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Factors Affecting Invertebrate Assemblages in Bryophytes of the Litovelské Luhy National Nature Reserve, Czech Republic

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Abstract: Invertebrates living in bryophytes were investigated to determine how the species of bryophyte and environmental factors affect them. 61 bryophyte samples were collected from which the animals were extracted by heat. In addition, a set of environmental variables was recorded for each sample. A total of 45 invertebrate species belonging to 13 higher taxonomic groups were identified from 15 bryophyte species. The richest assemblages of invertebrates were found in *Brachythecium curtum* growing on a decaying tree. The type of substrate and height above ground were the most important environmental factors affecting the distribution of invertebrates.

Key words: Chilopoda, Diplopoda, Oniscidea, Araneae, Pseudoscorpiones, Opiliones, Formicidae, Lumbricidae, Litovelské Pomoraví

Introduction

Bryophytes represent an important part of ecosystems. They play a pivotal role in peat bogs, forests, tundra, alpine ecosystems, spring areas, etc. and participate in photosynthesis, hydrological, chemical, decomposing and some other processes (Mägdefrau 1982, Vanderpoorten, Goffinet 2009). They have the ability to absorb water quickly and to release it gradually. As pioneer organisms they stabilize substrate, restrain erosion and produce litter (Longton 1992). Nowadays bryophytes are used as important bioindicators as they can indicate air and water pollution. They are also used in the monitoring of heavy metals, due to their ability to accumulate and retain heavy metals of up to 60 times elevated concentration (Vanderpoorten, Goffinet 2009).

Bryophytes also prevent their underlying substrate from drying-out; in the milder regions they represent a water refuge (Gerson 1982). Therefore, they often provide a shelter for aquatic invertebrates (e.g. Rotifera, Testacea), many of which are capable of adaptation to a regime of repeated drying and remoistening (Merrifield, Ingham 1998). The ability of bryophytes to provide a humid terrestrial microenvironment may have had a role in the evolution of dipterans (Gerson 1969). This may also explain the habitat preferences of bryobiont organisms, as they prefer the microclimate provided by mosses (Drozd *et al.* 2007). The ecological role of bryophytes lies also in their ability to protect invertebrates from climate oscillation. They provide insulation against rapid temperature and humidity changes (Merrifield, Ingham 1998). Their structure shapes

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available air spaces within a framework of plant tissue. Under extreme conditions, the survival and abundance of some invertebrates fully depend on the bryophytes present (Gerson 1969). Bryophytes can modify soil conditions and thereby affect the distribution of certain arthropods. Mites are among the most common species living in mosses with one group, Cryptostigmata, known as moss-mites due to their habitat (Gerson 1969). Other common invertebrate inhabitants of bryophytes are nematodes and tardigrades (Merrifield, Ingham 1998).

There are species, such as the crane fly *Dolichopeza* or mite *Eustigmaeus*, which oviposit their eggs in mosses (Gerson 1982). Cricket species *Pteronemobius palustris* and *Pteronemobius fasciatus* lay their eggs on *Sphagnum* (Gerson 1969). Some insects temporarily use bryophytes as a place to lay their eggs.

Bryophytes also serve as food for some invertebrates (Gerson 1969), such as beetles, orthopterans, collembolans, caterpillars or aphids. For example, mosses represent a food component of ground hoppers of genus *Tetrix*, who consume several species of mosses (Kočárek *et al*. 2008, 2011). As well, several detritophagous species (as millipedes, woodlice, earthworms) find food resources in bryophyte cushions.

Although some predators have the ability to hunt within mosses, mosses do provide good shelter for hiding from predators. Mosses can also be used as a camouflage by some invertebrates. A tipulid species *Trigoma trisulcata* lives in mountain streams where its larvae lives attached to the moss *Fontinalis antipyretica* (Gerson 1969) and the result of this association is a perfect mimicry as larvae resemble moss. Several bryophytes were found covering living curculionid beetles in New Guinea (Geressitt *et al.* 1968) as well as polydesmid millipedes in Columbia (Martínez-Torres *et al.* 2011).

Invertebrates can also be useful for mosses. *Dicranum flagellare* depends mostly on the dispersal of asexual branches to colonize disturbance gaps on decaying logs, and it has been found that forest slugs are a good dispersal vector (Kimmerer, Young 1995). Coprophilous species of flies can be enticed by the colour or secretions of coprophilous mosses of Splachnaceae and assist with the dissemination of spores (Gerson 1969). The important factor here is also the morphology of moss spores which are sticky and readily attach to the body of the fly.

The aim of the study is to describe the invertebrate communities inhabiting bryophytes in the Litovelské Luhy National Nature Reserve, Czech Republic, and to compare the influence of bryophyte species, size and thickness of the bryophyte cushion and selected environmental characteristics on the invertebrate assemblages.

Materials and Methods

Description of locality

The study was conducted in the Litovelské Luhy National Nature Reserve (49º 42' 30.5" N, 17º 5' 46.2" E, 208 m a.s.l.), which is a part of the Litovelské Pomoraví Protected Landscape Area, Czech Republic. Litovelské Luhy NNR has a total area of 344.45 ha, with an altitude span 229-231 m a.s.l. The centre of the reserve comprises the continental river delta of the Morava River with binding complexes of flood-plain forests, wet alluvial meadows and wetlands, and is located between the town of Litovel and the village Střeň. Flood-plain forest (*Querco-Ulmetum* association) is the dominant hard forest type but there are also stands of soft wood (*Salicetum albae* association). Dominant tree species are *Quercus robur*, *Fraxinus excelsior*, *Ulmus laevis* and *Populus nigra*. The age of the observed forest is ca. 130 years.

Sampling and extraction

In all, 61 bryophyte samples were collected in May 21st and October 5th 2007. Samples selected were biggish cushions formed by a single species of bryophyte. The extractions that were taken from the decaying tree and the ground were sampled together with a thin layer of substrate (bark / upper layer of soil). Samples taken from the living trees were mostly scratched off the tree into a net. Invertebrates were heat-extracted from the bryophytes in laboratory conditions using Tullgren funnels (Tuf, Tvardík 2005). Extracted invertebrates were then sorted, counted and, if possible, identified.

Measured parameters

Beside the **season** of sampling (spring, autumn), each sample was characterised by evaluation of several environmental parameters:

Bryophyte species –samples taken consisted of just one species, mixed cushions were ignored;

Size of sample – size (i.e. 20 × 20 cm, 5 × 20 cm or 5 × 15 cm, respectively) was chosen from the size of the bryophyte carpet;

Substrate – bryophyte samples were growing on either fallen decaying trees, living trees or on the ground;

Tree diameter – if the samples were taken from a log or tree, the tree diameter was measured;

Height above ground – was measured for all the samples except for the ones living on the ground;

Shading of the sampled bryophyte – was evaluated as a proportion of canopy closure using photographs taken towards the sky perpendicularly to the ground. Shading was scaled in percents (e.g. 80 % means that biggest part lies in shade, only 20 % in sun);

Bryophyte/sample area – was scaled from 1-4 (sample covered part of whole cushion: 1 = 100 %, 2 = 50-99 %, 3 = 20-49 %, 4 = 0-19 %);

Decay level – was scaled from 1-4 (1 = wood is hard, bark everywhere, 2 = wood is softish, bark on more than 50 %, 3 = wood is rather soft, bark on less than 50 %, 4 = wood is completely soft, without bark);

Thickness of the bryophyte cushion.

Statistical analysis

The quantitative data is analysed in the CANOCO programme for Windows 4.5© (Ter Braak, Šmilauer 1998). The effect of environmental parameters on the distribution of invertebrates at both species and higher taxonomic levels is evaluated by unimodal *canonical correspondence analysis* (CCA), and tested by Monte-Carlo permutation tests. To see the relations (dependences) between species and environmental factors from CCA analysis, we used *generalised additive models* (GAM) imaged in programme CanoDraw for Windows 4.0© (part of CANOCO software).

Results

Sampled invertebrate communities

In all, 15 species of bryophytes (Table 1) were found from 61 samples. *H. cupressiforme* was the most abundant species (13 samples). We evaluated 13 invertebrate groups in the moss samples. These groups were taxa at levels of classes (Gastropoda, Chilopoda, Diplopoda), orders (Isopoda, Araneae, Opiliones, Pseudoscorpiones, Acarina, Collembola), families (Formicidae, Lumbricidae, Enchytreidae) as well as an ecological group (insect larvae). The most abundant groups were Isopoda (439 specimens) and Diplopoda (240 specimens), and the least abundant were Opiliones (12 specimens) and Araneae (16 specimens). We identified 45 species in all: 9 species of Chilopoda, 7 of Diplopoda, 4 of Pseudoscorpiones, 6 of Isopoda, 4 of Opiliones, 6 of Lumbricidae, 4 of Formicidae and 5 of Araneae (juveniles were identified down to the genus or family level).

The moss species *B. curtum* has the highest mean number of invertebrate species per sample (7) and also the highest mean Simpson's index of diversity (0.7). *B. salebrosum* and *B. rutabulum* also possessed a high number of species per sample, 4 and 5.5 respectively. All three species of *Brachythecium* were found growing on decaying trees. *B. salebrosum,* growing on decaying trees, and *P. cuspidatum*, growing on both the ground and live trees, had one of the highest mean Simpson's index of diversity, 0.5.

A cluster analysis of dissimilarity of the 15 bryophyte species (Fig. 1) that takes into account the presence/absence of invertebrate species in these bryophytes has divided the species into two major groups. The first group of bryophytes (*A. serpens, I. alopecuroides, A. attenuatus, P. repens, B. salebrosum*, *H. trichomanoides*) and liverwort *M. furcata* consists of relatively rare bryophyte species (on the average 2.5 samples per bryophyte in this group) mostly growing on living trees, while the second group of mosses (*B. curtum, P. undulatum, E. hians, P. rostratum* and *P. cuspidatum*) consists of more frequent moss species (on the average 3.6 samples) found on the ground. Mosses growing on decaying trees were present in both groups. Standalone mosses *A. undulatum*, *B. rutabulum* and *H. cupressiforme* were the most frequent ones (on the average 8.3 samples) with a high number of species.

Environmental analysis of invertebrate groups distribution in moss cushions

According to analysis, the length of gradient in species data was high, for this reason we used the CCA model for evaluation of distribution of invertebrate groups (Fig. 2). The whole model was significant ($F = 2.956$, $p = 0.0020$), the first canonical axis shows 37.2 % variability; the second axis shows 20.9 %. According to the results of CCA, significant factors were the height above ground, bryophyte/sample area, season (i.e. spring vs. autumn), and living tree vs. decaying tree or ground (Table 2). All the other factors were not significant.

Table 1. List of invertebrate species extracted from moss samples with basic ecological characteristics. Abbreviations: D – dead tree, G – ground, L – live tree.

	Amblystegium serpens	*Anomodon attenuatus*	*Atrichum undulatum*	*Brachythecium curtum*	*Brachythecium rutabulum*	*Brachythecium salebrosum*	*Eurhynchium hians*	*Homalia trichomanoides*	*Hypnum cupressiforme*	*Isothecium alopecuroides*	*Metzgeria furcata*	*Plagiomnium cuspidatum*	*Plagiomnium rostratum*	*Plagiomnium undulatum*	*Platygyrium repens*
Chilopoda	0	3	6	1	3	1	1	3	6	0	1	1	3	2	0
Geophilus flavus (DeGeer, 1778)	-	-	-	-	+	-	+	-	+	-	-	-	-	-	-
Lithobius borealis Meinert, 1868	-	-	-	-	-	-	-	+	+	-	+	-	-	-	-
Lithobius erythrocephalus C. L. Koch, 1847	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lithobius forficatus Linnaeus, 1758	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-
Lithobius microps Meinert, 1868	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Lithobius mutabilis L. Koch, 1862	-	-	+	-	-	-	-	-	+	-	-	+	+	+	-
Lithobius spp. (juv)	-	+	+	-	+	+	-	+	+	-	-	-	-	-	-
Strigamia acuminata (Leach, 1814)	-	-	+	-	-	-	-	-	+	-	-	-	+	-	-
Schendyla nemorensis (C. L. Koch, 1836)	-	+	+	+	+	-	-	-	+	-	-	-	+	+	-
Diplopoda	1	0	5	2	4	2	2	2	1	0	0	1	3	1	1
Brachydesmus superus Latzel, 1884	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Glomeris tetrasticha Brandt, 1833	-	-	+	+	+	-	+	-	-	-	-	+	+	+	-
Leptoiulus proximus (Němec, 1896)	-	-	+	+	-	+	-	+	-	-	-	-	+	-	-
Melogona broelemanni (Verhoeff, 1897)	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-
Nemasoma varicorne C. L. Koch, 1847	-	-	-	-	+	+	-	-	+	-	-	-	-	-	+
Polydesmus denticulatus C. L. Koch, 1847	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-
Unciger transsilvanicus (Verhoeff, 1899)	-	-	+	-	+	-	+	-	-	-	-	-	-	-	-
Isopoda: Oniscidea	1	2	2	2	4	2	3	3	4	1	0	4	4	4	4
Androniscus roseus (C. Koch, 1838)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Hyloniscus riparius (C. Koch, 1838)	-	+	+	+	+	-	+	+	+	-	-	-	+	+	+
Porcellium collicola (Verhoeff, 1907)	-	+	+	-	+	+	+	+	+	+	-	+	+	-	+
Protracheoniscus politus (C. Koch, 1841)	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Trachelipus rathkii (Brandt, 1833)	+	-	-	-	+	+	-	+	+	-	-	+	+	+	+
Trichoniscus pusillus Brandt, 1833	-	-	-	+	+	-	+	-	+	-	-	+	+	+	-
Araneae	0	0	2	1	4	0	0	2	1	0	0	0	0	1	0
Clubiona sp.	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Diplocephalus sp.	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
Linyphiidae gen. sp.	-	-	+	+	+	-	-	+	+	-	-	-	-	+	-
Trochosa sp.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Xysticus sp.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Opilionida	0	0	0	0	1	1	2	0	2	0	0	1	0	1	0
Mitostoma chrysomelas (Hermann, 1804)	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Platybunus bucephalus (C. L. Koch, 1835)	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Rilaena triangularis (Herbst, 1799)	-	-	-	-	-	+	+	-	+	-	-	-	-	-	-
Trogulus tricarinatus (Linnaeus, 1767)	-	-	-	-	+	-	+	-	-	-	-	-	-	+	-
Pseudoscorpionida	0	0	1	0	1	1	0	1	2	0	0	0	0	0	1
Chernes hahnii (C. L. Koch, 1839)	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+
Pselaphochernes scorpioides (Hermann, 1804)	-	-	-	-	+	+	-	-	+	-	-	-	-	-	-
Neobisium sylvaticum (C. L. Koch, 1835)	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Neobisium carcinoides (Hermann, 1804)	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Hymenoptera:Formicidae	0	0	1	0	1	0	0	2	3	0	0	0	0	2	0

Lasius brunneus (Latreille, 1798)	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Lasius fuliginosus (Latreille, 1798)	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Leptothorax gredleri Mayr, 1855	-	-	-	-	-	-	-	+	+	-	-	-	-	+	-
Myrmica rubra (Linnaeus, 1758)	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-
Annelida: Lumbricidae	0	0	1	1	3	0	2	1	2	0	0	1	2	1	1
Aporrectodea caliginosa (Savigny, 1826)	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Dendrobaena octaedra Savigny, 1826	-	-	+	-	+	-	+	-	+	-	-	-	+	+	+
Dendrodrilus rubidus (Savigny, 1826)	-	-	-	-	+	-	-	+	+	-	-	-	-	-	-
Lumbricus castaneus Savigny, 1826	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Lumbricus rubellus Hoffmeister, 1843	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-
Octolasion lacteum (Örley, 1885)	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
main type of substrate	D	L	G	D	D	D	G	LD	DL	L	L	GL	G	G	DL
number of samples	2	2	6	1	6	2	6	4	13	1	1	3	5	3	6
number of species in all samples	2	5	18	7	21	7	10	14	21	1	1	8	12	12	7
mean number of species in a sample	1	3	4	7	5.5	4	2.8	5	2.9	1	1	3	3.2	3.3	1.7
mean Simpson´s index of diversity	0	0.4	0.4	0.7	0.3	0.5	0.3	0.3	0.3	0	0	0.5	0.4	0.3	0.2

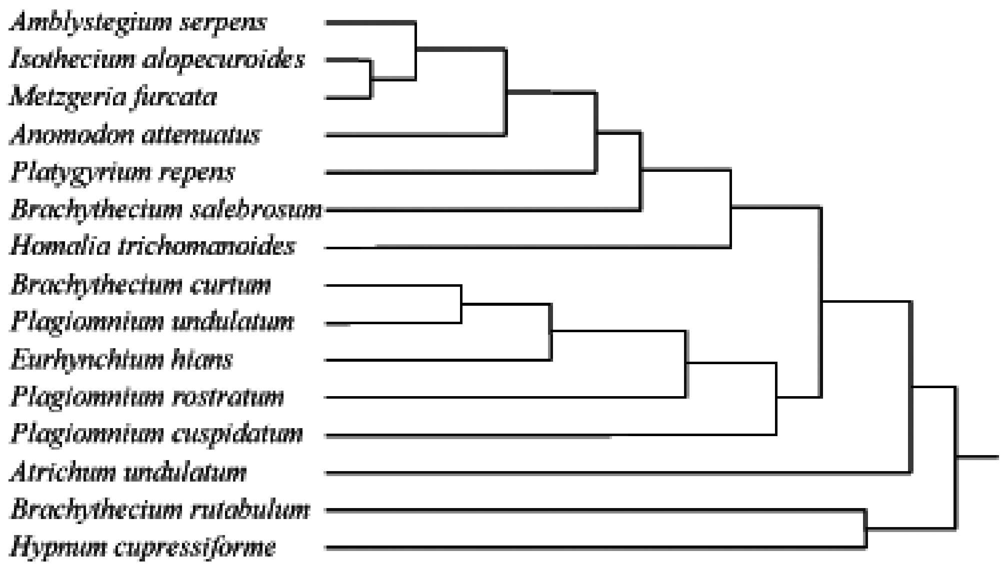

Fig. 1. Dissimilarity of bryophyte species according to presence/absence of invertebrate species in its cushions.

It is evident that the height above ground had a significant influence on Diplopoda as well as Gastropoda, insect larvae and Formicidae (Fig. 2). Collembola and Opiliones were numerous in the spring. The decay level of dead trees influenced the distribution of Pseudoscorpiones, even though this parameter was not significant.

Using GAM, we showed the influence and importance of parameters with significant effect to group distribution – height above ground and bryophyte/sample area. We discovered a significant relation between height above ground and 6 groups. Formicidae and Chilopoda preferred habitats on the ground or very near to it (Fig. 3a). Acari, Collembola and Pseudoscorpiones inhabited mosses growing at the base of a tree and dead fallen trees lying on the ground. Diplopoda were living in mosses, very high on trees, sometimes reaching as high as 160 cm above the ground. The relationship of this taxon with height above ground was the strongest one (Table 3). The relationship between bryophyte/sample area and invertebrates was significant for 6 groups (Table 3): insect larvae, Diplopoda, Chilopoda and Isopoda were numerous in the samples where we took a whole or almost whole moss carpet (Fig. 3b), i.e. they were abundant in small moss cushions contrary to Enchytreidae which were abundant in larger moss carpets.

Environmental analysis of invertebrate species distribution in moss cushions

Similarly we selected the CCA method to analyse the distribution of species in moss cushions

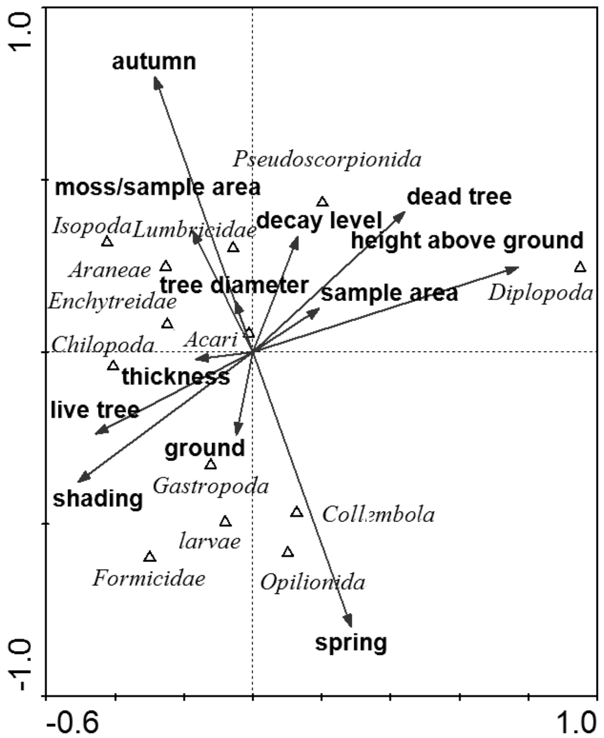

Fig. 2. Ordination plot of the influence of environmental parameters of bryophyte cushions on the distribution of invertebrate groups.

Table 2. Significance of environmental variables to prediction of abundance of invertebrate groups in moss pillows according to the CCA model.

Variable	Lambda	P	F
height above ground	0.26	0.002	7.41
spring	0.18	0.002	5.48
live tree	0.12	0.002	3.98
ground	0.08	0.008	2.69
moss/sample area	0.08	0.012	2.51
shading	0.04	0.162	1.44
decay level	0.04	0.152	1.37
thickness	0.03	0.34	1.06
sample area	0.03	0.65	0.76
tree diameter	0.01	0.822	0.56

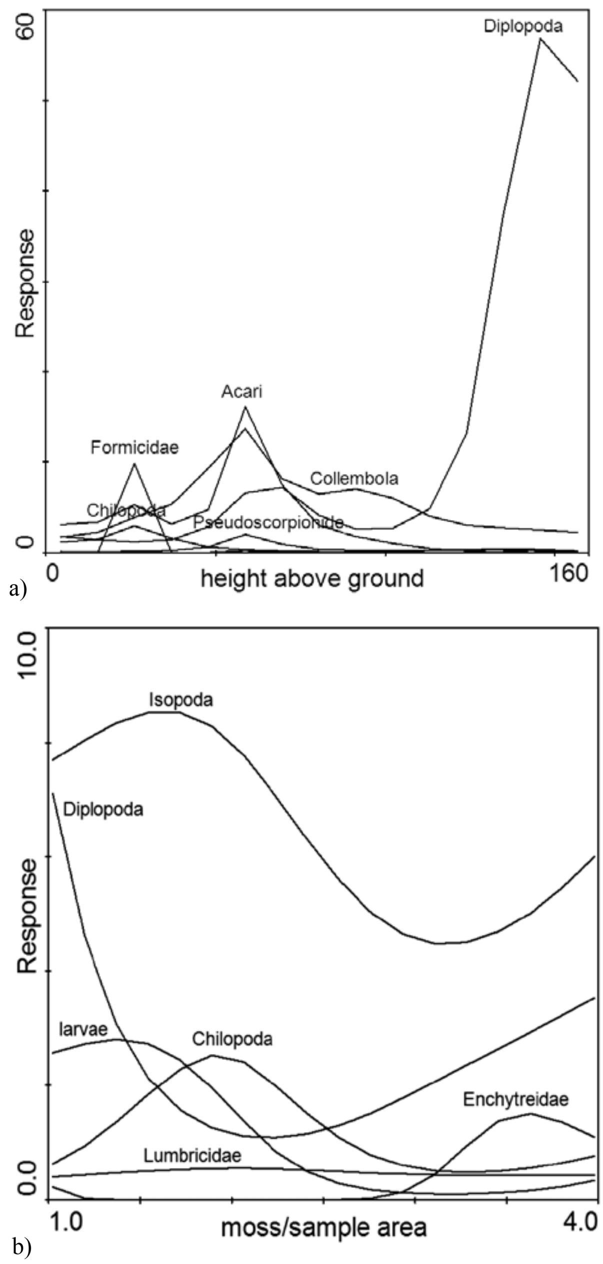

Fig. 3. Dependence of invertebrate group distribution in bryophyte cushions on: a) height above ground, b) moss/sample area of those cushions.

(Fig. 4): the whole model was significant (F = 2.264, p = 0.0020). According to the results of the CCA, significant factors predicting distribution of invertebrate species were height above ground, tree diameter, season (i.e. spring vs. autumn) and substrate (i.e. living tree and ground vs. decaying tree) (Table 4). Obviously, the group consisting of three *Lithobius* centipedes – *L. erythrocephalus, L. borealis* and *Lithobius* spp., and the ants *L. brunneus, L. fuliginosus* and *L. gredleri* were living on live trees (Fig. 4). At the opposite side of this graph we can see species that preferred decaying trees, such as the millipede *N. varicorne*, the pseudoscorpion *C. hahnii* and the earthworm *D. rubidus*. The harvestman *R. triangularis* was present in the spring season.

Height above ground showed a significant effect on 8 species (Table 5), and of those it had the strongest effect on the millipede *N. varicorne* (F = 37.53) and pseudoscorpion *P. scorpioides* (F = 22.49). The millipede *G. tetrasticha* and isopod *T. pusillus* were found on the ground, the centipedes *S. nemorensis, Lithobius* spp. and isopod *P. collicola* were found on the lower parts of the living trees or decaying trees lying close to the ground. In contrast, *N. varicorne*

Table 3. Influence of height above ground and moss/sample area on abundance of invertebrate groups (F-test of GAM). ** – p< 0.01; * – p< 0.05; n.s. – not significant. Only groups with a significant response to any factor are presented.

	Height above ground	Moss/ Sample area
Lumbricidae	n.s.	0.072*
Enchytreidea	n.s.	2.82*
Isopoda: Oniscidea	n.s.	0.113*
Acarina	4.50**	n.s.
Pseudoscorpionida	4.42**	n.s.
Diplopoda	13.51**	3.05*
Chilopoda	2.78*	3.56*
Colembola	2.81*	n.s.
Formicidae	3.23**	n.s.
Insect larvae	n.s.	4.99**

Table 4. Significance of environmental variables to prediction of abundance of invertebrate species in moss pillows according to the CCA model.

Variable	LambdaA	P	F
live tree	0.75	0.002	4.94
height above ground	0.65	0.002	4.63
spring	0.36	0.002	2.55
tree diameter	0.29	0.012	2.16
ground	0.23	0.014	1.7
shading	0.19	0.064	1.49
moss/sample area	0.19	0.078	1.43
decay level	0.14	0.424	1.02
thickness	0.1	0.644	0.82
sample area	0.1	0.794	0.73

Table 5. Influence of height above ground and tree diameter on abundance of invertebrate species (F-test of GAM). ** – p< 0.01 ; * – p< 0.05 ; n.s. – not significant. Only species with more than 10 specimens and a significant response to any factor are presented.

	Height above ground	Tree diameter
Lithobius mutabilis	n.s.	3.34**
Lithobius spp. juv	5.65**	4.38**
Schendyla nemorensis	2.43*	n.s.
Glomeris tetrasticha	2.41*	5.74**
Nemasoma varicorne	37.53**	21.25**
Hyloniscus riparius	n.s.	7.58**
Porcellium collicola	3.62**	5.10**
Trichoniscus pusillus	5.36**	4.98**
Trachelipus rathkii	3.44**	7.30**
Pselaphochernes scorpioides	22.49**	2.96**
Myrmica rubra	n.s.	0.366*

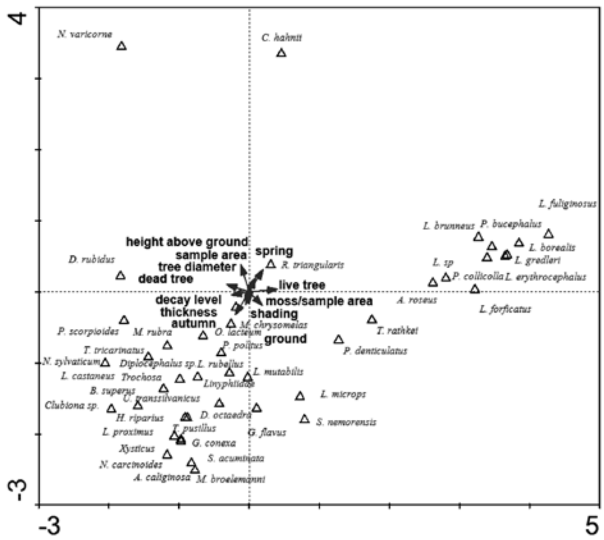

Fig. 4. Ordination plot of the influence of environmental parameters of bryophyte cushions on the distribution of invertebrate species.

was living in mosses growing approximately 160 cm above ground (Fig. 5a-b).

Tree diameter had a significant effect on 10 species (Table 5) and also had a very strong effect on *N. varicorne* (F = 21.25). Tree diameter had a big effect on *G. tetrasticha* (F = 7.58) and the isopod *T. rathkii* (F = 7.30) too. Smaller trees (tree diameters) were preferred by *G. tetrasticha* and *T. pusillus*, middle ones by the ant *M. rubra*, millipede *N. varicorne*, woodlouse *P. collicola* and pseudoscorpion *P. scorpioides*. The woodlice *H. riparius*, *T. rathkii*, centipedes *Lithobius* spp. and *L. mutabilis* preferred larger tree diameters (Fig. 5c-d).

Discussion

Comparison of bryophyte species according to their inhabitants

The Cluster analysis showed dissimilarity between mosses growing on living trees and the ground, but mosses growing on decaying trees were similar to both mosses growing on living trees and the ground. This depends on the decay level – when there is a lower decay level, mosses are more similar to ones on living trees. It is evident that congener species of the moss *Brachythecium* (*B. curtum, B. salebrosum* and *B. rutabulum*) growing on decaying trees (Fenton, Frego 2005) were highly dissimilar with respect to their inhabitants. Although thickness of their cushions is similar and high (ca. 2 cm), these species probably colonise the wood of different levels of de-

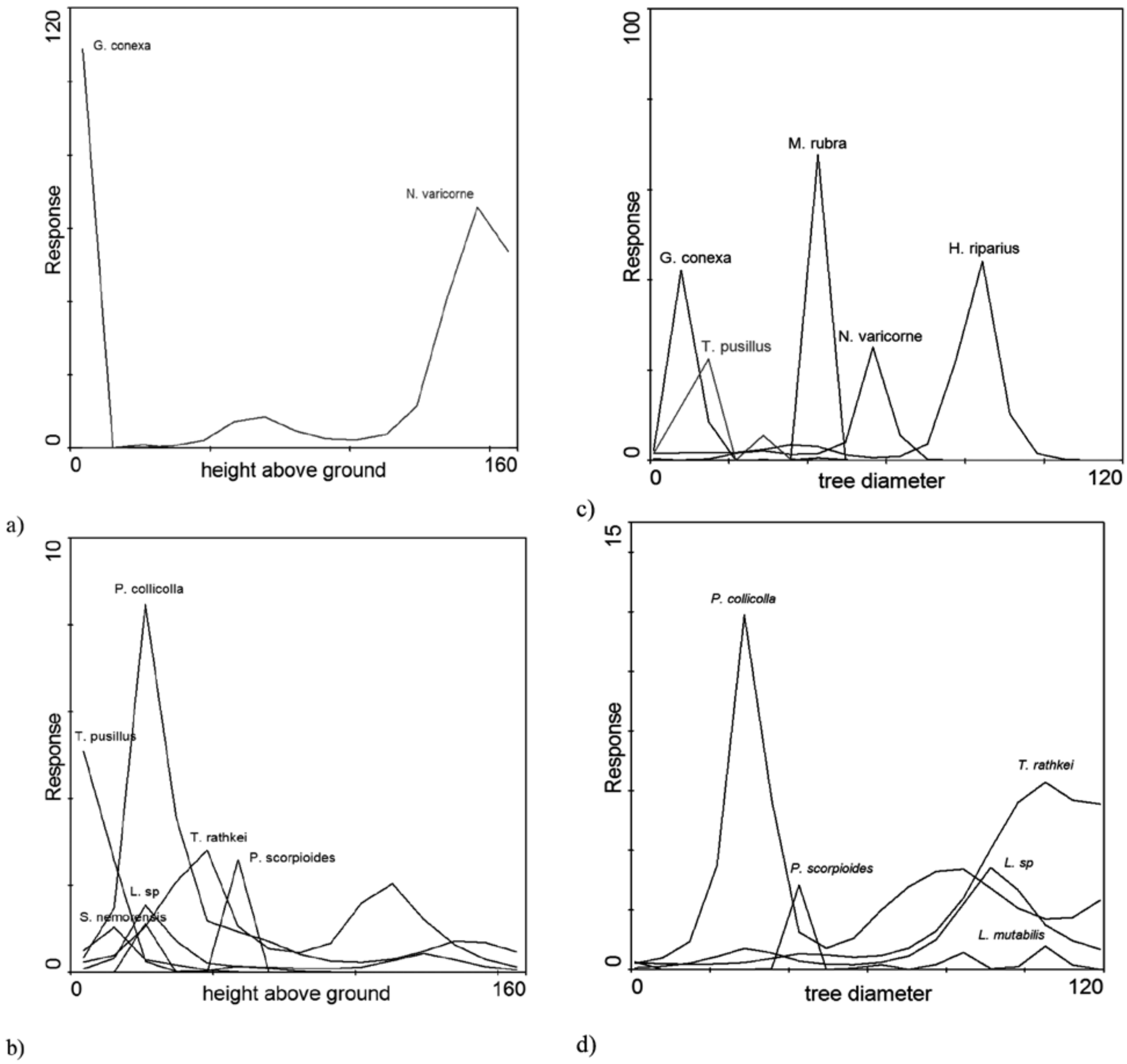

Fig. 5. Dependence of invertebrate species distribution in bryophyte cushions on height above ground: a) species with strong significant response, b) species with significant but weak response; and on tree diameter: c) species with significant strong response, d) species with significant weak response.

cay. Our data on mean decaying level of dead trees covered by *Brachythecium* supports this theory: *B. curtum*, inside a group of ground living mosses (cf. Fig. 1), covered a log of decaying level 3; *B. salebrosum* from live trees colonised a mosses group on a log of mean decaying level 2; and the standalone *B. rutabulum* covered a log of mean decaying level 2.5. These differences in preferences can reduce the interspecific competition of congeneric mosses.

The woodlice were most abundant in *Plagiomnium* samples growing on the ground. This is in line with the known preferences of *T. pusillus* and *H. riparius* with both species being mainly upper soil layer inhabitants (Tuf 2002, 2003).

Environmental factors affecting distribution of invertebrates

The analysis showed that the most significant factors were height above ground and bryophyte/sample area. The insect larvae, Diplopoda and Isopoda were abundant in smaller and more compact moss carpets (code 1 and partly 2 according to the bryophyte/sample area) probably because they found shelter against predators there.

It is very interesting that Diplopoda were mostly found higher in trees, around 160 cm above ground. Mosses growing at these heights were usually growing on dead, decaying trees, which are known to be suitable for Diplopoda (e.g. *N. varicorne*) as detritophagous species because their food is found there. While in the tropics there are arboricolous species of millipedes (e.g. Martínez-Torres *et al.* 2011), this behaviour is unusual in central European conditions. Although *N. varicorne* was found mainly in moss cushions covering decaying trees, it is extremely tolerant to high temperature and desiccation (Haacker 1968, Enghoff 1976). On the other hand *G. connexa,* although present at higher levels, was the most numerous in lower heights. Another member of the genus *Glomeris*, *G. tetrasticha*, is known as a species with relatively good tolerance to desiccation and is active throughout the whole day (Tuf *et al*. 2006). Presence of Formicidae in mosses near the ground is not surprising. All detected species build their nests mainly in soil, roots and fallen branches or in the base of trunks (e.g. Czechowski *et al.* 2002). We can expect that a high density of workers will be near a nest.

Juveniles of *Lithobius* (*Lithobius* spp. juv) look to avoid predation pressure of adult/bigger centipedes (Rawcliffe 1988) inhabiting the soil surface by escaping to mosses in the lower parts of living trees (or into deeper soil layers, not sampled in this project) (Biström, Pajunen 1989). The pseudoscorpion *P. scorpioides* was present in the same area as Acarina and that may be explained by the fact that the pseudoscorpion's food consists of Acarina, even hard-shelled Oribatidae (Kühnelt 1976).

Conclusions

As can be seen from the current study, bryophytes provide shelter to a large number of invertebrates. Our work showed that even though they are not rich in nutrients as other plants, they are still valuable habitats which invertebrates use in various ways. We found out that moss size and the height above ground are the most important factors that determine the spatial distribution. Cushions of mosses of the genus *Brachythecium* host the greatest diversity of invertebrates and the species with the richest community of invertebrates was *B. curtum* growing on the decaying tree. Of the environmental characteristics examined, the biggest role in invertebrate densities was height above ground, tree diameter and bryophyte/sample area. Bryophyte habitats higher above ground were the most preferred among millipedes, especially by the species *N. varicorne*. Acarina, Pseudoscorpiones and Formicidae stayed in the lower levels. In terms of tree diameter, the isopods *T. pusillus* and *P. collicolla* were in mosses living on smaller trees, whereas another isopod *T. rathkii*, together with the centipede *L. mutabilis* and juveniles of *Lithobius* spp. were found in mosses growing on larger trees.

This study contributes to a better knowledge of the ecology of both bryophytes and soil invertebrates. Bryophytes as an invertebrate habitat have not been studied thoroughly enough. They still, in a certain way, present a mystery. If we think that mosses were one of the first species to leave the aquatic environment and adjust to life on land we should be aware that, as we are facing climate changes, they could be one of the last resorts of some invertebrates. It is necessary to continue studying and observing them globally as a complex together with their invertebrate inhabitants.

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