obvious in FIR stands. The most probable reason was the higher heterogeneity of the stands due to the mosaic terrain microtopography and variable soil thickness after the clearing treatment and fire disturbance. The apparent increase in Collembola abundance observed in FIR3 in spring (in all samples taken) was caused by a high abundance of several dominant species, especially *I. minor* and *F. penicula* (see Appendix).

Windthrow might have a positive effect on arthropod communities with time. According to Wermelinger et al. (2003), windthrow caused an overall increase in biodiversity compared to the intact forest. We observed the same trend in our study of the influence of the windthrow and consecutive changes in the soil environment upon soil microarthropods with special reference to Collembola in the High Tatra Mts (Čuchta et al. 2009). According to our results, clearing practices in the spruce forests damaged by severe wind slightly enhanced diversity of soil microarthropod groups and species diversity of Collembola during the first year after the wind calamity. On the other hand, this kind of management strikingly diminished quantities of soil microarthropods, indicating overall inhibition of the soil processes at sites with intensive forest management, i.e. clear-cut with removal of tree logs. In the present study, we recorded the lowest value of collembolan abundance in EXT stands and the lowest species richness, which is contrary to the results of our previous study (Čuchta et al. 2009). We assume that the temporary increase of species richness observed early after the windthrow had faded away. Dense growths of grass and herbs covered the ground after clear-cutting of the former spruce forest stands. Epigeic species characteristic of meadows or forest edges colonised these formerly forested areas as also observed by Rusek and Brůhová (2007) in the study of the impact of a bark beetle outbreak on epigeic collembolan communities in spruce forests in the Šumava National Park (Bohemia). On the other hand, populations of montane collembolan species decimated after the windthrow were banished or totally wiped out. Moreover, our hypothesis concerning the detrimental impact of clearing treatments on collembolan species richness 3 years after the wind calamity was confirmed by the lowest values of both diversity indices counted.

Haimi et al. (2000) studied responses of soil decomposer animals to wood-ash fertilisation and burning in a coniferous forest stand in central Finland. They applied different treatments: a control, two level of wood-ash fertilisation and a fire treatment mimicking prescribed burning. After 3 years, they found increased arthropod densities and total numbers of collembolans in all study stands with no effect from any of the treatments. According to Henig-Sever et al. (2001), the size of the soil microarthropods community decreased with fire intensity, and fire intensity also affected the composition



of the arthropods and collembolan families. Isotomidae and Onychiuridae were present only in the burnt stands. The number of families decreased with increasing fire intensity: Isotomidae being dominant and some Entomobryidae, Hypogastriridae and Onychiuridae found in light fire, Isotomidae lowered to some extend and Hypogastruridae and Onychiuridae disappeared in medium fire and finally in the high fire intensity all collembolan representatives disappeared. We were not able to determine a fire intensity of the wildfire, but results of our study showed similar pattern in occurrence of collembolan groups with a light fire. On the other hand, Malmström (2008) studied temperature tolerance in soil microarthropods simulating forest-fire heating in the laboratory and found that among Collembola F. mirabilis was the most heat-tolerant species. In our study the species had, however, very low abundance at burnt stands. Admitting results of the previous author, we assume that despite higher survival of fire disturbance, F. mirabilis does not prefer changed conditions in the soil after fire.

Henig-Sever et al. (2001) and Kim and Jung (2008) also found a direct relationship between fire intensity and the pH of the ash layer. The increase in pH of the ash directly related to the impact of fire intensity on the chemical properties of the forest floor. Soil pH was higher in burnt stands than in control stands in their study due to release of mineral substances as oxides or carbonates usually having an alkaline reaction. They also observed that the abundances of oribatid and gamasid mites and collembolans negatively correlated with the soil pH. Similarly, we recorded increased soil pH in burnt stands compared to unharmed reference forest stands, however, with pH values in windthrown clear-cut stands being the highest. On the other hand, we did not find any correlations between soil pH and collembolan abundance. We recorded positive correlations between the abundance of several species and soil nutrients, mostly calcium and phosphorus. Similarly, Geissen et al. (1997) found positive correlations between abundances of one collembolan species group (Onychiurus furcifer, Folsomia qundrioculata and Isotoma notabilis) and the concentrations of potassium and, to a certain extent, phosphorus, while abundances of the second group (Onychiurus quadriocellatus and I. minor) were negatively correlated with the content of basic cations or the pH value. Generally, it is difficult to explain the reason of such correlation observations due to the indirect effect of soil nutrients on particular species.

The presented results are based on the case study of edaphic Collembola in Central European mountain spruce forests after disturbance. The sampling design of the study was adapted to the local natural conditions, especially to the smaller extent of the area affected by



fire (continuous area of 229 ha). Therefore, sampling plots resemble pseudoreplicates. We could obtain more reliable data on the effect of forest disturbance/treatment by sampling in different (more distant) locations; however, the burnt area was limited in extent. On the other hand, pronounced effects of particular disturbances studied (wildfire, deforestation) were documented not only by quantitative parameters of the communities (abundance, species richness). We also observed apparent differences between treatments in species composition and structure of edaphic Collembola communities with several indicator species strongly supporting the effect of the treatment studied. Probably, including more replicate plots would validate the observation.

Finally, in spite of the limitations outlined, the present paper contributes to the understanding of fundamental knowledge on the effects of forest wildfire and clear-cut management on communities of soil fauna.

5 Conclusions

The present study showed that in European montane spruce forests, following a 2 year period of recovery, wildfire may cause a temporary increase in the abundance and species richness of soil Collembola compared to clear-cut windthrown forest stands and to unharmed reference forest stands. Moreover, soil conditions after wildfire may be more favourable for rare or less abundant species. Direct effects of fire disturbance (immediate mortality of soil animals) have probably lesser impact to collembolan communities than the indirect effects of soil type, soil microclimate, nutrient content and biological interactions. Changed conditions in the disturbed forest are reflected in the composition and biomass of the herb vegetation as well as in the composition of the soil biota as the consequence of different trajectories of the secondary succession after the disturbance. The investigations presented in this study represent a part of the long-term observations of soil arthropods that may bring more light to mode of the secondary succession of the soil fauna in the mountain spruce forests differently affected by natural and human disturbance. The long-term study of soil Collembola communities in disturbed forest stands may have wider implications for the better understanding of forest ecosystem dynamics after perturbation.

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ALPU Altera face (Linue, 1758) S3 4,500 4,600 9,500 167 833 5,00 1,07 5,00	Abbrev	Species	EXT1 Apr	EXT1 Sep	EXT2 Apr	EXT2 Sep	EXT3 Apr	EXT3 Sep	FIR1 Apr	FIR1 Sep	FIR2 Apr	FIR2 Sep	FIR3 Apr	FIR3 Sep	REF1 Apr	REF1 Sep	REF2 Apr	REF2 Sep	REF3 Apr	REF3 Sep
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$ \begin{array}{llllllllllllllllllllllllllllllllllll$	FRMI	Friesea mirabilis (Tullberg, 1871)	167		333		1,400	500	167	167		167			1,167		1,000	2,333		2,167
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	FRTR	Friesea truncata Cassagnau, 1958	333	167	833	1,000	200				1,500	333			1,500	1,000	500	667		833
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3 Microphonic disolati 333 167 200 667 167 333 333 333 333 67 333 0 formula predionary disolati 163 100 167 107 107 107 107 107 107 103 <td>MIPY</td> <td>Micranurida pygmaea Börner. 1901</td> <td>1,333</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>167</td> <td>167</td> <td></td> <td>167</td> <td></td> <td></td> <td></td> <td></td> <td></td>	MIPY	Micranurida pygmaea Börner. 1901	1,333									167	167		167					
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Principino mata (Gisin, 1922) 333 1,500 1,833 800 1,333 816 813 813 816 816 813 816	PRAU	Protaphorura aurantiaca (Ridlev 1880)	3,500	667	167	2,333			667	833	1,333	1,833	667		167	167				167
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	PRCM	Protaphorura campata (Gisin, 1952)		333	1,500	1,833	800	1,333			333	833			500		167	167	333	167
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	PRFI	Protaphorura fimata (Gisin, 1952)									167									
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	PRGI	Protaphorura gisini (Haybach, 1960)							167		333				167					
$\begin{tabular}{ c c c c c c c c c c c c c c c c c c c$	PRPA	Protaphorura pannonica (Haybach, 1960)	3,667	1,000	833		1,800	333	2,833	2,833	833	333	8,500	333	667	333	167	333	167	500
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	PRSA	Protaphorura subarmata (Gisin, 1957)														167				
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 Table 4 (continued)

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	2,833	167		
	167 2,	333 167	107 667 333	Bretfeld G (1999) Symphypleona. In: Dunger W (ed) Synopses on palaearctic Collembola, vol. 2. Abhandlungen und Berichte des Naturkundemuseums, Görlitz, 318 p
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