Centipedes, millipedes, terrestrial isopods and their relationships to physical and chemical properties of forest soils

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The quality of soil environment in forest ecosystems of mountain zones was characterised by skeleton content and particle size as well as soil moisture and chemistry and used for deepening the knowledge of ecological requirements of centipedes, millipedes and terrestrial isopods. Soil skeleton and size of the particles were significant environmental factors, with *Lithobius austriacus*, *Lithobius erythrocephalus* and *Lithobius nodulipes* preferring stony soils. The isopods *Ligidium hypnorum* and *Hyloniscus riparius* were closely bound to heavy soils with a high clay content, which was related to increased soil moisture and indication of waterlogged soils. Soil reaction (pH/KCl) was less associated with the occurrence of the studied invertebrates. The soils with higher skeleton content and a favourable moisture regime containing more Ca^{2+} and Mg^{2+} were more attractive to some centipedes (*Strigamia acuminata*, *Lithobius microps*) and isopods (*Trachelipus ratzeburgii*, *Oniscus asellus*, *Porcellio scaber*).

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1. Introduction

Knowledge of interactions between the soil environment and soil fauna forms an important background for objective assessment of other factors affecting the complex of relationships such as impacts of climate change (Briones *et al.* 1997, Dollery *et al.* 2006, David & Handa 2010), changes in species composition of woody plants in native stands (Schreiner *et al.* 2012), differences in the setting of ravines (Schlaghamerský *et al.* 2014) or reforestation of grasslands (Carpenter *et al.* 2012). Earlier observations also suggest the possibility of occurrence of different soil invertebrates based on different characteristics of soil environment (Scheu & Schulz 1996).

To understand the differences in behavior of invertebrates, it is necessary to know the basic characteristics of soils in forest ecosystems. Soil is based on the soil-forming substrate (Bedrna 1977, Němeček *et al.* 1990), which affects through its quality of the edaphon (Mařan & Káš 1948) that consequently influences the ongoing soil-forming processes. Soil chemistry affects weathering of the parent rock, and thus also particle size and skeleton content. Soil texture is the most stable characteristic of the soil environment, influencing to a critical extent the porosity, air and water regimes, infiltration and humus formation processes and fertility of soil (Brady & Weil 2008). Knowledge of soil chemistry is a precondition of the possibility to study the manifestations of soil invertebrates.

Diplopoda and Lumbricidae play an important role in transformations of the soil environment of the ecosystem (Schaefer 1991) and fulfil the criterion as suitable individual invertebrates for the bioindication of the soil quality and in this context of global climate change (Blackburn *et al.* 2002, Tuf & Tufová 2008, Dunger & Voigtländer 2009). Soil properties and their influence on the distribution and presence of the species of the orders Lithobiomorpha and Geophilomorpha were studied by Scheu & Poser (1996), Blackburn *et al.* (2002) and Jabin (2008). Blackburn *et al.* (2002) and Jabin (2008) suggested that assessing the soil environment using solely the chemical composition of the soil may not estimate some of the soil properties correctly. The results so far show only a minor importance of soil reaction for Lithobiomorpha, in contrast to soil moisture. Some partial results defining the relationship of soil environment and individual centipede, millipede and terrestrial isopod species have been published but no conclusive data exists so far.

Faunistic data on centipedes, millipedes and terrestrial isopods of the Moravian-Silesian Beskyds were published by Kula *et al.* (2011). This study aimed at assessing the preferences of soil-epigeic centipedes, millipedes and terrestrial isopods along the gradients of chemical and physical properties of soil. The presence of centipedes, millipedes and terrestrial isopods was monitored using pitfall traps in 2007–2012 over each year's growing season.

2. Materials and methods

2.1. Study area

The sites forming the monitoring grid (38 plots, Fig. 1) encompass a broad spectrum of mesoclimatic conditions of the massifs of Smrk and Kněhyně mountains of the Moravian-Silesian Beskyds (the Czech Republic). They are situated within the altitudinal range of 540–1,220 m above the sea level. The climate is characterised by average annual precipitation of 690–934 mm and average annual temperature of 2.6 °C with the minimum in January (–6.1 °C) and maximum in July (11.7 °C), the absolute minimum and maximum temperatures being –30.9 °C and 29.5 °C, respectively (weather station: Lysá hora, 1,323 m a. s. l.). For other details, see Kula *et al.* (2011).

The network of research plots covers an area of 58 km^2, where the distances between the most remote locations are 8.45 km in east-west direction and 6.85 km in north–south direction (Fig. 1). The average distance between the plots is 1.2 km. All study sites are located on soils covered with forests that have been used for forestry for a long time. Close-to-natural forest management is realised in the studied territory.

2.2. Collecting the invertebrates

To capture epigeic fauna, five pitfall traps (glass round-neck-shaped jars with the diameter of 93 mm and overall height of 263 mm), each with 4,000 ml of formaline (4% formaldehyde) as a fixative solution were set on each study site. The traps were sheltered with roofs and situated along a transect with 10 m spacing. The traps were inspected every six weeks from 1 April to 30 October in 2007–2012. Mixed samples were formed by pooling the material from all the five traps at each site on each of the inspection dates and were kept in 75% ethanol. In the years 2007–2009, the invertebrates were determined under the direct supervision of RNDr. & Mgr. Ivan Hadrian Tuf, Ph.D. and Mgr. Jana Tufová, Ph.D. (Faculty of Science, Palacký University Olomouc) while the material from the years 2010–2013 was determined by one of the authors (M. L.).

2.3. Soil sampling

A rectangular soil pit was excavated at each site (August 2009) allowing us to describe the soil profile, determine the depth of the individual horizons and carry out the chemical analysis in line with the Taxonomic Soil Classification System of the Czech Republic (Němeček *et al.* 2001). The pit must be deep enough (70 – 120 cm) to uncover all the soil horizons. The width × length was 70 ×

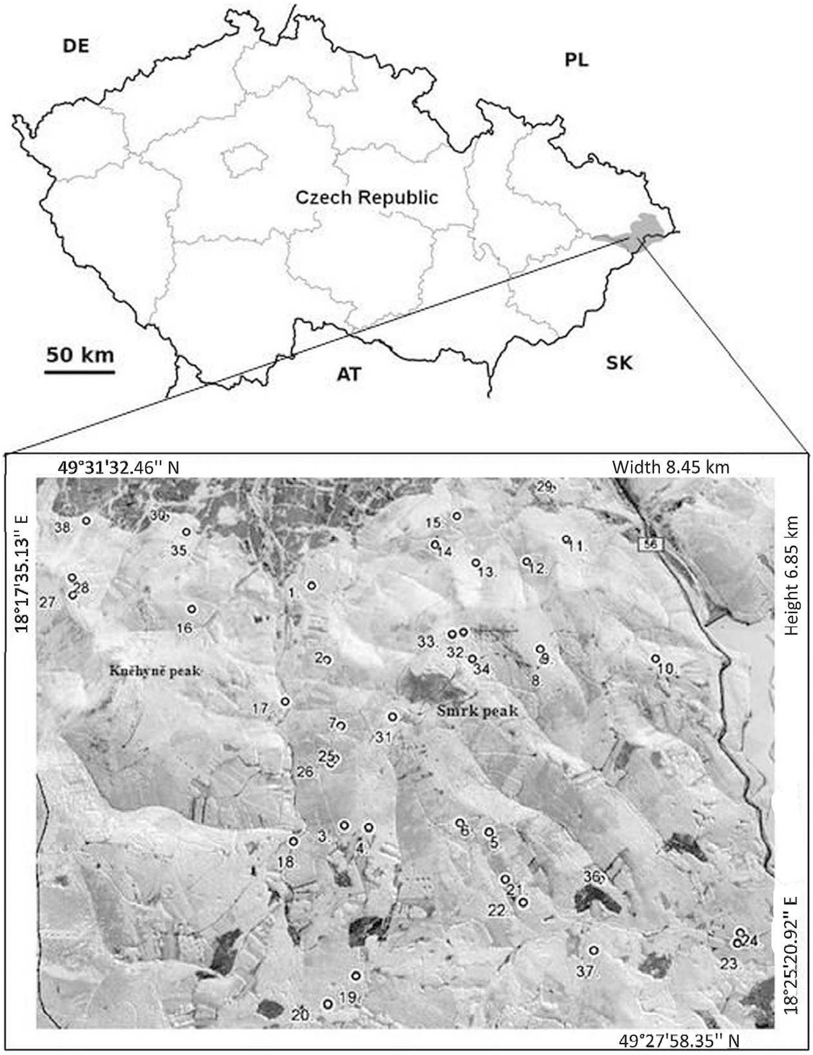

Fig. 1. Locations of study sites in the mountains Beskids massifs in the Spruce and Kněhyně and along the river Čeladenka. A ring beside the number represents the location of the site. Shown is an area of 58 km^2.

100 cm, The excavation of the soil pits was performed manually with spades, shovels and pickaxes. In flat terrains, the back side of the soil pit was oriented to the north. On the slopes, the backside of the pit must be oriented against the slope, which means that the longitudinal axis of the pit was perpendicular to the contour. The face, back side and the two side edges were vertical (perpendicular to the ground of the pit).

To determine the physical properties and characteristics of water and air regime of the soil, we collected undisturbed soil samples in the so-called Kopecky cylinders. The cylinders are made of stainless steel, capacity of 100 cm^3 and the height of 5 cm (Čurlík & Šurina 1998, Jandák 2003).

2.4. Skeleton content and particle size

Skeleton content was defined as the weight percentage of solid particles larger than 2 mm. Soil samples were taken from each horizon of the soil pit, the sample specific weight being 500 g. Each sample was washed through sieves with mesh sizes gradually decreasing to 2 mm. The skeleton sample was then dried at 105 °C and weighed. The weight percentage of the skeleton was determined as the proportion of dry weight of the skeleton and weight of a 500 g sample converted to dry matter under ČSN ISO 11464 (1998).

Particle size was determined by the standard sedimentation method where each of the fine-earth fractions was converted to the percentage of

Table 1. Characterization of study sites. Site numbers refer to those in Fig. 1.

A. Type of top soil layers (horizons A and B) with ionic concentrations (cmol^{+}/kg) and pH.

Site	Soil type	Al^{2+}	H^{+}	Ca^{2+}	Mg^{2+}	K^{+}	Na^{2+}	pH/KCl
1	Leptosols	12.40	7.26	2.48	0.81	1.17	0.23	2.80
2	Leptosols	2.61	3.82	11.66	2.27	1.42	0.10	3.50
3	entic Podzols	2.63	3.90	11.15	1.94	1.72	0.20	3.47
4	haplic Podzols	7.25	4.85	3.82	0.84	1.04	0.15	3.02
5	haplic Podzols	2.09	5.02	8.11	1.53	1.87	0.09	3.32
6	Cambisols	1.11	1.04	24.03	3.08	1.50	0.22	4.29
7	Leptosols	1.64	2.24	18.16	2.46	1.46	0.10	3.75
8	haplic Podzols	7.99	8.59	4.64	0.75	0.86	0.18	2.99
9	Cambisols	10.80	2.18	1.35	0.43	0.52	0.09	2.74
10	Leptosols	11.12	2.97	4.62	0.78	0.72	0.12	3.15
11	Leptosols	9.44	5.20	4.28	0.95	0.87	0.21	2.95
12	entic Podzols	7.40	0.96	5.04	0.71	0.65	0.08	3.31
13	Leptosols	6.98	2.22	1.23	0.49	0.49	0.08	2.78
14	Cambisols	10.08	1.30	4.47	0.91	0.93	0.10	3.41
15	Leptosols	1.09	0.47	38.88	14.71	1.04	0.14	4.43
16	Leptosols	6.22	6.10	7.89	1.02	1.15	0.09	3.11
17	Fluvisols	9.24	4.11	4.45	0.91	1.08	0.10	3.07
18	Fluvisols	13.33	3.98	2.17	1.15	1.16	0.09	3.13
19	Gleysols	11.89	8.22	3.67	2.05	1.88	0.55	3.03
20	Histosols	0.73	0.11	50.66	4.03	0.19	0.35	5.01
21	Cambisols	2.47	4.44	17.01	2.34	2.29	0.12	3.95
22	Cambisols	7.53	11.19	4.48	0.95	1.11	0.12	2.97
23	Histosols	7.60	1.36	13.27	4.10	0.17	0.18	3.77
24	Stagnosols	23.49	3.47	3.05	1.44	1.70	0.22	3.34
25	entic Podzols	1.76	1.10	18.63	2.59	1.14	0.15	4.11
26	Leptosols	10.70	4.41	9.50	2.26	0.99	0.18	3.00
27	Cambisols	7.86	1.43	4.88	1.02	0.81	0.07	3.18
28	Cambisols	9.56	1.74	6.28	2.02	0.96	0.09	3.29
29	Leptosols	8.00	4.59	9.01	1.08	0.99	0.09	3.05
30	Cambisols	9.73	5.19	6.93	1.14	1.01	0.09	2.98
31	Cambisols	12.86	2.98	2.55	0.82	0.75	0.11	2.74
32	Leptosols	7.72	9.03	5.16	1.67	2.75	0.18	3.14
33	haplic Podzols	12.61	7.13	3.17	1.09	1.01	0.17	2.79
34	haplic Podzols	7.36	5.52	5.26	1.04	1.45	0.17	3.00
35	Cambisols	1.37	1.72	16.67	2.36	1.16	0.08	4.04
36	Cambisols	10.41	4.69	3.41	1.21	1.39	0.14	3.09
37	Cambisols	9.66	5.27	5.27	1.20	1.14	0.10	2.87
38	haplic Podzols	8.01	7.92	5.62	1.15	1.20	0.07	3.12

B. Soil moisture (in soil horizons A and B) (%) and composition (%) as well as altitude (m) and main tree species (S – Norway spruce; B – beech).

Site	Moisture		Composition$^{\#}$				Alt.	Trees
	HA	HB	Clay	f.dust	g.dust	f.sand		
1	–	–	6.5	7.4	26.1	60.0	600	S
2	28.45	28.77	1.0	11.4	26.4	61.2	815	B
3	29.43	31.26	1.9	7.5	33.7	56.9	880	B
4	29.09	27.48	3.6	6.9	39.1	50.4	890	S
5	25.96	31.08	16.7	15.5	26.8	41.0	850	B
6	29.57	39.15	0.0	9.2	41.7	49.1	915	B
7	–	–	1.5	10.1	21.3	67.1	855	B
8	–	–	2.2	5.8	33.7	58.3	1,010	S
9	40.87	37.91	2.4	11.3	22.3	64.0	1,045	S
10	19.87	23.36	13.1	17.1	26.1	43.8	845	S

Table 1, continued

11	–	–	6.0	11.9	22.8	59.3	840	S
12	32.98	32.02	0.8	9.4	29.3	60.6	835	B
13	29.86	35.47	0.0	9.1	16.6	74.3	850	S
14	24.36	30.14	11.0	25.3	39.8	23.9	830	S
15	–	–	1.9	4.7	15.3	78.1	780	S
16	20.86	15.30	20.0	22.2	36.4	21.3	785	S
17	–	–	12.2	8.2	16.6	62.9	560	S
18	29.87	24.34	7.9	8.0	15.3	68.8	610	S
19	42.53	49.41	22.0	21.6	35.1	21.4	680	S
20	48.05	49.34	–	–	–	–	660	S
21	30.77	30.57	18.6	15.5	24.5	41.1	730	B
22	–	–	15.2	17.4	31.4	36.0	695	S
23	49.85	48.69	27.1	17.0	20.1	35.8	530	S
24	38.17	39.54	1.0	13.9	46.4	39.7	540	S
25	24.75	25.78	0.4	8.4	32.1	59.1	870	B
26	29.52	24.59	–	–	–	–	825	S
27	33.52	31.93	8.9	18.4	28.4	44.3	1,015	B
28	–	–	11.2	13.2	37.4	38.2	1,025	B
29	17.40	21.9	3.5	12.8	25.5	58.3	620	S
30	–	–	4.9	9.9	23.1	62.0	630	S
31	27.10	29.32	1.5	10.0	30.1	58.3	1,100	S
32	–	–	1.3	8.3	12.9	77.5	1,190	S
33	33.72	34.32	0.4	10.1	16.8	72.7	1,220	S
34	33.06	34.06	11.6	11.5	16.6	60.3	1,100	S
35	29.03	25.49	12.7	30.6	37.8	18.9	635	B
36	26.61	23.11	16.6	19.1	33.1	31.1	620	S
37	22.67	21.74	2.6	11.1	15.9	70.4	645	S
38	29.76	26.98	20.2	17.2	23.1	39.5	635	S

f.dust: fine dust, g.dust: gross dust, f.sand: fine sand.

the total weight of each sample collected. The classification scale by Casagrande (1948) was used for the fractions:

- Clay < 0.002 mm,
- Fine dust (f.dust) 0.002–0.01 mm,
- Gross dust (g.dust) 0.01–0.05 mm,
- Fine sand (f.sand) 0.05–2 mm.

2.5. Soil moisture

Soil moisture was determined by measuring soil resistivity at hourly intervals using the Virrib sensor that was attached to the Virrib data logger (Amet Velké Bílovice). The Virrib Sensor has two concentric rings of stainless steel, connected to the sensor body. The sensor body is a mechanically fixed mass, which prevents water from penetrating to the electronic part. The diameter of the outer ring is 280 mm and its measuring capacity is from 15 to 20 l of soil. The function of the sensor is based on the principle of electromagnetic wave propagation in the environment. The power supply of the sensor is 12–20 V from an external source. The sensor operates on the principle of the current loop, where an electric pulse is sent between the circles of the sensor at set intervals. Consequently, the size of the output current is proportional to the percentage of moisture. Volumetric soil moisture is the water content of total soil volume. At each study site, two Virrib sensors were installed in the middle of the transect from where the invertebrate samples were collected (by the third pitfall trap); one sensor was placed in the centre of the top layer of the A horizon and another one in the centre of the organo-mineral layer of the B horizon. The measuring range was 5–50% of volumetric soil moisture. The data were recorded from April 2008 to October 2009.

To classify the levels of soil moisture, the scale by Kutílek (1971) was used:

- Dry (DryHA, DryHB) < 25%,

- Moist (MoistHA, MoistHB) 25.1–35%,
- Wet (WetHA, WetHB) 35.1–45%,
- Slush (SlushHA, SlushHB) 45.1–50%, wherein the target soil layer is identified in the humus horizon (HA) and in the organo-mineral horizon (HB).

2.6. Exchangeable soil reaction

Exchangeable soil reaction depends on the activity of aqueous hydrogen ions bound to soil colloidal complex (solid part of the soil). The activity of hydrogen ions causes alkaline reaction of soil. Soil reaction strongly influences the process of formation and development of soil. Exchangeable soil reaction was measured for each soil pit and its horizons under laboratory conditions by potentiometer in a suspension formed of a 1 M of KCl solution (2.5 parts) and soil (1 part) within one hour (Zbíral 2002).

2.7. Chemical properties of soil

A subsample of each soil sample was taken from each soil horizon. After removal of undecomposed parts of plant and coarse skeleton, the sample was turned into a fine fraction by crushing. The sample was sifted using a screen of the mesh size of 2 mm and analysed as described below.

2.7.1. Exchangeable elements (e)

The chemical analysis determined the concentration of exchangeable protons H^+ and Al^- (by titration potentiometer) and exchangeable elements Ca^{2+}, Mg^{2+}, K^+ and Na^+ in the humus horizon (HA and HB combined) after extraction by the method according to Göhler (Soukup *et al.* 1987) and in the organo-mineral horizon (HA) after extraction by the method according to Mehlich III (Mehlich 1984, Zbíral 1997) under ČSN ISO 11260 (1998).

The exchangeable elements present in the soil environment bound in colloids are easily accessible to plants and were included as a part of the analyses in this study: exchangeable hydrogen proton (eH), exchangeable calcium (eCA), magnesium (eMg), potassium (eK) and sodium (eNa) ($cmol^+ \times kg^{-1}$).

2.7.2. Accessible elements (pa)

Accessible elements form a group of elements soluble in soil solution, immediately surrounding the roots of plants and bodies of animals. They were determined using the Mehlich III method by extracting the leachate from the soil solution (Mehlich 1984). The group includes of accessible phosphorus oxide (paP), accessible potassium oxide (paK), accessible calcium oxide (paCa) and accessible magnesium oxide (paMg) ($mg \times kg^{-1}$).

2.7.3. Bound elements (t)

Bound elements are engaged in chemical bonds and they are hard to be accessed by plants and animals. Their release often depends on the weathering process. The content of these elements was determined by the technique of decomposition in 20% HCl. The group consists of bound iron oxide (tFe), bound aluminium oxide (tAl), bound manganese oxide (tMn), and the content of oxidised forms of calcium (tCa), bound magnesium oxide (tMg), bound potassium oxide (tK) and bound phosphorus oxide (tP) ($mg \times kg^{-1}$).

2.8. Data analysis

The correlations of environmental variables were analysed along with the occurrence of invertebrates using redundancy analysis (RDA) or canonical correspondence analysis (CCA). A suitable analysis was selected by Detrended Canonical Analysis (DCA). The DCA results of eigenvalues formed the basis for determining the use of RDA or CCA. If all canonical eigenvalues in DCA are less than 3.0, it is more appropriate to use RDA, while if they are over 3.0, CCA is more appropriate. RDA is closely linked to Multivariate linear regression, and is used in cases where a linear relationship is expected whereas CCA allows nonlinearity. Distances split-plot and permutation of the Monte Carlo test (999 permutations) for CANOCO were applied in the CCA or RDA analyses. Data were log(y+1) transformed and rare species were down

Table 2. Mean and total number of specimens of different species of Diplopoda, Chilopoda and terrestrial Isopoda in 38 study sites, and number of sites with specimens.

Species	Abbrev.	Mean no.	Total no.	No. of sites
Chilopoda				
Cryptops parisi Brölemann, 1920	C_par.	2.1	44	21
Goephilus flavus (DeGeer, 1778)	G_fla.	1.5	32	21
Geophilus insculptus Attems, 1895	G_inst.	1.0	1	1
Lithobius austriacus Verhoeff, 1937	L_aus.	13.7	123	9
Lithobius biunguiculatus Loksa, 1947	L_biu.	1.0	1	1
Lithobius borealis Meinert, 1868	L_bor.	1.7	7	4
Lithobius burzenlandicus Verhoeff, 1934	L_bur.	1.0	2	2
Lithobius cyrtopus Latzel, 1880	L_cyr.	19.6	747	38
Lithobius erythrocephalus C.L.Koch, 1847	L_eryt.	50.8	1,931	38
Lithobius forficatus Linnaeus, 1758	L_for.	111.0	4,219	38
Lithobius micropodus (Matic, 1868)	L_mpod.	2.0	6	3
Lithobius microps Meinert, 1868	L_mic.	5.6	186	33
Lithobius mutabilis L.Koch, 1862	L_mut.	99.0	3,761	38
Lithobius nodulipes Latzel, 1880	L_nod.	6.1	158	26
Lithobius pelidnus Haase, 1880	L_pel.	2.0	28	14
Lithobius piceus L.Koch, 1862	L_pic.	1.0	1	1
Lithobius tenebrosus Meinert, 1872	L_ten.	2.8	54	19
Strigamia acuminata (Leach, 1814)	S_acu.	5.9	170	29
Strigamia transsilvanica (Verhoeff, 1928)	S_tran.	1.2	5	4
Diplopoda				
Brachydesmus superus Latzel, 1884	Br_sup.	1.3	8	6
Brachyiulus bagnalli (Curtis, 1845)	Br_bag.	1.4	7	5
Cylindroiulus nitidus (Verhoeff, 1891)	Cy_nit.	1.5	6	4
Glomeris connexa C.L.Koch, 1847	Gl_con.	25.3	785	31
Glomeris hexasticha Brandt, 1833	Gl_hex.	7.3	51	7
Glomeris pustulata Latreille, 1804	Gl_pus.	1.0	1	1
Haasea flavescens (Latzel, 1884)	Ha_fla.	6.0	12	2
Julus scandinavius Latzel, 1884	Ju_scan.	2.8	67	24
Julus terrestris Linnaeus, 1761	Ju_terr.	1.7	5	3
Leptoilus trilobatus (Verhoeff, 1894)	Le_tri.	8.6	318	37
Ophyiulus pilosus (Newport, 1842)	Oph_pil.	2.8	42	15
Polydesmus complanatus (Linnaeus, 1761)	Po_com.	10.5	379	36
Polydesmus denticulatus C.L.Koch, 1847	Po_den.	3.0	3	1
Polyzonium germanicum Brandt, 1831	Py_germ.	1.6	8	5
Tachypodoiulus niger (Leach, 1815)	Ta_nig.	5.3	179	34
Isopoda				
Protracheoniscus politus (C.Koch, 1841)	Pr_poli.	38.3	1,110	29
Hyloniscus riparius (C.Koch, 1838)	H_rip.	21.2	170	8
Lepidoniscus minutus (C.Koch, 1838)	L_min.	1.0	1	1
Ligidium germanicum Verhoeff, 1901	Li_ger.	1.0	1	1
Ligidium hypnorum (Cuvier, 1792)	Li_hyp.	12.7	51	4
Oniscus asellus Linnaeus, 1758	O_asell.	1.0	1	1
Trachelipus ratzeburgii (Brandt, 1833)	T_ratb.	9.6	163	17
Porcellio scaber Latreille, 1804	Pe_scab.	2.0	6	3

weighted (Ter Braak & Šmilauer 2002, Lepš & Šmilauer 2003).

To assess the significance of the association of different invertebrates with soil skeleton, the study localities were divided into two groups. The first group consisted of locations with high skeleton contetnt (>40%, Ske. H.) and the second group of sites with low skeleton content (<40%, Ske. L.). Based on the results of DCA and RDA the relationships between the two groups of the skeleton content and the occurrence of individual species were compared.

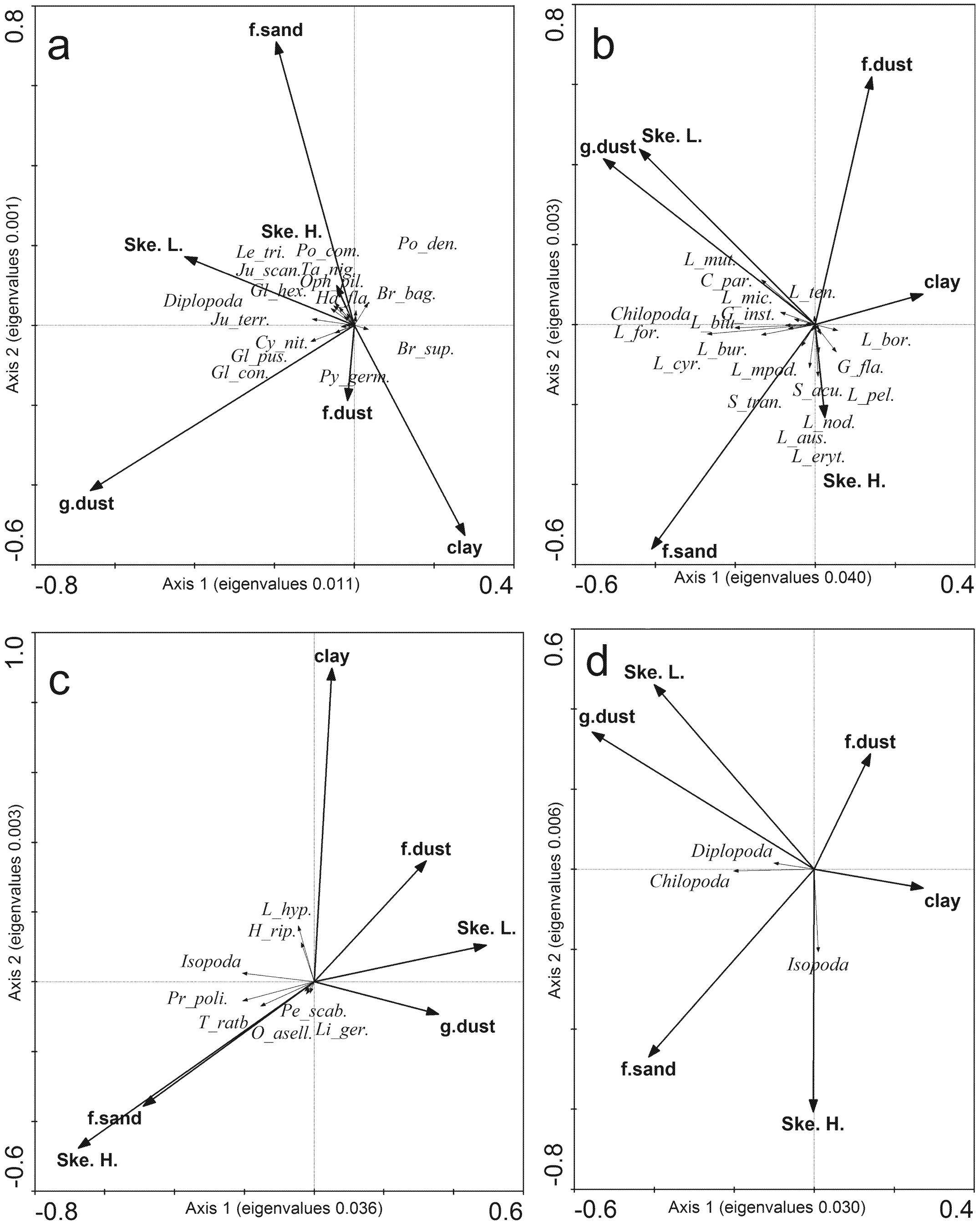

Fig. 2. Results of redundancy analysis ordination of invertebrate assemblages with the environmental skeleton content and particle size of soil. – a. Millipedes. – b. Centipedes. – c. Terrestrial isopods. – d. All species of each group combined. Abbreviations: Ske. H – skeleton high, Ske. L – skeleton low, f.dust – fine dust, g.dust – gross dust, f.sand – fine sand. For abbreviations of species, see Table 2.

CCA was used to find the links between the occurrence of individual soil arthropod species and each of the following environmental variables: soil moisture, soil reaction and chemical properties. For soil reaction, the input data were split into two categories: pH-katA (soil reaction with a value of <3.5 pH/KCl – a very strongly acidic soil reaction) and pH-katB (soil reaction with a value of >3.5 pH/KCl – a strongly acidic soil reaction), while the highest measured pH reached 5.1 (acidic). The input data of chemical properties were divided into three groups (exchangeable, accessible, bound elements).

The level of significance was set at $p < 0.05$ for all testing procedures. Statistical analyses were performed by the STATISTICA Cz software, version 9.2 (StatSoft, Inc.).

3. Results

Overall information on the soil properties and numbers of specimens of different species trapped in the 38 study sites is provided in Table1 and 2, respectively.

3.1. Skeleton content and particle size

At 16 sites, soil skeleton content and particle size were classified to be the major site-specific factors, meaning that large stones (boulders) were represented throughout the soil profile, the range being 44.0% to 64.9% (for the 16 sites, mean ± *S.D.*: 52.3% ± 5.8%). In these sites, individual boulders protruding above the soil surface formed barriers for growth of herbaceous vegetation. The sites were also generally lacking undergrowth, at best, moss and lichen communities were found on the boulders.

In these sites, mainly terrestrial isopods occurred, representing 97.9% of the dominant species; *Trachelipus ratzeburgii* and *Protracheoniscus politus* demonstrate this finding (Fig. 2c). In contrast, the isopods *Ligidium hypnorum* and *H. riparius* showed a positive relationship to the soils with low skeleton content, colonising particularly soils with high content of clay particles. *Porcellio scaber* and *Oniscus asellus* were indifferent in relation to these environmental factors (Fig. 2c).

Millipedes had a positive correlation with the factor of lower presence of skeleton and particle size in the 0.01–0.05 mm fraction (gross dust), where axis 1 represents 90.4% and axis 2 represents 97.9% of all cases of occurrence of millipedes (Fig. 2a). The species *Glomeris connexa*, *Glomeris pustulata* and *Cylindroiulus nitidus* were positively correlated to the particle size fraction 0.01–0.05 mm (gross dust) (Fig. 2a). In contrast, a portion of the species, dominated by *Leptoiulus trilobatus* and *Polydesmus complanatus*, showed a positive relationship to the sites with a higher share of skeleton and the particle size fraction of 0.05–2 mm (fine sand).

Chilopods showed a significant correlation with the factors of coarse dust and fine sand, and accordingly, their vector forms an acute angle with the skeleton low vector (Fig. 2b, d). From this we can conclude that centipedes were more abundant in the locations with lower content of the skeleton. The individual species are dispersed between the Skeleton Low and Skeleton High vector, of which *Lithobius mutabilis* has a positive relationship to the sites with low skeleton content, while *L. erythrocephalus* has a positive relationship to the sites with a higher content of skeleton (Fig. 2b).

3.2. Moisture

The sites were divided into two groups of which the one comprising sites with lower volumetric moisture was found to be predominant, while the other one consisted of three heavily waterlogged sites (No. 19, 20 and 23, Table 1B).

Situated in flat terrain and being the richest in terms of moisture, the site No. 23 showed an average volumetric moisture (Table 1B) and low incidence of soil arthropod fauna (415 individuals). At this site, millipedes featured sporadic representation in terms of both species and numbers (27 ind.), with *P. complanatus* accounting for a half of them (13 ind.). The highest species diversity occurred in centipedes (16 species), which was represented by nine species. Of these, *L. mutabilis* (42%) and *Lithobius forficatus* (19%) prevailed. The relict species, *Lithobius biunguiculatus*, was represented by one individual. The largest numbers were those of Isopoda (279 ind.) that were represented by only three species, *H. riparius* (54%), *P. politus* (30%) and *L. hypnorum* (16%).

Another site (No. 20), a peat bog, had also a notable and permanent groundwater level. It was

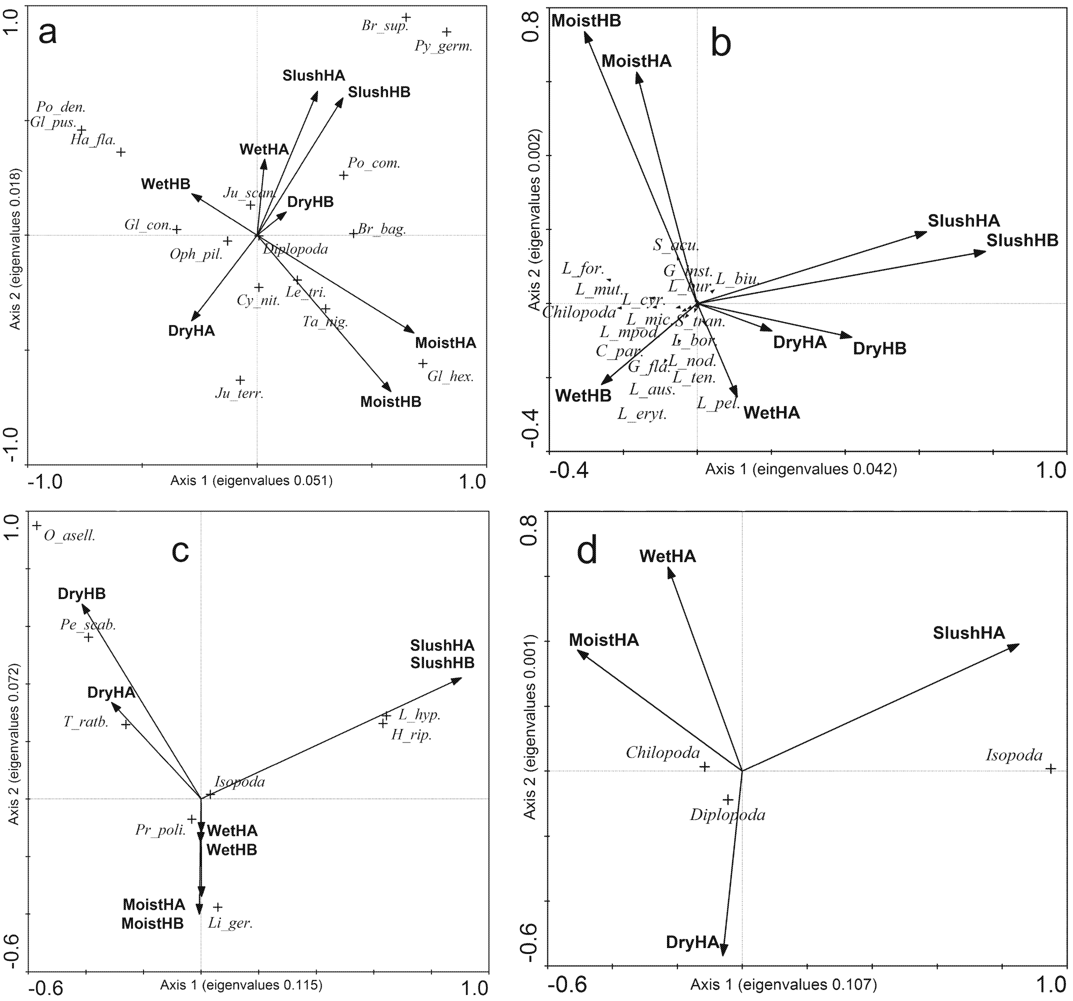

Fig. 3. Results of canonical correspondence analysis ordination of invertebrate assemblages with soil moisture. – a. Millipedes. – b. Centipedes. – c. Terrestrial isopods. – d. All species of each group combined. Abbreviations: DryHA – dry soil in horizon A, DryHB – dry soil in horizon B, WetHA – wet soil in horizon A, WetHB – wet soil in horizon B, MoistHA – moisture soil in horizon A, MoistHB – moisture soil in horizon B, SlushHA – slush soil in horizon A, SlushHB – slush soil in horizon B. For abbreviations of species, see Table 2.

characterised by consistency of the average value of volumetric soil moisture in both upper (48.05 ± 1.01%) and lower (49.34 ± 0.56%) soil layer and, just like the site No. 23 above, a low occurrence of soil arthropods (45 ind.). Millipedes were represented only by *P. complanatus* (5 ind.) and centipedes by six species: *L. mutabilis* (25 ind.), *L. erythrocephalus* (6 ind.), *Lithobius cyrtopus* (3 ind.), *Lithobius tenebrosus* (3 ind.), *L. forficatus* (3 ind.) and *L. microps* (1 ind.). Terrestrial isopods absented here.

In the third site (No. 19) influenced by water, the average volumetric moisture reached 42.53 ± 2.45% in the upper and 49.41 ± 0.21% in the lower layer of the soil, with occasional drop of the groundwater level during the summer. The latter fact was not reflected in rising abundance of individual species compared with the above-mentioned sites more strongly influenced by water. The population of millipedes was very low (13 ind.): *L. trilobatus* (15%), *P. complanatus* (62%) and *Tachypodoiulus niger* (23%). Centipedes were more numerous (74 ind.): *L. mutabilis* (49%), *L. erythrocephalus* (39%), *L. forficatus*

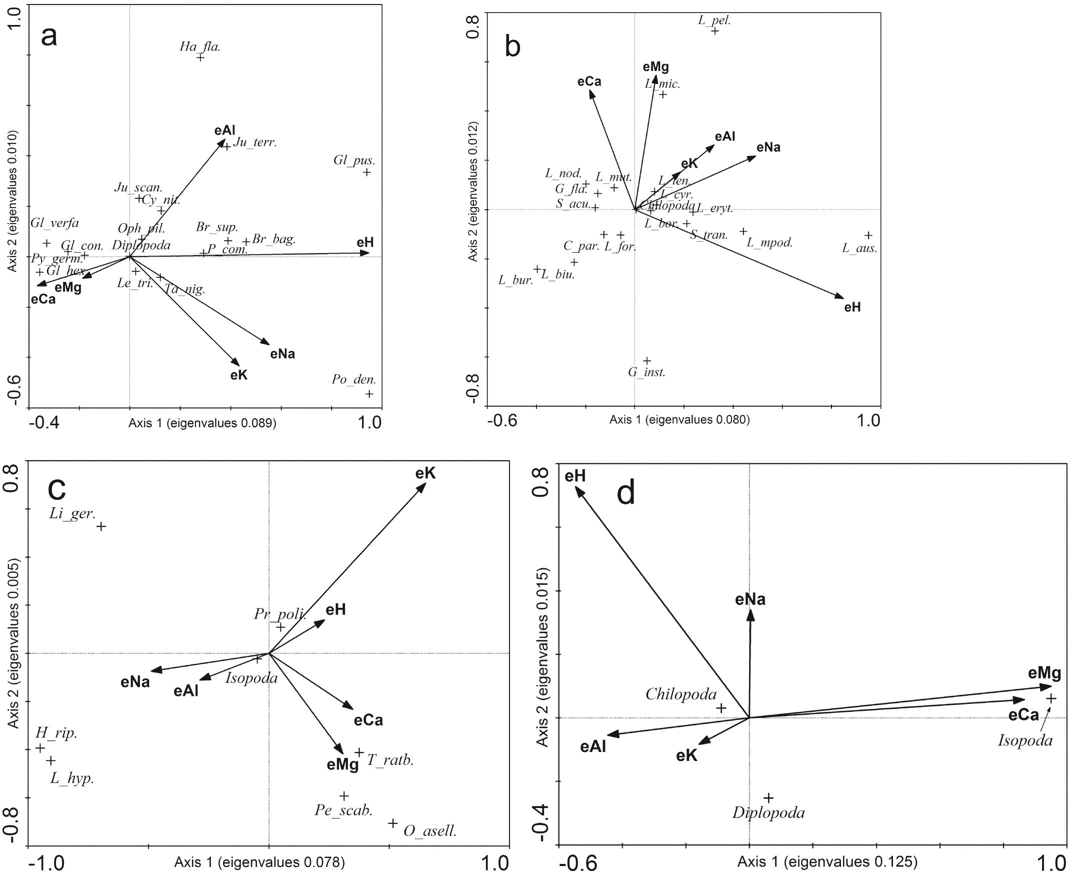

Fig. 4. Results of canonical correspondence analysis ordination of invertebrate assemblages with exchangeable macroelements in soil. – a. Millipedes. – b. Centipedes. – c. Terrestrial isopods. – d. All species of each group combined. For abbreviations of species, see Table 2.

(3%), *L. cyrtopus* (3%), *L. tenebrosus* (1%) and *S. acuminata* (1%).

For Chilopoda, CCA analysis was applied. The chilopod vector passes between those of of moist soil (MoistHA, MoistHB) and wet soil (WetHA, WetHB) with a slight tendency to the wet soil (Fig. 3d). This means that centipedes were associated with sites of moist soil. Between the WetHA and WetHB vectors, there is a noticeable difference in moisture, which is related to the difference in the skeleton content in the soil.

Lithobius erythrocephalus and *L. austriacus* (Fig. 3b) are different from the rest of the centipede species due to their association with increased soil moisture in the lower layers and lower moisture content in the top part of the soil. *Strigamia acuminata* is a species that almost follows the gradient vector of moist soil (MoistHB) with higher content of soil moisture in the lower layers, confirming its ecological niche. *Lithobius biunguiculatus* suggests to some extent a bond to the sites with strong waterlogging and groundwater level projecting as far as the upper layers of soil throughout the year. The vector of dry soil (DryHA, DryHB) lacked any species, which confirms the necessity of soil moisture for the success of centipede representatives in forest soil.

The individual millipede species are so adaptable that they clustered into the centre of all the gradient vectors of CCA, making determination of any precise correlations impossible. However, some tendencies are worth of mentioning. *Cylindroiulus nitidus* and *Ophyiulus pilosus* (Fig. 3a) are species tending towards the vector of dry soil (DryHA), while *L. trilobatus*, *Julus terrestris* and *Tachypodoiulus niger* rather showed associations with the vector of moist soil in the lower layers (MoistHB). *Glomeris hexasticha* and *Brachyiulus bagnalli* had a positive relationship with moisture in the upper soil layers (Moist HA). Species recorded at wet sites (WetHB), where primarily the lower layer of soil was moist, involved *Julus scandinavius*, *G. connexa*, *G. pustulata*, *Haasea flavescens* and *Polydesmus denticulatus*. Slush sites (WetHA) with water often rising up to the ground level, were colonised by *Brachydesmus superus* and *Polyzonium germanicum* (Fig. 3a).

For the community of terrestrial isopods, only a weak correlation in CCA with the gradient axis of slush soil (SlushHA, SlushHB) was detected when taking into account all the species. *Ligidium hypnorum* and *H. riparius* showed positive correlation with slush soils. In contrast, *P. scaber* and *O. asellus* occurred in dry areas (DryHB), where drying was extending as far as the lower soil layer (Fig. 3c). *Porcellio scaber* (6 ind.) and *O. asellus* (1 ind.) were captured at the site no. 29, which is a dry habitat. *Trachelipus ratzeburgii* occurred most frequently at the sites where soil moisture in the upper layers was low (DryHA). *Protracheoniscus politus* and *Ligidium germanicum* were recorded on the wet sites (WetHA, WetHB) with values of soil moisture very similar to those measured at the moist sites (MoistHA, MoistHB).

3.3. Soil reaction

Soil reaction was determined in all the horizons of the soil profile down to the parent rock level. The study sites had very low pH, fully equalling that of sites in mountainous/sub-mountainous spruce stands (Table 1A). The average pH/KCl value reached 3.29 ± 0.46 (min. 2.48 at site No. 1, max. 5.01 at site No. 20). As regards soil reaction and the presence of individual species, CCA confirmed that there were no statistically significant relationships of the studied invertebrate species with the range of the observed soil pH values (results not shown). With generally no relationship of chilopods to soil pH in this study, we even found a tendency to a positive one with *Lithobius burzenlandicus* and *Ligidium germanicum*, while other studies have found, if any, negative relationship of chilopods with soil pH (Blackburn *et al.* 2002, Jabin 2008).

3.4. Macroelements in soil

Soil analysis determined the contents of individual elements and their oxides that are usually important with respect to flora, while their relationships with fauna are not generally defined. Since mostly a negative relationship with the content of individual elements in the soil was determined for centipedes, millipedes and terrestrial isopods, which was manifested in a regular distribution of the individual species with respect to all the elements monitored, each species was evaluated separately for its relationship to macroelements in soil.

Lithobius pelidnus indicated a strong bond to calcium and magnesium, both the exchangeable (eCa, eMg, Fig. 4b) and accessible (paCa, paMg, Fig. 5b) form. The relationship with Mg was even more distinct in *L. microps*, which followed the gradient vector of soil magnesium (Mg) in both its accessible and exchangeable form (Figs. 4b, 5b). A positive correlation appeared also for Ca and Mg in five other species of Chilopoda (*S. acuminata*, *Geophilus flavus*, *L. biunguiculatus*, *L. nodulipes* and *L. tenebrosus*), in four species of Diplopoda (*G. hexasticha*, *G. pustulata*, *J. terrestris* and *P. germanicum*), and in three species of Isopoda (*O. asellus*, *P. scaber* and *T. ratzeburgii*). Interestingly, along with the change in the forms (exchangeable, accessible, bound) of oxides of Ca and Mg, there was no change of the species relationships with those elements. The chilopods *Cryptops parisi* and *G. flavus*, colonising deeper soil layers, exhibited a correlation with the content of bound iron (tFe) (Fig. 6b), which, due to strongly acidic pH, occurred in substantial quantities (site No. 14; 39,000 mg × kg^{-1} of Fe oxide). *Lithobius cyrtopus*, *L. erythrocephalus*, *L. austriacus* and *Lithobius borealis* correlated with the increased content of accessible, oxidised phosphorus (paP) in the soil (Fig. 5b).

Although most of the millipede species showed a negative association to all the elements monitored, *P. denticulatus* had a strong positive association to accessible potassium (paK, Fig. 5a) and exchangeable sodium (eNa, Fig. 4a). Julus terrestris and *H. flavescens* occurred in the soils

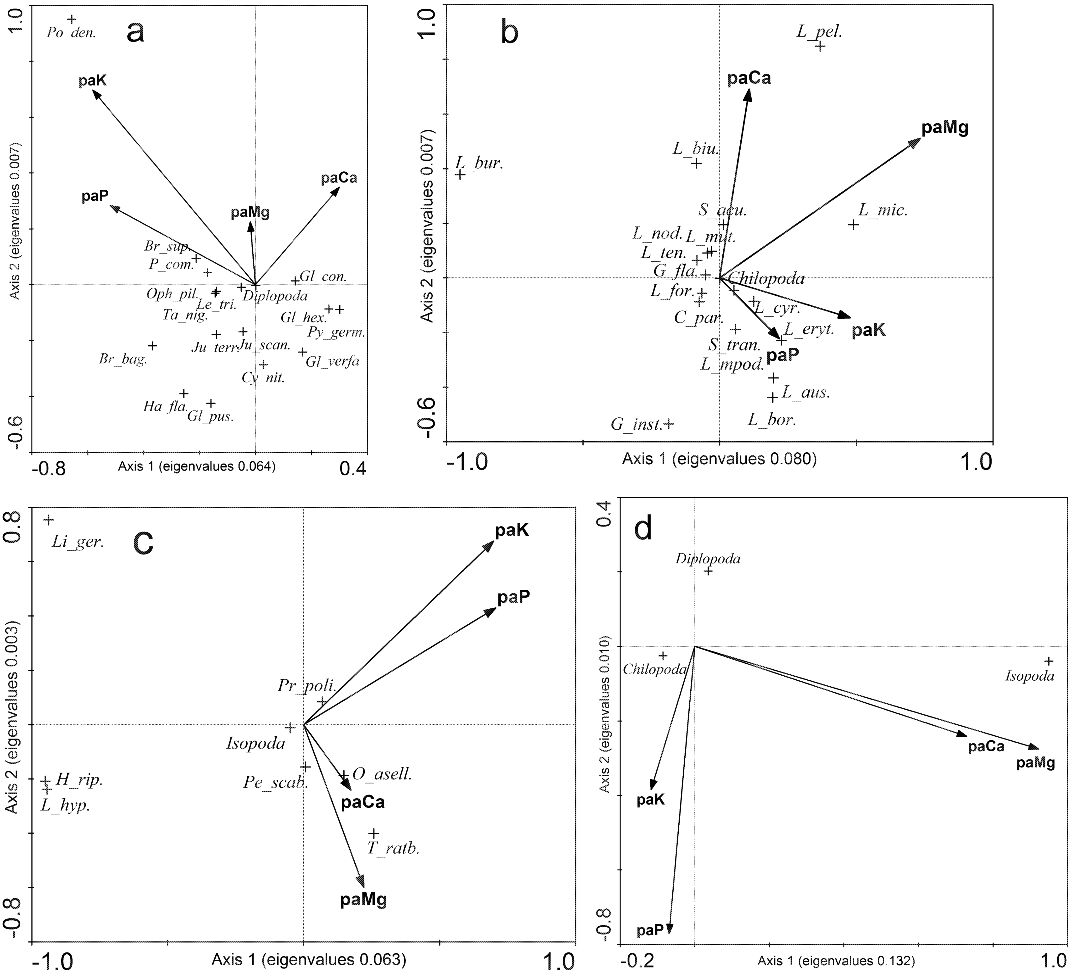

Fig. 5. Results of canonical correspondence analysis ordination of invertebrate assemblages with accessible macroelements in soil. – a. Millipedes. – b. Centipedes. – c. Terrestrial isopods. – d. All species of each group combined. For abbreviations of species, see Table 2.

with increased content of exchangeable aluminium (eAl) (Fig. 4a), indicating soils with high contents of clay particles and acidic soil reaction. The species such as *G. connexa*, *G. hexasticha* and *P. germanicum* were found in soils with increased content of exchangeable calcium and magnesium (eCa, eMg) (Fig. 4a), with the maximum contents of exchangeable calcium and magnesium being recorded at the sites No. 20 (50.66 cmol$^+$ × kg^{-1}) and No. 1 (14.71 cmol$^+$ × kg^{-1}), respectively.

Terrestrial isopods were slightly negative in their relation to the content of potassium, magnesium and calcium in all forms, but they showed more frequent associations with heavy soils of acidic reaction and increased content of aluminium (eAl). *Ligidium hypnorum* and *H. riparius* were significantly associated with the content of both exchangeable (eAl, Fig. 4c) and bound aluminium (tAl, Fig. 6c). The most frequently occurring isopod species, *P. politus*, had a positive relationship with the soils rich in potassium in all forms (eK, paK, tK), indicated by the fact that the vector spacing distance to the vector (K) was balanced in all forms of the element (Figs. 4c, 5c, 6c). The sites with a high content of calcium and magnesium supported *T. ratzeburgii*, *P. scaber* and *O. asellus*. They occurred mostly in the presence of exchangeable calcium and magnesium (eCa, eMg, Fig. 4c) which are

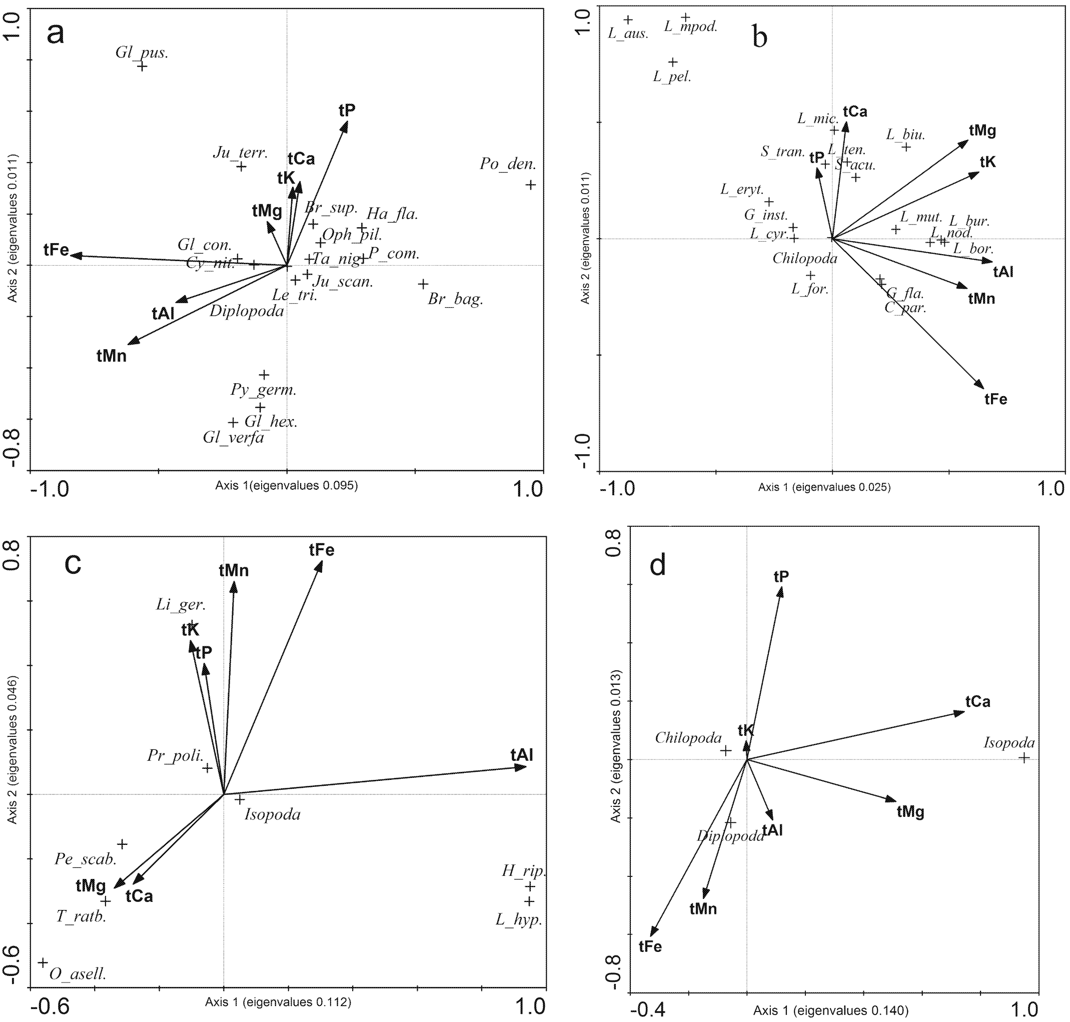

Fig. 6. Results of canonical correspondence analysis ordination of invertebrate assemblages with bound macroelements in soil. – a. Millipedes. – b. Centipedes. – c. Terrestrial isopods. – d. All species of each group combined. For abbreviations of species, see Table 2.

part of the soil solution on the surface of colloids and immediately affect the habitat of organisms. In contrast, *L. hypnorum* had a negative association to the presence of both accessible and exchangeable calcium and magnesium (eCa, paCa, eMg, paMg, Figs. 4c, 5c) and was indistinctively positive in its relation to bound potassium (tK, Fig. 6c).

4. Discussion

Soil environment as the basis for an ecosystem has not been comprehensively analysed in terms of the relationships between pedological characteristics and epigeic fauna (Schaefer & Schauermann 1990, Scheu & Poser 1996, Blackburn *et al.* 2002, Scheu & Setälä 2002, Jabin 2008). The relationship between the amount of organic matter and the pH of soil is variable (Salamon *et al.* 2008, Fierer *et al.* 2009) and influences the biomass of fungi and bacteria, and thus the food supply for the consumer level. It has been shown that Lithobiomorpha (*Lithobius crassipes* L. Koch 1862, *L. mutabilis*), according to the content of fatty acids, are consumers of fungi and also hunters of springtails and oribatid mites feeding on fungi (Maraun *et al.* 2003, Chahartaghi *et al.*

2005, Maraun *et al.* 2011, Ferlian *et al.* 2012). The members of Geophilomorpha (*S. acuminata*, *Geophilus ribauti* Brölemann, 1908) prefer bacteria eaters (Ferlian *et al.* 2012).

In order to shed light on relationships between the soil environment and representatives of Chilopoda, Diplopoda and Isopoda, a detailed account of soil variables and abundance of the above mentioned invertebrates was undertaken in this study in the area of the mountains of Moravian-Silesian Beskyds. Among the major factors of soil environment for centipedes, millipedes and terrestrial isopods are the nutritional components of soil-forming processes, soil moisture, pH, the level of skeleton content as well as the height of accumulated humus, and soil air content, of which the two latter ones were not included in this study.

4.1. Skeleton content and particle size

Centipedes have been recorded in corridors formed by members of Lumbricidae or those left by rotted roots of trees (Albert 1982). Jabin (2008) mentioned the direct influence of airspace in soil on the presence of epigeic Lithobiomorpha and Geophilomorpha. However, soil skeleton content and particle size have not been studied to the extent that would allow us to link gained knowledge to the occurrences of the individual soil arthropod species. These factors, however, are significant for changes in soil moisture, air capacity, soil fertility and associated soil chemistry, which is related to the content of colloidal solutions. In this study, centipedes, millipedes and terrestrial isopods were associated with the sites with increased skeleton content and they were less abundant on soils with high content of clay (Fig. 2d). Centipedes do not colonise clayey soils with reduced interstitial air volume (Attems 1926, Albert 1982). Therefore, it is assumed that soil aeration is an important factor influencing the presence of centipedes, millipedes and terrestrial isopods in the soil profile. *Porcellio scaber* and *O. asellus* were indifferent in their relation to skeleton content and particle size (Fig. 2c), which could be due to the low representation of these species. Therefore, it was not possible to establish any indisputable relationships with the individual environmental factors. The finest soil particles, clay, had no connection with the occurrence of species, which means that centipedes, millipedes and isopods prefer places with aerated soil profile. However, information on underground species would be required.

4.2. Moisture

Moisture is an important soil property for the distribution of epigeic fauna. For example, Schlaghamerský *et al.* (2014) found the greatest species diversity of centipedes, millipedes and isopods, in wet sites on the bottom of ravines, i.e. in the places offering favourable conditions in winter in addition to other seasons. In accordance, since the mountains of Moravian-Silesian Beskyds are characterised by high precipitation (average annual total of >1,200 mm), there were no sites with a dry soil profile, which contributed to the wide range of the species caught. Myriapoda are among the organisms particularly sensitive to drying (Curry 1974, Lewis 1981) due to the weak epicuticular wax layer on the epidermis (Blower 1951, Mead-Briggs 1956). Albert (1983) mentions preference of moist habitats by myriapods with close to 100% relative humidity, with Lithobiomorpha preferring relative humidity above 96% (Fründ 1987). They are able to find even a very small soil niche with increased moisture (Weil 1958). Centipedes occur abundantly on wet soil surface and increase activity in the rain (Zapparoli 1997). However, they are not always able to survive periods of flooding (Zerm 1997). According to Cloudsley-Thompson and Crawford (1970), there is no evidence of centipedes taking up moisture from saturated air.

Overall, centipedes preferred freshly moist sites (Moist HA, Fig. 3d) with the volumetric moisture of the soil never decreasing below 25%. The increased presence of Lithobiomorpha and Geophilomorpha in moist habitats is related to the availability of food, because in moist habitats, molds are more abundant than bacteria due their better moist resistance (Bardgett *et al.* 2005, Gordon *et al.* 2008). According to Jabin (2008), *S. acuminata*, *L. mutabilis* and *L. forficatus* show a greater drought resistance compared to smaller centipedes, such as *L. microps* or *L. austriacus*.

Brachydesmus superus, *P. germanicum* and *G. connexa* were the diplopod species colonising sites with waterlogged soil (Fig. 3a). *Cylindroiulus nitidus* and *O. pilosus* appeared to be quite resistant to drying (Fig. 3a). These species were found on drying soils as well as on the others, because some species are more drought resistant than other ones. However, it is not clear how some species can survive periods of short-term drought in the course of the growing season.

Terrestrial isopods require moist soil, too (Vasconcellos *et al.* 2013). Accordingly, increased numbers of members of this group on agricultural, all-year-round irrigated soils, were confirmed by Morón-Rios *et al.* (2010). In this study, association to wet soils was found in two other species, *L. hypnorum* and *H. riparius* that were closely bound to waterlogged soils (Fig. 3c).

4.3. Soil reaction (pH)

As regards soil reaction, there was no significant differentiation in respect to the study sites in the studied species spectrum of Diplopoda, Chilopoda and terrestrial Isopoda in this study. Similar conclusion for chilopods was reached by Jabin (2008). In general, information on soil arthropods in relation to soil reaction is not sufficient. However, Blackburn *et al.* (2002) found a strong link of the chilopod *Brachygeophilus truncorum* (Bergsoë & Meinert, 1886) to acidic soils. This is due to the availability of food, i.e. fungi are more abundant in an acid medium than bacteria (Francis 1986).

In the study by Scheu and Poser (1996), soil pH affected the macrofauna near tree trunks, with the importance of pH decreasing with increasing distance from the trunks. Increased acidity was preferred by the centipede *S. acuminata*, while the abundance of *G. insculptus* was reduced in the same setting (Scheu & Poser 1996). In another study, the millipede *Mycogona germanica* (Verhoeff, 1892) colonised an acidic environment (Ellenberg *et al.* 1986). In our study, the habitat conditions were mainly acidic (pH/KCl 2.74 to 5.01), providing suitable environment for a wide range of centipedes, millipedes and terrestrial isopods.

4.4. Soil chemistry

Soil chemistry affects soil-forming processes and, indirectly, the quality of soil as a source of food for soil fauna through the development of microbial activity (Wardle 1992, Blackburn *et al.* 2002).

Scheu and Schaefer (1998) found high contents of phosphorus, nitrogen and carbon to be the limiting factors for soil microorganisms. Increased acidification reduces the diversity and generally increases the abundance of mesofauna in forest soils through high representation of some of the dominant species (Hågvar & Kjøndal 1981, Hågvar 1984, Baas & Kuiper 1989).

The results of the present study indicate preference of sites with increased levels of calcium and magnesium in centipedes, particularly *L. pelidnus* and *L. biunguiculatus* and in the terrestrial isopods *T. ratzeburgii* and *O. asellus*, in contrast to millipedes. This may be related to the finding that increased calcium and magnesium contents have a favourable influence on the occurrence of arthropods with calcium-based exoskeletons (Hopkin & Read 1992, Jabin 2008).

The availability of nutrients can be a limiting factor. Millipedes were found to respond negatively to accessible Ca and Mg (Fig. 5d) in the proton forms, which are better accessible for plants than their exchangeable, oxidized forms. Centipedes showed no associations to the level of individual elements, except for *S. acuminata* and *L. microps*, the species with a positive link to the presence of Ca and Mg (Figs. 4b, 5b, 6b). In terrestrial isopods, the response was clear with *T. ratzeburgii*, *O. asellus* and *P. scaber* having positive responses to increased content of Ca and Mg in all forms (Figs. 4c, 5c, 6c). *Ligidium hypnorum* and *H. riparius* confirmed the relationship to heavy soils through their bond to Al and Na (Figs. 4c, 6c). *Protracheoniscus politus* preferred the sites with increased levels of K in all forms (Figs. 4c, 5c, 6c).

5. Conclusion

The study indicated how millipedes, centipedes and terrestrial isopods are affected by selected soil characteristics. Soil skeleton content and particle size were indicated as important factors. The sites with the most boulders on the soil surface have a favourable hydric regime of soil associated with high representation of centipedes and terrestrial isopods. Species like *L. austriacus*, *L. erythrocephalus* and *L. nodulipes* occurred specifically in areas with increased content of boulders. Of these, *L. nodulipes* reached increased incidence especially in valleys where mountain streams expose boulders on the soil surface and where soil moisture regimes are good. Influence of soil reaction (pH / KCl) did not show a significant trend. The most marked response to nutrient levels was shown in isopods *T. ratzeburgii*, *O. asellus* and *P. scaber*, i.e. in species with a tendency to seek increased content of Ca and Mg. The isopods *L. hypnorum* and *H. riparius* were associated to heavy soils with high levels of Al. In contrast, the chemical composition of soil did not show a significant link to the occurrence of centipedes and millipedes in the soil environment.

General understanding of the ecological demands of individual centipede, millipede and terrestrial isopod species is insufficient, although with their living habits, they form an important part of nutrient cycling in the ecosystem. Such lack of general knowledge disallows any deeper confrontation of the results of this study with those of other studies.

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