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Relationship Between Soil Type, Humus Form and Macrofauna Communities (Myriapoda and Isopoda) in Forests of the Moravskoslezské Beskydy Mountains, Czech Republic

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Abstract: The effect of soil type, form of humus and altitude on the species composition and density of soil invertebrate communities was studied. Pitfall traps was used to examine diversity of selected epigeic invertebrate groups, i.e. Diplopoda, Chilopoda and Isopoda. A total of 40 species of these groups were captured in traps in a set of 38 sites in forests of Beskydy Mountains, Czech Republic, and monitored for 2007-2012. Overall findings showed the presence of species with wide tolerance to the soil type. High numbers of species were found on Cambisols and Leptosols; Histosols and Stagnosols exhibited smaller number of species and lower abundance. Regarding the form of humus, most abundant populations occurred in soils with Moder humus. Sites with Mor humus were dominated by representatives of the Chilopoda (Lithobiomorpha). Soils with Mull humus were characterised with the presence of species resistant to drying. Sites with Tangl humus were characterised by the presence of *Hyloniscus ryparius* (Isopoda). The altitudinal analysis revealed the preference of Isopoda to lower altitudes, Chilopoda to middle and Diplopoda to middle and high altitudes.

Key words Diplopoda, Chilopoda, Isopoda, type of soil, form of soil humus, altitude

Introduction

Forest communities are strongly dependent on soil types and the peculiarities of their humus (Kauz, Topp 1998, Schue *et al.* 2003), elevation and slope position (Mudrick *et al.* 1994, Ponger *et al.* 1997) and chemical characteristics of soil (Schaefer, Schauermann 1990). The structure of the soil and the composition of the epigeic invertebrate communities reflect qualitative changes of the soil and are sensitive to local endogenous and exogenous factors (Blackburn *et al.* 2002, Jabin 2008). Several groups of invertebrates have great importance as bioindicators for the soil quality, i.e. Aranea (Buchar 1983), Oribatoidea (Curry 1978), Carabidae (Hůrka *et al.* 1996) and Staphylinidae (Boháč 1990). Recent studies have demonstrated the bioindicative value of Myriapoda and Isopoda (Tuf, Tufova 2008). The knowledge of ecological preferences of various invertebrates contributes to their assessment as bioindicators. The strong connection of invertebrates to the soil characters requires further examinations of site conditions in relation to the usefulness of various groups as bioindicators (Scheu, Poser 1996, Blackburn *et al.* 2002, Jabin 2008, Tuf, Tufova 2008, Dunger, Voigtländer 2009).

The subphylum Myriapoda includes invertebrates predominantly dwelling in soil (Kautz, Topp 1998, Hopkin, Read 1992, Scheu *et al.* 2003, Golovatch, Kime 2009, Mudrick *et al.* 1994, Ponge *et al.* 1997). Its class Chilopoda is the prevailing group in relation to the biomass; although known as carnivores, intake of detritus is not uncommon in centipedes (Lewis 1965, Gunn, Cherrett 1993). Organic matter containing bacteria, fungi and moulds is the main food resource for diplopods and isopods (Stephen

1992, Lang 1954, Frankenberger 1959). Ferlian *et al.* (2012) reported some species of Lithobiomorpha [*Lithobius crassipes* L. Koch 1862, *L. mutabilis* L. Koch 1862] as consumers of fungi, along with hunting collembolans and oribatids (Maraun *et al.* 2003, 2011, Chahartaghi *et al.* 2005).

In forest ecosystems, the relationship between soil conditions and the epigeic fauna was recently analysed (Blackburn *et al.* 2002, Schaefer, Schauermann 1990, Jabin 2008, Scheu, Poser 1996, Scheu, Setälä 2002). Experimental evidence suggested that, in natural ecosystems, where several species co-occurred in close temporal and spatial proximity, there were interactions between the different types of litter decomposition (Blair *et al.* 1990, McTiernan *et al.* 1997, Wardle *et al.* 1997, Hoorens *et al.* 2003, Smith, Bradford 2003).

Important factors of soil environment affecting myriapods include the height of accumulated humus, the nutrient component of soil-forming processes, soil moisture, pH, and contents of skeleton and air (Scheu, Poser 1996, Blackburn *et al.* 2002, Jabin 2008). Schreiner *et al.* (2012) have shown a significant influence of successional change defined by the stand age on the communities of diplopods and chilopods. *Julus scandinavius* Latzel, 1884 was a species that indicated successional changes in deciduous forests (Topp 1998), while Scheu, Schulz (1996) revealed the different responses of soil invertebrates to successional changes as per trophic group. Topp *et al.* (1992) observed links between synanthropic and eurytopic members of diplopods in woodlands. Decrease in the number of species and the number of subjects was studied in urban, rural and suburban areas. It has been shown a decrease of the impact of urbanization on the diversity and the expansion of synanthropic species (Bogyó *et al.* 2015). Changes in the water regime influenced communities of isopods and millipedes in forested montane wetlands (Sterzyńska *et al.* 2015). Altitude was also recorded as a factor limiting the distribution of isopods and millipedes (Tajovsky 1997, Sterzyńska *et al.* 2015). Impact of tree species has been studied in the Arboretum Borová Hora (Slovakia), where there were significant differences in the composition of millipedes under various tree species (Stašiov *et al.* 2012).

In the context of above-described knowledge of soil invertebrate communities and their dependence on various factors in forest ecosystems, the aims of the present study are (1) to characterise the structure of communities of Diplopoda, Chilopoda and Isopoda under the conditions of different soil types in a selected mountain areas; (2) to examine whether the form of humus can influence these communities; and (3) to test whether myriapods can be used as bioindicators for undisturbed forest soils in mountain zones.

Material and Methods

The study area

We used 38 plots being sites of a monitoring grid (Fig. 1) and representing a broad range of mesoclimatic conditions of the massifs of Smrk and Kněhyně in the Moravskoslezské Beskydy Mountains, Czech Republic. The altitudinal gradient of plots was 540-1220 m. The diversity of soils included from oligobasic soils (Cryptopodzols and Podzols) to eumesobasic soils (Cambisols, Leptosols); their hydric range varied from soils without hydromorph influence to such permanently affected by water (Histosols), with microecologically significantly differing stand types of beech (11 stands) and spruce (27 stands). The stand age was between 49 to 160 years and 60 to 259 years, respectively. The climate of the area is characterised by av. annual precipitation 690-934 mm, av. annual temperature 2.6°C, with the mini-

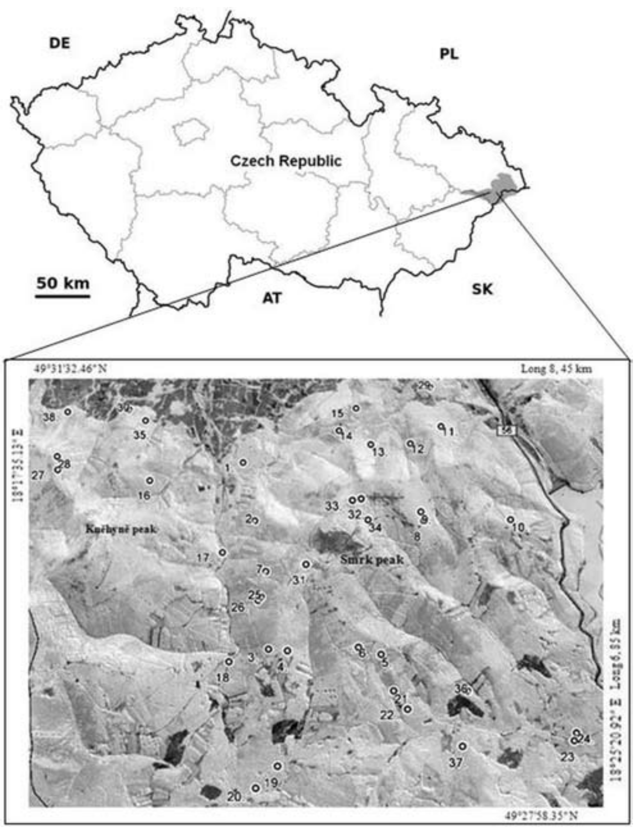

Fig. 1. Location of sites in the mountains Moravskoslezské Beskydy in the massifs Smrk and Kněhyně and along the Čeladenka river. A ring of the number represents the location of the site. The coordinates for the corners of the viewport indicate the position of the upper left and lower right corner of the viewport. Length is a real length field

Table 1. Habitat characteristics of permanent research plots (Beskydy, 2007–2012)

Localities	GPS localities	Type of soil	Tree species	Altitude (m)	Form of humus
1	N 49°30´47.5´´ E18°20´37.1´´	Leptosols (LP)	S	600	Mor
2	N 49°30´10.7´´ E18°20´51.5´´	Leptosols (LP)	B	815	Mor
3	N 49°29´02.5´´ E18°21´08.7´´	entic Podzols (eP)	B	880	Moder
4	N 49°29´01.9´´ E18°21´23.0´´	haplic Podzols (haZ)	S	890	Mor
5	N 49°29´02.0´´ E18°22´33.3´´	haplic Podzols (haZ)	B	850	Moder
6	N 49°29´04.5´´ E18°22´16.0´´	Cambisols (CM)	B	915	Moder
7	N 49°29´42.6´´ E18°21´03.0´´	Leptosols (LP)	B	855	Mor
8	N 49°30´10.9´´ E18°23´04.4´´	haplic Podzols (haZ)	S	1010	Mor
9	N 49°30´15.5´´ E18°23´02.0´´	Cambisols (CM)	S	1045	Moder
10	N 49°30´13.5´´ E18°24´14.2´´	Leptosols (LP)	S	845	Mor
11	N 49°31´08.6´´ E18°23´19.9´´	Leptosols (LP)	S	840	Mor
12	N 49°30´57.1´´ E18°22´54.4´´	entic Podzols (eP)	B	835	Moder
13	N 49°30´55.0´´ E18°22´22.1´´	Leptosols (LP)	S	850	Moder
14	N 49°31´03.9´´ E18°21´55.9´´	Cambisols (CM)	S	830	Moder
15	N 49°31´19.1´´ E18°22´09.4´´	Leptosols (LP)	S	780	Mor
16	N 49°30´31.7´´ E18´19´24.3´´	Leptosols (LP)	S	785	Moder
17	N 49°29´55.2´´ E18°20´26.1´´	Fluvisols (FL)	S	560	Moder
18	N 49°28´57.0´´ E18°20´38.2´´	Fluvisols (FL)	S	610	Moder
19	N 49°28´07.0´´ E18°21´19.6´´	Gleysols (GL)	S	680	Tangel
20	N 49°27´56.5´´ E18°21´04.6´´	Histosols (HS)	S	660	Tangel
21	N 49°28´44.6´´ E18°22´43.3´´	Cambisols (CM)	B	730	Moder
22	N 49°28´36.2´´ E18°22´54.0´´	Cambisols (CM)	S	695	Moder
23	N 49°28´24.6´´ E18°24´59.5´´	Histosols (HS)	S	530	Tangel
24	N 49°28´28.4´´ E18°25´01.5´´	Stagnosols (ST)	S	540	Mor
25	N 49°29´29.3´´ E18°21´00.6´´	entic Podzols (eP)	B	870	Moder
26	N 49°29´27.8´´ E18°20´58.1´´	Leptosols (LP)	S	825	Mor
27	N 49°30´32.6´´ E18°18´13.2´´	Cambisols (CM)	B	1015	Moder
28	N 49°30´40.6´´ E18°18´10.7´´	Cambisols (CM)	B	1025	Moder
29	N 49°31´38.5´´ E18°23´12.9´´	Leptosols (LP)	S	620	Mor
30	N 49°31´17.1´´ E18°18´57.4´´	Cambisols (CM)	S	630	Moder
31	N 49°29´45.2´´ E18°21´34.2´´	Cambisols (CM)	S	1100	Mor
32	N 49°30´18.9´´ E18°22´14.8´´	Leptosols (LP)	S	1190	Mor
33	N 49°30´17.4´´ E18°22´08.1´´	haplic Podzols (haZ)	S	1220	Mor
34	N 49°30´08.5´´ E18°22´20.6´´	haplic Podzols (haZ)	S	1100	Moder
35	N 49°31´09.6´´ E18°19´13.2´´	Cambisols (CM)	B	635	Mull
36	N 49°28´46.6´´ E18°23´39.6´´	Cambisols (CM)	S	620	Moder
37	N 49°28´19.5´´ E18°23´34.9´´	Cambisols (CM)	S	645	Moder
38	N 49°31´13.5´´ E18°18´06.6´´	haplic Podzols (haZ)	S (Fir)	635	Moder
Note: Tree species: S-spruce, Norway spruce, B-beech					

mum in January (-6.1°C) and the maximum in July (11.7°C), the absolute minimum -30.9°C and the absolute maximum (29.5°C) (weather station: Lysá hora, 1323 m a.s.l.).

Sampling methods

To capture epigeic fauna, five pitfall traps filled with formalin (4% formaldehyde) were placed in each of the 38 stands studied (Table 1). Pitfall traps were set in working condition every year at the end of April. The volume of each trap was 4 litres, and the diameter of the trap mouth was 93 mm. The traps were sheltered with metal roofs and installed linearly within each stand, with a space of 10 m between the traps. The traps were collected every six weeks (15 June, 31 July, 15 September and 30 October) in 2007–2012.

Soil types and forms of humus

A soil probe was used at each site to allow describing the soil profile, determining the depths of the individual horizons and taking a sample (September 2009) to carry out the chemical analyses of the overlying humus layer (horizon H) and the soil (horizon Ah). The soil analysis followed the methodology of the Taxonomic Soil Classification System of the Czech Republic (Němeček *et al.* 2001). For determining the type of soil and humus forms, an analysis was performed on one sample. Changes in the soil environment were not studied.

The soil type was determined at the research sites based on the soil horizon structure using the methodology according to WRB 2006 (The World Reference Base for Soil Resources), which involves a two-stage system of soil classification with 32 major soil groups ("Reference Base") and over 120 clearly defined traits to describe the specific properties of the soil. Eight main soil types were defined on the monitored sites (Table 1): Leptosols (LP), Haplic Podzols (haZ), Entic Podzols (eP), Stagnosols (ST), Histosols (HS), Cambisols (CM), Gleysols (GL) and Fluvisols (FL).

Simultaneously, the form of soil humus was determined, i.e. Mor, Moder, Mull and Tangle (Table 1). While characteristic of the Mor form is the accumulation of non-humified dead organic matter on the soil surface, low pH and combined cold and wet mesoclimate, the Mull form features a rapid humification process, decaying organic matter, a rich herb layer and activity of actinomycetes and bacteria; the Moder form represents a transition between Mor and Mull. Finally, Tangle as a separate form of humus is characterised by intense accumulation of undecomposed organic matter on wet sites (peat bogs).

Altitudinal vegetation zones (AVZ)

Four altitudinal vegetation zones were recognised: 530-700 m, 701-875 m a.s.l., 876-1050 m and 1050-1220 m. The comparison was performed by using canonical correspondence analysis (CCA) after log-transformation and with downweighted race data. CCA results are presented as an ordination diagram of vectors axis shows the distribution of the environmental variables (AVZ) and illustrating the position of species.

Statistical processing

The module of basic characteristics was applied to determine the position of data relative to normal distribution (STATISTICA 10). Subsequently, the data were tested in the environment of the CANOCO 4.5 program using Detrended Canonical Analysis (DCA), where suitability of subsequent analyses was determined on the basis of the resulting eigenvalues. To assess environmental variables that do not differ between structures, but are related to myriapod turnover, we performed a Canonical Correspondence Analysis (CCA) or Redundance Analysis (RDA) in CANOCO 4.5 (ter Braak, Šmilauer 2002, Lepš, Šmilauer 2003). Densities were log transformed (x+1) and rare species were downweighted. We entered all environmental factors, used interspecies distances, Hill's scaling, and extracted seven best-fitting environmental variables using the forward selection procedure with 999 Monte-Carlo permutations for significance testing. In cases where the input data were evaluated as linear combination, we used redundancy analysis (RDA); this method was used for defining the relationship of each myriapod and isopod species to the form of humus.

Results

Impact of soil type

Eight soil types were characterised in the set of 38 stands monitored on the basis of morphological traits found in the soil probes. Cambisols (CM; 12 sites) and Leptosols (LP; 10 sites) were the predominant types. The soil environments were diverse, ranging from dystric to mesotrophic scree subtypes. A group of soils showing processes of podzolisation (11 sites), including the soil types of Entic Podzols (eP), Haplic Podzols (haZ) and Stagnosols (ST), were also recorded; these soils indicate acidification and nutritional deterioration of soil humus with a deceleration process.

Isopods were clearly connected to sites with a high content of undecomposed organic matter with Histosols (HS) (Fig. 2A). Diplopods were more frequent on Cambisols (CM), and chilopods were rather common on Fluvisols (FL) and Gleysols (GL) (Fig. 2A).

From the Chilopoda, several species such as *Lithobius forficatus* L., 1758, *L. mutabilis* L. Koch, 1862, *L. cyrtopus* Latzel, 1880 and *L. erythrocephalus* C.L. Koch, 1847 colonised Cambisols and Leptosols, i.e. soils that provide good moisture conditions (Fig. 2B). In contrast, *Lithobius pelidnus* Haase, 1880, *L. austriacus* Verhoeff, 1937, *L. tenebrosus* Meinert, 1872 and *L. micropodus* (Matic, 1980) favoured Leptosols (LP), i.e. the soil type with a high content of skeleton and reduced moisture. Cambisols (CM) suited to *Lithobius burzenlandicus* Verhoeff, 1934. *Geophilus insculptus* (Attems, 1895) and *Lithobius biunguiculatus* Loksa, 1947 exhibited clear preference to Haplic Podzols and Entic Podzols, respectively. *Lithobius forficatus* L., 1758 a very common species, was recorded to a wide range between Haplic Podzols and Cambisols (Fig. 2B).

A wide range of diplopod species, *Leptoiulus trilobatus* (Verhoeff, 1894), *Ophyiulus pilosus* (Newport, 1842), *Tachypodoiulus niger* (Leach, 1815), *Cylindroiulus nitidus* (Verhoeff, 1891), *Brachyiulus bagnalli* (Curtis, 1845) and *Julus terrestris* L., 1758, showed a positive relationship with Leptosols (LP) (Fig. 2C). *Glomeris hexasticha* Brandt, 1833 was mostly found on Entic Podzols, where the process of podzolisation only occurs in the deeper soil layers. *Glomeris connexa* C. L. Koch, 1847 and *Haasea flavescens* (Latzel, 1884) have colonised Cambisols (CM), a soil which ranks among types rich in nutrients. The species prevailing in water-influenced soils was *Julus scandinavius* Latzel, 1884; its presence, however, was not as significant as that of *Glomeris pustulata* Latreille, 1804. Out of isopods, *Hyloniscus riparius* (C. Koch, 1838) was strongly bound to Histosols (HS). *Trachelipus ratzeburgii* (Brandt, 1833), *Porcellio scaber* Latreille, 1804 and *Oniscus asellus* L., 1758 were species that preferred Haplic Podzols (haZ) (Fig. 2D). *Protracheoniscus politus* (Koch, 1841) was found most frequently on Cambisols (CM) and *Ligidium germanicum* Verhoeff, 1901 mostly occurred on Entic Podzols (eP).

Impact of humus form

The Moder was the most frequently found form of overlying humus in the stands monitored (20 stands). At these stands, not all the horizons were fully developed, some of them being greatly reduced or absent. The Mor form was predominant at 14 sites, as a result of low pH and slow soil-forming processes; at these sites, all the horizons were present and the total overlying humus was accumulating to a depth of 15–18 cm. Only a single site (No. 35) was recorded to contain the Mull humus. By contrast, three sites contained the Tangle form (No. 19, 20 and 23) where overlying humus was extending to a depth of 60 cm (Table 1).

The form of the overlying humus considerably influenced various myriapod groups (Fig. 3A). For the Diplopoda, a positive correlation with the Moder form was registered for *Glomeris verhoeffi fagivora* (Verhoeff, 1906), *Glomeris hexasticha* Brandt, 1833, *Polyzonium germanicum* Brandt, 1837 and *Haasea flavescens* (Latzel, 1884). *Julus scandinavius* Latzel, 1884, *Brachyiulus bagnalli* (Curtis, 1845), *Leptoiulus trilobatus* (Verhoeff, 1894) and *Ophyiulus pilosus* (Newport, 1842) were the species found to a variable extent on the sites with Mor and Moder humus forms (Fig. 3B). Species with a positive response to Mor and Tangle included *Brachydesmus superus* Latzel, 1884, *Cylindroiulus nitidus* (Verhoeff, 1891), *Tachypodoiulus niger* (Leach, 1815), *Polydesmus denticulatus* C.L. Koch, 1847, *Glomeris pustulata* Latreille, 1804 and *Polydesmus complanatus* (L., 1761).

The Chilopoda was the group found mainly on sites with Mor and Moder humus. *Lithobius austriacus* Verhoeff, 1937, *L. erythrocephalus* C. L. Koch, 1847, *L. cyrtopus* Latzel, 1880, *L. nodulipes* Latzel, 1880, *L. pelidnus* Haase, 1880, *Geophilus insculptus* Attems, 1895 and *Strigamia acuminata* (Leach, 1814) occurred at sites with a predominance of the Mor form (Fig. 3C). A positive relationship with Moder was revealed for *Geophilus flavus* (DeGeer, 1778) and *Lithobius biunguiculatus* Loksa, 1947. *Lithobius borealis* Meinert, 1868 was the only species that exhibited a slightly increased occurrence on sites with the Tangle humus form.

Isopods were abundant on sites with Mor and Tangle humus forms. While *Ligidium hypnorum* (Cuvier, 1792) and *Hyloniscus riparius* (C. L. Koch, 1844) showed a positive connection to the Tangle form (Fig. 3D), *Protracheoniscus politus* (C. Koch, 1841), *Trachelipus ratzeburgii* (Brandt, 1833) and *Oniscus asellus* L., 1758 occurred at sites with a predominance of the Mor form. *Ligidium germanicum* Verhoeff, 1901 was confirmed to have a positive relationship to the Moder form, when the vector axis is nearly identical to that of the gradient. In Moder, 52% of individuals were caught using pitfall traps (33 species), while Tangle uncovered 4% of captured individuals (21 species), which could have been caused, to some extent, by the location of sites in valleys or migration. For most of the species, only several individuals were trapped.

Impact of altitude

We used canonical correspondence analysis to examine the impact of altitude on abundance of millipedes, centipedes and isopods. To simplify the analysis, the altitude was presented as four altitudinal vegetation zones (AVZ). Axis 1 explained 24.5% of the variance ($p = 0.001$) and Axis 2 explained 12.6% ($p = 0.001$). According to the ordination diagram (Fig. 4), diplopods occurred in all four AVZ. Significant abundance was revealed for *Polydesmus denticulatus* and *P. complanatus* (Fig. 4); these two species represented 19.8% of the total number of captured millipede individuals. Another important species is *Glomeris connexa*, which is more common in AVZ 5. Representatives of the Chilopoda occurred in AVZ 4 and AVZ 5 representing altitudes of 530-875 m. Several frequent species such *Lithobius forficatus*, *L. erythrocephalus*, *L. mutabilis* and *L. cyrtopus* did not show pronounced differentiation along the altitude

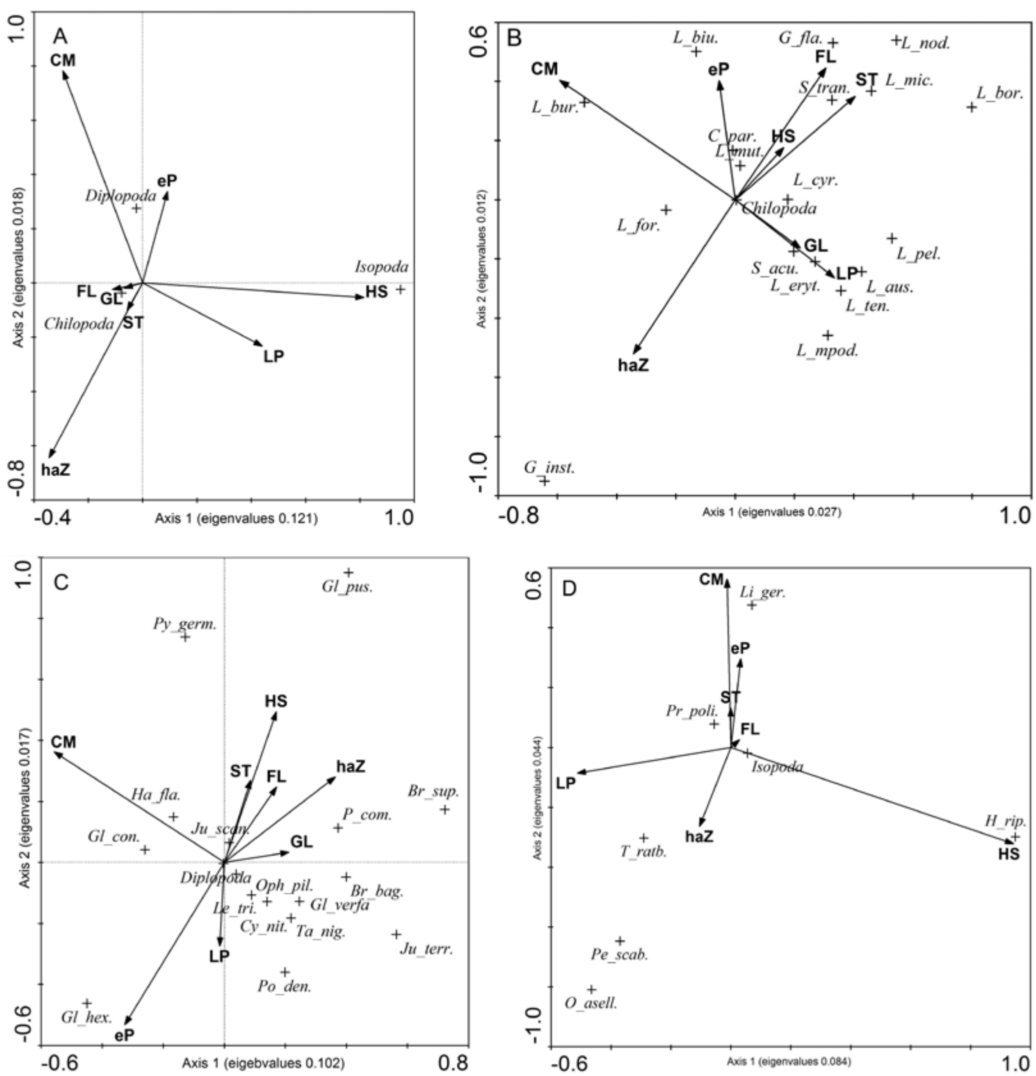

Fig. 2. Ordinations of species data for one animal groups (section A) and three animal groups (B – Chilopoda C – Diplopoda, D – Isopoda) by species using the CCA analysis, where the arrows represent the dominant ecological relationships together. The values listed on the species itself are marked with a cross. Generic points and key together reflect the distribution of species on each environmental variable

range. However, species such as *Lithobius austriacus*, *L. borealis* and *L. micropodus* occurred mainly in lower zones (Fig. 4). Isopods occurred mostly in zones lower than the altitude of 850 m; the most abundant representative *Protracheoniscus politus* occurred at the transition between AVZ 4 and AVZ 5.

Discussion

Impact of soil type

We studied the effect of different soil conditions on the distribution of the soil macrofauna of three groups, i.e. millipedes, centipedes and isopods. The overall distribution of the individual species substantially varied. The most abundant group was the Chilopoda, especially in Cambisols and Leptosols. This corresponds to the results of Jabin (2008) on areas with Dystric Cambisols in Germany as well as to the observations on soils with good aerobic regimes and with sufficient free living space (Kleber, Jahn 2007, Jabin *et al.* 2006). When comparing the occurrence of individual species in the studied area, we found an increased proportion of the Lithobiomorpha (*Lithobius pelidnus*, *L. austriacus*, *L. tenebrosus*, *L. micropodus*, *L. erythrocephalus*) and Geophilomorpha (*Strigamia acuminata*) on ranker soils. Leptosols are characterised by the presence of stones, aeration and good permeability, which favours the occurrence of the Chilopoda. The ground traps in localities with high skeleton and lower humidity have captured mostly species (*Lithobius pelidnus*, *L. tenebrosus*) characterised by a strong link to trunks of trees (Summers, Uetz 1979, Schatzmann 1990, Spitzer *et al.* 2010, Kula, Lazorík 2014). Members of the genus *Lithobius* (*L.*

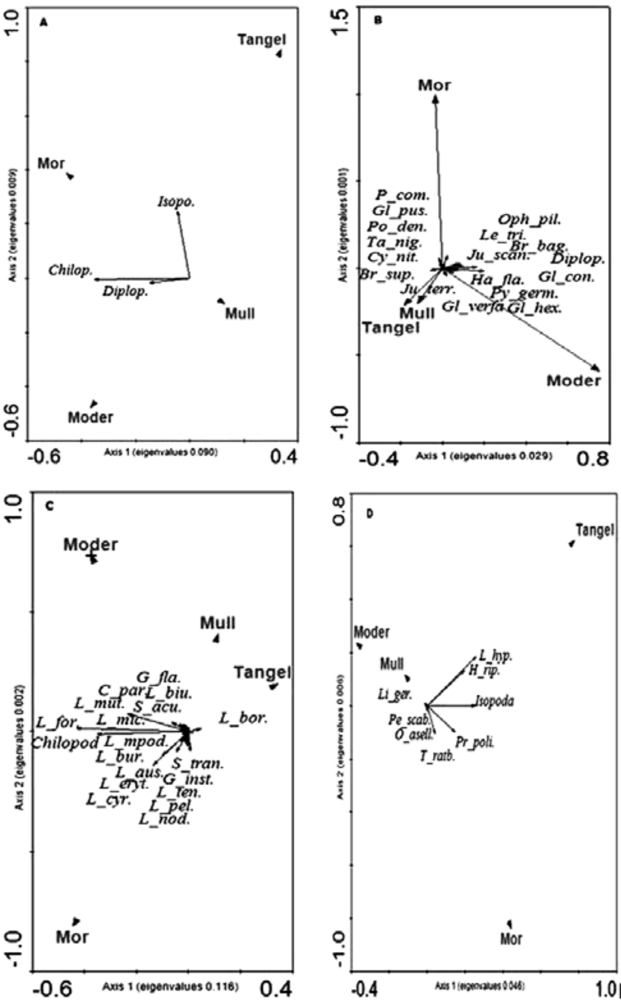

Fig. 3. Ordinations of species data for one animals groups (section A) and three animal groups (B – Chilopoda C – Diplopoda, D – Isopoda) by species using RDA analysis, where the triangles represent the dominant ecological relationships of soil humus forms. Other values listed themselves are indicated by arrows. Generic arrows reflect relationships to soil humus forms

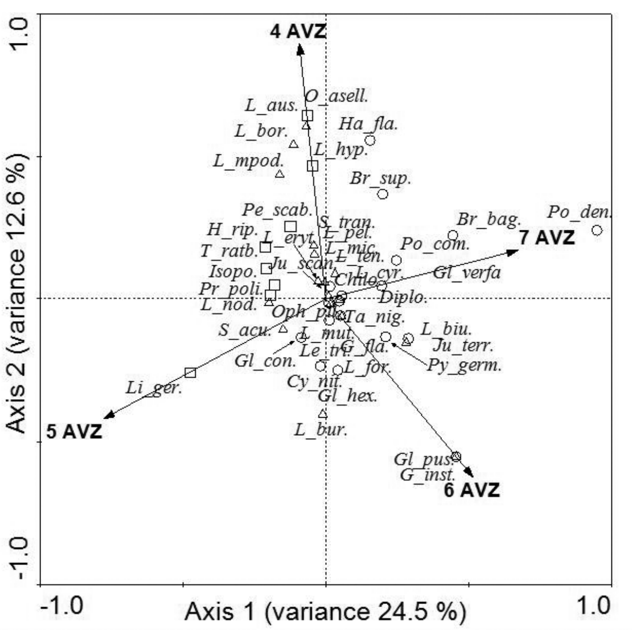

Fig. 4. Ordination diagram showing the distribution of the Diplopoda, Chilopoda and Isopoda in relation to the altitude (CCA). Two predetermined axes explaining 24.5% and 12.6%, respectively. The vector shows the altitude vegetation zone. Circle, Diplopoda; triangle, Chilopoda; square, Isopoda

borealis, *L. nodulipes* and *L. microps*) and *Strigamia acuminata* are represented in soils with suitable moisture regime, which is consistent with the data of Barber, Keay (1988). While *Lithobius borealis*, *L. microps* and *Strigamia acuminata* are connected to habitats affected by high levels of water, the peat species *Lithobius nodulipes* may occur mostly near springs (Spitzer *et al.* 2007).

Diplopods occur mostly at locations with Cambosols and Leptosols. However, the most numerous records were on Entic Podzols and Haplic Podzols. These soils are characterized by a reduction in pH, slowing the process of humification and accumulation of forest litter. On the prevalent soil type, Cambisols, the dominating species are *Glomeris connexa* and *Hassea flavescens*. In particular, *G. connexa* is defined in relation to the habitat as eurythermic to thermophilic, indifferent to bedrock (Stašiov *et al.* 2007) or as eurytopic woodland species, with preference to xeric shrub communities (Voigtländer 2011). Soils affected by water were dominated by *Julus scandinavius*, which is considered among the representatives adapted to multilevel habitats with vegetation and different humidity (Voigtländer 2011). As diplopods occurring in soils with lower levels of moisture are *Ophyiulus pilosus* and *Brachyiulus bagnalli* (Fründ, Ruszkowski 1989) while *Julus terrestris* is characteristic for inundated habitats (Bogyó *et al.* 2012, Jedryczkowsky 1992). The occurrence of *Tachypodoiulus niger*, being a species resistant to drought, in skeletal soils is in accordance with previous data (Haackert 1968).

Isopods are recorded in Histosols representing environment with the necessary levels of moisture. However, *Protracheoniscus politus* and *Trachelipus ratzeburgii* are captured on stony Leptosols. In addition, Cambisols also provide suitable habitats for the occurrence of these species. Notably, *Hyloniscus riparius* and *Lygidium hypnorum* occur to some extent at all locations but the most significant numbers of them are on Histosols.

We can confirm that representatives of diplopods, chilopods and isopods are suitable for bioindication of soil habitats. However, it is necessary to extend the knowledge of their ecological requirements and responses to a wider range of soil characteristics.

Impact of humus form

The humus layer involves a border area, in which there is contact between plants, animals and microbial organisms. Significant biological processes are underway as part of the woodland ecosystem (Ponge 2003), resulting in humus forms (Rusek 1975, Kubiena 1955) that in turn influence terrestrial plant and animal communities (Ponge *et al.* 1997, Ponge, 1999, Hooper *et al.* 2000). The Mull form is characterised by (i) rapid decomposition of tree litter as a result of operating animal decomposers and white-rot fungi, and (ii) soil fertility (Ponge 2003). The presence of macrofauna, particularly Lumbricidae, may transform the form of humus, e.g. Mull to Moder, thus creating variations in the Myriapoda coenose (Scheu, Poser 1996). Petersen, Luxton (1982) report that acidification of the soil results in the different soil fauna of the Moder form (mesofauna – Acari, Collembola) compared with the Mull form (macrofauna – Lumbricidae, millipedes, isopods). Increased acidity reduces fragmentation of beech litter mass and its decomposition and results in the formation of Mull due to the limited representation of macrofauna decomposers (Scheu, Wolters 1991).

The effect of humus forms on the myriapod fauna was studied in a broader area with relatively similar habitat characteristics (O'Neill, Reichle 1979, Petersen, Luxton 1982, Bornebusch 1930, Schaefer, Schauermann 1990, David *et al.* 1993).

The area of the mountains of Moravskoslezské Beskydy was affected by acid rain in the past. Predominant in the middle zones with occurrence of spruce stands is Moder (overlying humus with moderate accumulation of undecomposed organic matter and the onset of mineralisation processes, increased carbon content and a higher C to N ratio along with low pH). The decrease in the rate of mineralisation and decomposition arrives with the stand's age (45-95 years), while the metabolic activity and microbial activity recede (Chauve *et al.* 2005) and the fungal biomass increases. The monitored stands of spruce and beech in the mountains of Moravskoslezské Beskydy were older than 60 years and correspond to this stage of the soil process. The Mull form is reported from a spruce forest (Bernier, Ponge 1994) only at the stage of senescence.

Moder (33 myriapod species) primarily profiled through eurytopic species (*Lithobius forficatus*, *L. mutabilis*, *L. erythrocephalus*), through adaptive species (*Glomeris connexa*, *Leptoiulus trilobatus*) and the relict *Lithobius cyrtopus.* Mor (34 species of Myriapoda) can be described with the range of adaptable species such as *Protracheoniscus politus*. Mull created unfavourable conditions for the Myriapoda (11 species), with the shares of the eurytopic members *Lithobius mutabilis*, *L. forficatus* and *L. cyrtopus* being the most distinct. Tangle (21 species) can be characterised by *Hyloniscus riparius*, a species that was in fact absent in other forms of humus. The density and species diversity of Chilopoda, especially Geophilomorpha, and saprophagous macrofauna (Diplopoda, Isopoda) is reported to be higher in the Mull form of a restored stand compared with the Moder form of an adult spruce stand (Salmon *et al.* 2008), which is in accordance with the data of Athias-Binche (1982), Schaefer (1991b), David *et al.* (1993), Lavelle, Spain (2001), Schaefer, Schauermann (1990) and Ponge (2003). Generally, the species diversity is higher in dys-moder and amphi-mull of young woodland than in the dys-moder and amphi-mull forms of old stands (Salmon *et al.* 2008).

An elevated layer of undecomposed litter mass creates space for movement and provides a source of prey for predatory species of lithobiid centipedes (Scheu, Poser 1996). Similar findings are presented by David *et al.* (1993) from beech stands with increased carbon content. The increase in the Diplopoda abundance in the Moder form may be caused by the onset of fungal decomposers in the organic matter serving as food (Schaefer, Schauermann 1990).

The Mor form is recorded to have an increased presence of *Lithobius austriacus*, *L. erythrocephalus*, *L. cyrtopus*, *L. nodulipes*, *L. pelidnus*, *Geophilus insculptus* and *Strigamia acuminata*. The common factor for most of the listed species is their preference to soils with a thick layer of undecomposed organic matter with low pH, located in cold mountain and foothill areas (Jabin 2008, Tuf, Tufová 2008, Tajovsky, Wytwer 2009, Poser 1990, Blackburn *et al.* 2002, Tajovský 2001, Grgič, Kos 2005, Voigtländer 2005). Higher abundance of the Chilopoda in the Mor form with a thicker layer of overlying humus has been demonstrated by Schaefer, Schauermann (1990) due to ease movement in corridors formed by the Lumbricidae and food supply. For the Isopoda, David *et al.* (1993) have reported a higher representation in the Moder form, which is not confirmed in the present study. Our results show higher proportions of Isopoda in the Mor and Tangle humus forms, where soil moisture is the limiting factor as demonstrated by moisture measurements. The Chilopoda are reported by Jabin (2008) as occurring in soils with wood decaying on the soil surface, suitable microclimate conditions and the occurrence of natural prey.

Impact of altitude

Comparing the abundance of diplopods, chilopods and isopods from various altitudes, it is possible to find some significant differences. Previous studies (Tajovsky 1997, Sterzyńska *et al.* 2015) have demonstrated this for mountain wetlands in relation to populations of diplopods and isopods. As prominent representatives of the Diplopoda occurring at high altitudes, we can mention *Brachyiulus bagnalli*, *Polydesmus complanatus* and *P. denticulatus*, which have been recorded in high mountains (Read, Golovatch 1994, Špelda 1996, Kime, Golovatch 2000, Mikhaljova 2000). The total trend can be detected that isopods occur at lower altitudes, chilopods are frequent in middle altitudes, while diplopods are adapted to medium and higher altitudes.

Conclusions

According to our results, the soil type, the form of humus and the altitude are important factors for the distribution and abundance of epigeic species of Diplopoda, Chilopoda and Isopoda in forest soils in Beskydy Mountains. Cambisols and Leptosols contain more abundant macrofaunal communities, while Histosol and Stagnosols are the poorest soil types in relation to abundance of these three groups. The Moder humus form provides favourable conditions for the abundance and species diversity of myriapods and isopods. Mor humus form is also suitable for myriapods and isopods, with its thick layer of decomposed organic matter enabling shelter and food availability as well as providing conditions for mobility within the soil. Mull humus form is inhabited mostly by species tolerant to dry habitats. Tangel form is characterised by high accumulation of organic matter and good moisture regime, which is suitable for *Hyloniscus riparius* (Isopoda), which is suggested to be used as a bioindicator for wet soils.

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