

Occurrence of collembolan fauna in mofette fields (natural carbon-dioxide springs) of the Czech Republic

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Abstract

Mofette fields are naturally occurring, cold, volcanic gas vents that emit geogenic CO₂ through surface waters or the soil into the atmosphere. Soil CO₂ concentrations can reach 100% in the centre of these fields. High ground-level CO₂ concentrations can accumulate and become lethal traps, as evidenced by undecomposed vertebrate and invertebrate remains littering the areas. Nonetheless, plant growth is possible, and an adapted, partly azonal vegetation often occurs in mofette fields. The obvious impossibility of above-ground animal life in such fields led to the question of the occurrence of endogeic soil fauna, which are generally considered to be adapted to elevated soil CO₂ concentrations. For this reason a series of small pilot studies were undertaken in mofette fields in the north-western Czech Republic to ascertain (1) whether Collembola occur at all at such high soil CO₂ concentrations and (2) if so, does a specific collembolan fauna occur analogous to the mofettophilous vegetation of such habitats. Twelve collembolan species in, at times, substantial populations were found even at soil CO₂ concentrations approaching 100%. It can be assumed that these species are at least temporarily able to survive the anaerobic conditions. At 20–40% CO₂, 13 species were found and 23 species at ‘normal’ CO₂ concentrations, so that species richness decreased with increasing soil CO₂ concentration. The highest total densities were found at intermediate concentrations. Possibly azonal species (i.e. *Tullbergia simplex*, *Folsomia hissarica*) as well as a previously undescribed species (*Folsomia mofettophila*) were found only at high soil CO₂ concentrations. Many species registered at normal soil CO₂ concentrations were not found at higher concentrations. The registered species could thus be separated into mofettophilous, mofetotolerant and mofetotoxic species. Interestingly, males of otherwise parthenogenetic *Mesaphorura* species were regularly found at high soil CO₂ concentrations.

Keywords: Collembola, soil CO₂, mofette fields, natural carbon-dioxide springs, extreme habitats

1. Introduction

Mofette fields are geogenic, cold CO₂-exhaling gas vents occurring in regions of tectonic or volcanic disturbances (Pfanz 2008). The origin of CO₂ in the lithospheric mantle and the pathways the gas takes reaching the atmosphere are relatively well known (Bräuer et al. 2003, Geissler et al. 2005, Kämpf et al. 2007). As carbon dioxide is heavier than air, it forms gas

lakes when there are holes, depressions or valleys. Otherwise the gas becomes diluted within the atmosphere by convective or turbulent air (Pfanž et al. 2004).

When the gas flux within the soil is high and soil oxygen correspondingly low, even plants die off. Yet, if the CO₂ flux is lower and the concentrations in the rooting horizon of the plants do not exceed a certain threshold, several plants can grow within at least European mofette areas and some of them even seem to have advantages (Pfanž et al. 2007, Vodnik et al. 2006). Some plant species, among them *Carex nigra*, *C. acutiformis*, *Eriophorum angustifolium* or *E. vaginatum*, can be considered mofettotolerant. Other plant species, i.e. *Agrostis canina* ssp. *monteluccii*, have only been found in mofette fields (Selvi 1994) and thus are possibly mofettobiont.

Even for mofettotolerant species, soil CO₂ affects plant growth, structure and performance (Pfanž et al. 2004, Raschi et al. 1997). Turk et al. (2001) showed that in bog rush (*Juncus effusus*) the ratio of shoot length to width well as the amount of sclerenchymatous tissue changes as with increasing CO₂ concentrations. The number and size of leaves, the number and fertility of flowers, and the seed number may also change with the soil CO₂-regime (Pfanž et al. 2004, 2007, Pfanž 2008, Vodnik et al. 2002a,b, 2006).

It is assumed that, above concentrations of 15% CO₂, no animals can survive and carcasses of different animals (insects, reptiles as well as mammals) can often be found in mofette fields (Raschi et al. 1997, Pfanž et al. 2004, Paoletti et al. 2005). The activities of soil mammals, i.e. moles (*Talpa* spp.), has been observed to stop fairly sharply at the borders of high soil CO₂ concentrations (Pfanž 2008). On the other hand, soils normally contain CO₂ concentrations that are 10–100 times higher than normal atmospheric levels (Zinkler 1966, Dunger 1983, Lavelle & Spain 2005). Aboveground species of Collembola have been shown to strongly reduce locomotion at CO₂ concentrations of only 1–2%, whereby endogeic species maintain full activity even at CO₂ concentrations of 35% (Rüppel 1953, Moursi 1962, Zinkler & Rüssbeck 1986). However, Tosi & Parisi (1990) also identified viable populations of epedaphic species at high CO₂ levels. Thus, an ability of at least some soil-animal species to tolerate the high CO₂ concentrations of mofette fields can be expected.

Since the existence of endogenous soil fauna in mofette fields is practically unknown, a series of small pilot studies on soil Collembola in such an area in the Czech Republic were undertaken in 2008 and 2009. The first of these studies aimed primarily at answering whether Collembola can occur and survive at the high soil CO₂ concentrations. If this proved to be the case, these studies further asked if differences in the composition and structure of soil collembolan communities exist at different soil CO₂ concentrations and whether a specific mofettotolerant and/or azonal collembolan fauna (analogous to the plant communities) occurs in mofette fields.

2. Material and Methods

2.1. Study area

The pilot studies occurred in the Cheb Basin, Czech Republic, which is a shallow Neogene intracontinental basin formed at the intersection of the ENE-striking Eger Graben, the NW-striking Cheb-Domažlice Graben and the N-striking Regensburg-Leipzig-Rostock fault zone (Bankwitz et al. 2003, Kämpf et al. 2007). The CO₂-dominated degassing area (dimensions: ca. 7 km in length and ca. 0.5 km in width, located between the villages of Milhostov and Nebanice) is situated along the N-striking Počátky-Plesná fault zone (PPZ), being part of the eastern Cheb Basin (Bankwitz et al. 2003). The Počátky-Plesná Zone forms

an escarpment in Pliocene and Pleistocene sediments and was probably active since the late Pleistocene (Bankwitz et al. 2003). North of Milhostov, the Počatky-Plesná fault zone is seismically active at a length of approximately 10 km, causing so-called swarm earthquakes typical for areas in which mofette fields are found.

Within this region, the main study area (Hartousov Meadow; 12° 27' E, 50° 07' N, 423 m a.s.l.) is a meadow in which the vegetation is harvested regularly once or twice each year. The vegetation is very heterogeneous due to the varying composition of the soil gas atmosphere and consists of perennial, non-woody herbs and grasses mainly belonging to the Valeriano-Filipenduletum, the Arrhenateretalia or Molinietales types, depending on soil water and the prevailing soil gas regime. Up to 110 different plant species occur (Saßmannshausen & Pfanz unpubl.), with perennial grasses and sedges dominating. The soil surface is mostly covered by vegetation, except for sites at which the CO₂ flux exceeds certain thresholds, then the ground is bare of vegetation.

The prevailing soils have developed from fluvial Holocene sediments (Bankwitz et al. 2003) and are clayey silts, representing Reductosols/Cambisols. The Ah horizon reaches depths of ca. 20 cm. Soil pH values were generally around 4.1, but in the area can occasionally be reduced to values as low as pH 3 or 2 when soil CO₂ concentrations reach nearly 100% (Hohberg et al. in prep., Pfanz et al. in prep.). Soil moistures were on average between 18% and 27%, total soil C concentrations between 38 and 88 g/kg.

2.2. Sampling and laboratory methods

During these pilot studies, the sampling area was the location of ongoing botanical and geological studies. As the sampling plots generally were very small, and soil cores can potentially influence CO₂ output from mofette fields and thus alter the results of the other workgroups in the area, sampling for soil Collembola was severely limited. As the studies presented here were viewed as pilot studies, the limited sampling was determined to be adequate to answer the above-mentioned study questions.

Soil Collembola were sampled via soil cores (diameter: 5 cm, depths: see below), which were taken directly adjacent to measurement points for soil gases (CO₂ and O₂) carried out by the botanists working in the area. Soil gases concentrations were measured at four different soil depths (10, 20, 40 and 60 cm) at the intersection of botanical grids laid out over the study area. As a consequence, at each measurement point four values for each type of soil gas at each depth were obtained and were averaged afterwards. These values were used for characterising the sampling plots for Collembola as well as in the data analyses (see below). The soil gas measurements were carried out with the portable landfill gas analyser GA2000 (Geotechnical Instruments, Warwickshire, England).

The main sampling area was within the Hartousov Meadow (approximately 300 m by 200 m). The studies began with sampling of various plots (usually <0.25 m²) at the measurement points of 100% soil CO₂ concentration (Fig. 1). The plots, sampling depths and number of cores per plot are given in Table 1. Three of the plots were vegetated areas of the Hartousov Meadow. Within the Hartousov Meadow a further plot was in a small depression void of vegetation and bordered by *Eriophorum vaginatum* tussocks called Little Italy due to its shape. A similarly small (ca. 4 m²) unvegetated circular structure adjacent to the Hartousov Meadow, Weg Mofette, was briefly sampled. The Bog Mofette is located within the flooding zone of the Plesna River about 2000 m from the Hartousov Meadow. It is slightly elevated (100–850 cm) above a wet stand of *Filipendula* and *Urtica* and mainly dominated by *Deschampsia caespitosa*. The Nardus Mofette is a further 500 m distant within an occurrence of mat-grass (*Nardus stricta*).

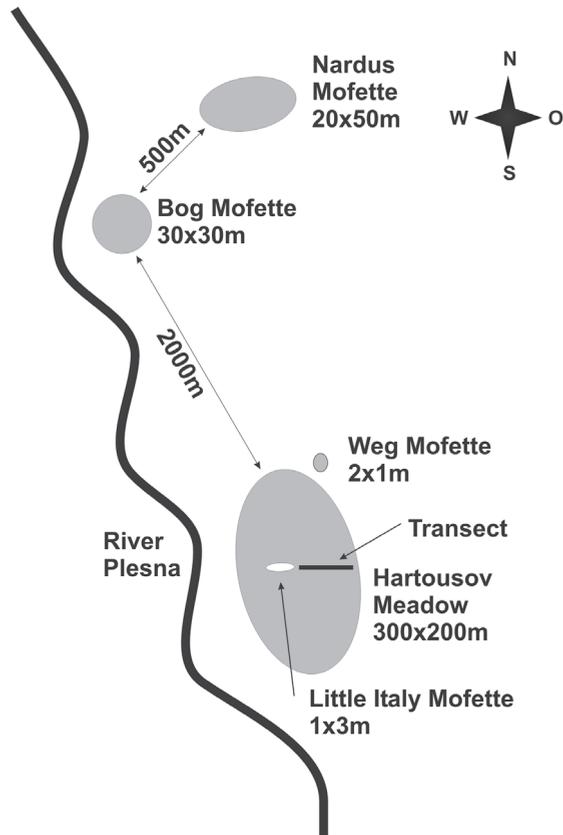


Fig. 1 Sketch of the study area showing the spatial relationship between the various study plots. For a description of the sampling plots, see text; for sampling details, see Table 1.

Tab. 1 Plots within which sampling for Collembola at 100% soil CO₂ concentrations occurred, including sampling dates, number of cores and sampling depth.

Plot	Vegetation present	Sampling date	Number of cores	Sampling depth
Hartousov-1	Yes	14 May 2008	3	0–5 cm
Hartousov-2	Yes	3 Sept. 2008	4	0–10 cm
Hartousov-3	Yes	3 June 2009	6	0–10 cm
Little Italy	No	3 Sept. 2008	1	0–5 cm
Weg Mofette	No	3 Sept. 2008	2	0–10 cm
Bog Mofette	Yes	2 Sept. 2008	4	0–5 cm
Nardus Mofette	Yes	3 June 2009	4	0–10 cm

Additionally in 2008, a few samples were taken in areas where various soil CO₂ concentrations were measured. In the Hartousov Meadow two samples each were taken on 14 May 2008 in plots where 'normal' (1.8%), 38% and 100% CO₂ were measured directly adjacent. In the Bog Mofette samples were taken on 3 Sept. 2008 in plots of 'normal' (1%; 5 samples), 20% (3 samples) and 100% CO₂ (4 samples).

Due to the non-systematic sampling in all of these areas, the various sites mentioned above are not considered to be replicates and are viewed here simply as separate sampling plots for registration of occurring species and are not analysed statistically. Only the CO₂ gradient plots of the Hartousov Meadow were included in the gradient study described next.

Based on the results of the sampling in May 2008 (including others not reported here), more systematic sampling was undertaken on 3 Sept. 2008 in a transect through the Hartousov Meadow representing a CO₂ gradient. In the 30 m long transect, two (pseudoreplicated) plots each at normal (0.1%), medium (22.1%) and high (100%) CO₂ concentrations were sampled with four cores each, which again were subdivided into the depths 0–5 and 5–10 cm. The plots were located within the transect at 0 m (directly adjacent to where 0.1% CO₂ was measured), 2.5 m (0.1% CO₂), 12.5 m (22.1% CO₂), 15 m (28.8% CO₂), 24 m (100% CO₂) and 26 m (100% CO₂).

In the laboratory the soil Collembola were extracted from the samples on the day after field sampling in Berlese-Tullgren funnels over 5 days at 20–22 °C. The samples were kept as intact as possible and were placed inverted in the funnels, i.e. with the sample upper surface placed downward. The animals were extracted sample-specifically into a fixation and conservation agent (modified Törne mixture: 50% isopropanol with 3% glacial acetic acid and 0.3% formalin; Dunger & Fiedler 1997). Collembola were sorted under a stereomicroscope at maximally 40x magnification, embedded in microscopic cavity slides in 90% aqueous lactic acid solution and determined to species level using a differential interference contrast microscope (Leica DM2500) at maximally 1000x magnification. Species determination followed mainly Fjellberg (1998, 2007), Potapov (2001), Thibaud et al. (2004), Zimdars & Dunger (1994) as well as generic revisions and original descriptions.

2.3. Statistical analyses

Since a main study question was simply whether Collembola can occur at the high soil CO₂ concentrations of mofette fields, species identity was the most important registered parameter. Due to the different sampling limitations and thus heterogeneous sampling effort in the different plots, for comparative purposes species abundances were extrapolated to average densities (individuals m⁻²) for each plot.

Since only the transect of the CO₂-gradient in the Hartousov Meadow was sampled systematically with sufficient, albeit low sample numbers, only the results from these plots were analysed statistically to obtain first impressions of CO₂-related differences in the collembolan assemblages. To test for significant spatial differences in the collembolan communities, the data on total abundances and species richness was submitted to a variance analysis with sampling plot (= CO₂ concentration) as the main factor. Due to the non-normal distribution of soil animals, differences in the densities and species richness (as individual and species number per sample, respectively) between sampling sites were tested for significance using a non-parametric one-way ANOVA for multiple observations (= samples) per cell (= sampling site) (modified Friedman test; Zar 1999). This ANOVA is based on ranked per sample data for each sampling site, on the χ^2 rather than the F distribution and can easily handle unbalanced sampling designs. A post-hoc Tukey-like multiple comparison procedure for this

non-parametric ANOVA (Zar 1999) tested for significant differences between sampling sites.

As a first test of community dependence on CO₂ concentration, correspondence analyses were carried out on the available environmental and individual species' abundance data (log+1 transformed) of the Hartousov Meadow gradient using CANOCO v.4.5 (Leps & Smilauer 2003). Since gradient lengths of detrended correspondence analyses were well above 4, the species 'reactions' were assumed to be unimodal and canonical correspondence analyses (CCA) were performed. Rare species were thereby downweighted and the results centred on species. To visualise the relationship between CO₂ concentration and species occurrences, CO₂-concentration isolines were plotted onto the species-ordination diagram by a regression of the CO₂ values of the individual samples using the local linear Loess model of CANOCO.

3. Results

At the 100%-CO₂ sampling sites, a total of 22 species were registered (Tab. 2). At most sites, only 1 or 2 species were found. However, at two sampling dates in the Hartousov Meadow multiple species were recorded (13 and 7, respectively). This was partly due to

Tab. 2 Collembolan species and their average densities (in individuals m⁻²) found in the various plots of 100% soil CO₂ concentrations (for plot characteristics and sampling dates, see Tab. 1).

	Hartousov-2	Hartousov-1	Hartousov-3	Nardus	Little Italy	Bog	Weg
<i>Ceratophysella</i> Börner, 1932 sp. juv.			150				
<i>Desoria trispinata</i> (MacGillivray, 1896)			590				
<i>Desoria violacea</i> (Tullberg, 1876)						220	
<i>Folsomia</i> cf. <i>hissarica</i> Martynova, 1971				440			
<i>Folsomia manolachei</i> Bagnall, 1939	330						
<i>Folsomia quadrioculata</i> (Tullberg, 1871)			9,990				
<i>Friesea mirabilis</i> (Tullberg, 1871)	110						
<i>Isotomiella minor</i> (Schäffer, 1896)	330						
<i>Lepidocyrtus cyaneus</i> Tullberg, 1871	220						440
<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)						220	
<i>Lepidocyrtus lignorum</i> (Fabricius, 1775)	3,090		440				
<i>Mesaphorura hylophila</i> Rusek, 1982	110						
<i>Mesaphorura macrochaeta</i> Rusek, 1976			290				
<i>Metaphorura affinis</i> (Börner, 1902)	990						
<i>Proisotoma minima</i> Absolon, 1901		290			2,550		3,530
<i>Protaphorura armata</i> (Tullberg, 1869)			2,650		1,020		
<i>Protaphorura pannonica</i> (Haybach, 1960) s. str.	110						
<i>Pseudosinella alba</i> (Packard, 1873)	660						
<i>Sminthurides schoetti</i> Axelson, 1903	660		150				
<i>Sminthurinus aureus</i> (Lubbock, 1862)	110						
<i>Sphaeridia pumilis</i> (Krausbauer, 1898)	1,980						
<i>Xenylla boernerii</i> Axelson, 1905 & sp. juv.	110			440			
Total densities	10,690	290	14,260	880	3,570	440	3,970

increased sampling effort, but the increased species richness at these sites and dates were unproportionally higher than the increased number of samples. Individual densities were generally very low at the sampled sites, but again in the Hartousov Meadow densities reached $> 10,000$ Ind. m^{-2} (Tab. 2). Most of the registered species were found in only one of the sites and in low individual numbers. Only *Proisotoma minima*, for instance, occurred in three different sites and at different dates.

First sampling within different areas of the Bog Mofette revealed general small-scale differences in the collembolan communities at different soil CO_2 concentrations. Within this area, the number of registered species increased from 2 to 18 species with decreasing soil CO_2 concentrations (Tab. 3). At the same time total collembolan densities increased. However, the highest densities of $<100,000$ Ind. m^{-2} were revealed at medium CO_2 concentrations (ca. 20%) due to strong populations of, i.e., *Desoria violacea* and *Folsomia manolachei* (Tab. 3). Interestingly, the samples from normal CO_2 concentrations and those of the higher concentrations had almost no species in common.

Tab. 3 Species and their densities (individuals m^{-2}) found on 2 Sept. 2008 in plots of different measured soil CO_2 in the Bog Mofette.

	1% CO_2	20% CO_2	100% CO_2
<i>Ceratophysella scotica</i> (Carpenter & Evans, 1899)	1,587		
<i>Choreutinula inermis</i> (Tullberg, 1871)	705		
<i>Desoria tigrina</i> Nicolet, 1842		294	
<i>Desoria violacea</i> (Tullberg, 1876)		77,300	220
<i>Folsomia bisetosa</i> Gisin, 1953		1,175	
<i>Folsomia quadrioculata</i> (Tullberg, 1871)	1,763		
<i>Folsomia manolachei</i> Bagnall, 1939		15,577	
<i>Friesea mirabilis</i> (Tullberg, 1871)	1,234		
<i>Isotoma viridis</i> Bourlet, 1839	529		
<i>Isotomiella minor</i> (Schäffer, 1896)	882		
<i>Isotomurus palustris</i> (Müller, 1776)	1,410		
<i>Lepidocyrtus cyaneus</i> Tullberg, 1871	705	882	
<i>Lepidocyrtus lignorum</i> (Fabricius, 1775)	3,174		
<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)			220
<i>Megalothorax minimus</i> Willem, 1900	1,940		
<i>Mesaphorura tenuisensillata</i> Rusek, 1974	353		
<i>Neanura muscorum</i> (Templeton, 1835)	176		
<i>Neelides minutus</i> (Folsom, 1901)	1,940		
<i>Parisotoma notabilis</i> (Schäffer, 1896)	4,761		
<i>Pogonognathellus flavescens</i> (Tullberg, 1871)	4,409		
<i>Protaphorura armata</i> (Tullberg, 1869)		8,817	
<i>Protaphorura quadriocellata</i> (Gisin, 1947)	176		
<i>Sminthurides malmgreni</i> (Tullberg, 1876)	176		
<i>Sminthurides schoetti</i> Axelson, 1903	5,114		
Total densities	31,034	104,045	440

These faunal differences between areas of differing soil CO₂ concentrations separated by only a few metres were also observed after somewhat more systematic sampling in the Hartousov Meadow. Combining all sampling dates, species richness significantly increased from 1 to 18 species per plot with decreasing soil CO₂ concentrations ($\chi^2 = 10.826$, $P = 0.004$; Fig. 2). Total densities increased from approx. 5,000 Ind. m⁻² next to 100% CO₂ measurements to on average 15,000 Ind. m⁻² at medium CO₂ concentrations (25–38%) (Fig. 3). Again, intermediate densities were found at near-normal CO₂ concentrations. Only the densities at 100% were significantly lower than the other CO₂ concentrations ($\chi^2 = 8.234$, $P = 0.016$), with no significant differences between intermediate and normal CO₂ concentrations.

The CCA analysis of the Hartousov Meadow revealed strong correlations between soil CO₂ concentration measured in the close proximity of soil samples and collembolan community. The eigenvalue of axis 1 and correlations as well as explained variance of both axes were relatively high (axis 1: eigenvalue: 0.457, species-environmental correlation: 0.885, explained variance: 46.7%; axis 2: eigenvalue: 0.261; species-environmental correlation: 0.812; explained variance: 26.6%). The strongest environmental vectors were for soil CO₂ and O₂ concentrations, which pointed in opposite directions (results not shown). Other environmental factors with relevant vectors were month of sampling and sampling depth. These analyses

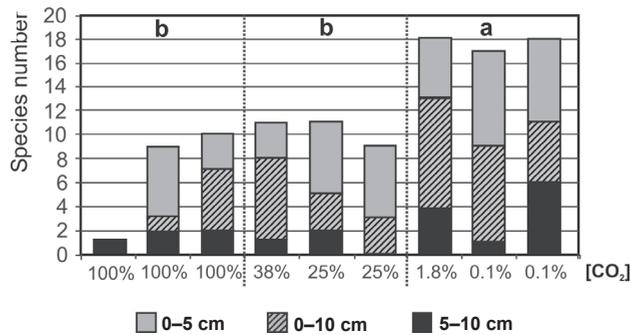


Fig. 2 Average collembolan species richness of the sampling plots from the CO₂-concentration gradient (sampling from both May and September 2008) of the Hartousov Meadow. Three plots each from high (ca. 100%), medium (25–38%) and ‘normal’ (0.1–1.0%) soil CO₂. Different letters denote significantly different species richness (total samples 0–10 cm depth) of the three CO₂ levels.

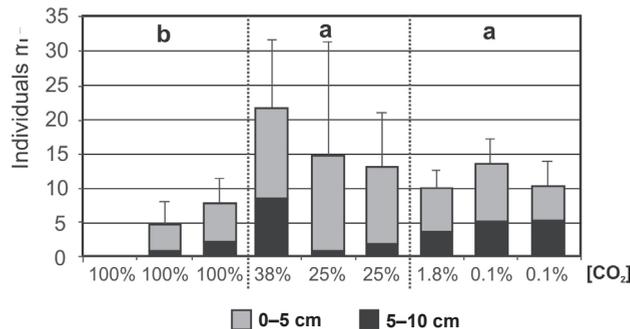


Fig. 3 Average collembolan densities of the sampling plots from the CO₂-concentration gradient of the Hartousov Meadow. Details as in Fig. 2.

showed an obvious distribution of species occurrence along the CO₂-gradient (Fig. 4). Most species corresponded to 'normal' soil CO₂ concentrations on the left-hand side of the diagram. While a number of species corresponded to intermediary concentrations or were widely distributed and plotted near the origin of the diagram, only a few species corresponded to high CO₂ concentration on the right-hand side of the diagram.

Based on these results, it was possible to create an ordination table of species in relation to their occurrence at different soil CO₂ concentrations within the Hartousov Meadow (Tab. 4). Many species found at high CO₂ levels were not found in the samples from 'normal' concentrations (i.e. *Proisotoma minima*, *Desoria violacea*, *Folsomia mofettophila* or *F. ancestor*). Of these species *F. mofettophila* is new to science (Schulz & Potapov 2010). Conversely, many species were only found at normal but not in higher CO₂ concentrations (i.e., *Friesea truncata*, *Metaphorura affinis*, *Mesaphorura hylophila*, *Lepidocyrtus ruber*, *Pseudosinella alba*, to name only the most abundant). Only some species were registered throughout all CO₂ concentrations (i.e. *Folsomia quadrioculata*, *Isotomiella minor*, *Protaphorura armata*, *Lepidocyrtus cyaneus*). An interesting sidenote is that of the individuals found at high CO₂ concentrations of otherwise parthenogenetic species (*Mesaphorura macrochaeta*, *Mesaphorura tenuisensillata*), approximately 10% were males.

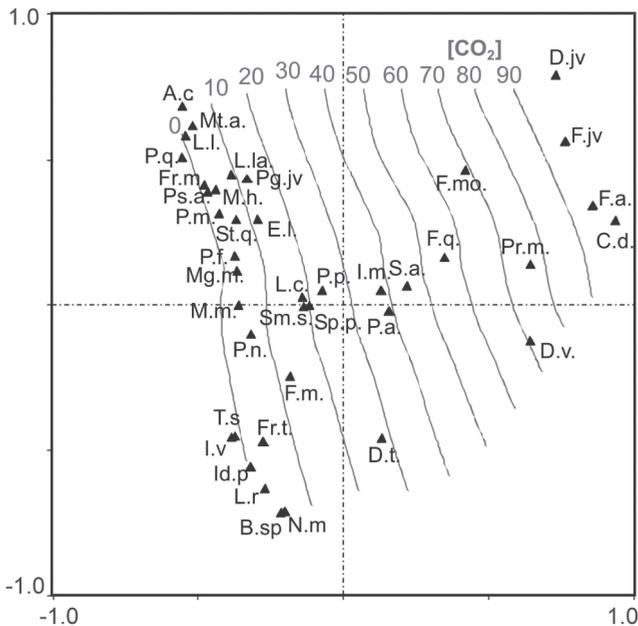


Fig. 4 CCA plot of the registered collembolan species' abundances from the CO₂-concentration gradient of the Hartousov Meadow. Abbreviations of species names given in Table 4. In grey are the CO₂-concentration isolines plotted in the ordination space in relation to the species' occurrences.

E.l.	<i>Entomobrya lanuginosa</i> (Nicolet, 1842)	220	441
Fr.t.	<i>Friesea truncata</i> Cassagnau, 1958	220	220 1,323
M.h.	<i>Mesaphorura hylophila</i> Rusek, 1982		220 661
E.jv	<i>Entomobrya Rondani</i> , 1861 sp. juv.		1,543
L.r	<i>Lepidocyrtus ruber</i> Schött, 1902		220
B.sp	<i>Bourletiella</i> Banks, 1899 sp. juv.		220
N.m	<i>Neanura muscorum</i> (Templeton, 1835)		661
Id.p	<i>Isotomodes productus</i> (Axelson, 1906)		220
I.v	<i>Isotoma viridis</i> Bourlet, 1839		220
T.s	<i>Tullbergia simplex</i> Gisin, 1958		1,763 441
Mt.a.	<i>Metaphora affinis</i> (Börner, 1902)		3,747
St.q.	<i>Stenaphorura quadrispina</i> Börner, 1901		220
L.l.	<i>Lepidocyrtus lignorum</i> (Fabricius, 1775)		220
A.c.	<i>Arrhopalites caecus</i> (Tullberg, 1871)		220
L.la.	<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)		220
Ps.a.	<i>Pseudosinella alba</i> (Packard, 1873)		661 1,543
Fr.m.	<i>Friesea mirabilis</i> (Tullberg, 1871)		220 1,323
P.q.	<i>Protaphorura quadriocellata</i> (Gisin, 1947)		220
I.jv	<i>Isotoma</i> Bourlet, 1839 sp. juv.		441
Mg.m.	<i>Megalothorax minimus</i> Willem, 1900		220
P.f.	<i>Protaphorura fimata</i> (Gisin, 1952)		1,102
P.m.	<i>Protaphorura meridiana</i> (Gisin, 1952)		1,323
X.jv	<i>Xenylla</i> Tullberg, 1869 sp. juv.		220

4. Discussion

Studies of the effects of high natural CO₂ emissions from mofette field on soil organisms are practically non-existent. Of the few published reports, Cotrufo et al. (1999) found severe negative effects on soil fauna at extreme CO₂ concentrations. Yeates et al. (1999) examined the nematode fauna in mofette fields and observed significant decreases in total abundance and diversity, but also increases in the dominance of bacteriovores. Thus, the present studies represent first species-level community investigations of the soil collembolan fauna at different CO₂ concentrations in mofette fields.

Despite the necessarily minimal sampling design, the results of these pilot studies unequivocally show that a specific CO₂-influenced soil collembolan fauna exists in mofette fields. Firstly, Collembola apparently occur at very high soil CO₂ concentrations. The methods employed here cannot prove that the registered individuals were active at such high CO₂ levels. Estimation of CO₂ concentrations in the extracted soil cores may also not be perfect. Subsequent investigations have shown high variability of CO₂ concentrations in the field at very small spatial scales (centimetres), especially within the 0–5cm layer of soil (Hohberg et al., in prep.). Furthermore, although the samples were capped tightly during transport, a reduction of the CO₂ concentrations and some increase in soil O₂ levels, especially during the subsequent short extraction procedure, is likely. Nonetheless, very high CO₂ concentrations in the soil samples during sampling were highly probable, so that the species found in these samples did experience high CO₂ levels. They necessarily were active during the dynamic extraction procedures, proving their viability. Despite the lack of proof of activity at very high CO₂ concentrations, the point remains that the collembolan species found here were able to survive high CO₂ output and at the least became active again at low output periods.

Secondly, as in plant communities of mofette fields, a number of species not typical for the zoogeographical region were found only in the high CO₂-concentration plots. For instance, *Folsomia ancestor*, described from the Magadanskaya region from a *Dryas* community and birch wood with *Calamagrostis*, is normally distributed in northern Asia (Potapov & Babenko 2000). Further records are only from several biotopes of the type locality. *Tullbergia simplex* is known only from the Arctic tundra (Fjellberg 2007) or, more rarely, alpine habitats in Austria (Haybach 1971). *Folsomia hissarica* is known only from the region around the type locality (Middle Asia, Tadjikistan, in moss of rocks and litter under stones, Potapov 2001). These species may thus possibly be considered mofettotolerant azonal species. The occurrence of azonal species appears to be typical for mofette fields (Selvi 1994). *Folsomia mofettophila* is a species new to science described from the Hartousov mofette meadow (Schulz & Potapov 2010). It is a member of the circumpolarly distributed *Folsomia bisetosa* group (Potapov 2001). Baring further records, *F. mofettophila* may possibly even represent a specialized mofettobiont species.

Furthermore, in the samples taken from high soil CO₂ concentration, an altered species composition was found relative to the normal CO₂ samples. Many species were not found at high concentrations and thus are probably intolerant of highly increased CO₂ (mofettotoxic species). Some species were registered at many CO₂ concentrations, but with their highest abundances at elevated CO₂ concentrations, i.e. *Folsomia quadrioculata*, *Isotomiella minor*, *Desoria tigrina* or *Protaphorura armata*. These all are common and abundant species occurring in a large variety of habitats without clear preferences (Potapov 2001, Fjellberg 2007). Their distribution in the present studies show them to be CO₂ tolerant. On the other hand, a number of otherwise common species was only found at high CO₂ concentrations.

These species are thus also obviously tolerant of elevated CO₂ levels and like the species above can be considered to be mofettotolerant. For instance, *Ceratophysella denticulata* is a widespread species and typical inhabitant of rich organic litter (Fjellberg 1998). It was also found to be tolerant of, i.e., insecticides, under the influence of which it was found to dominate Collembola communities (Fountain et al. 2007). *Proisotoma minima* is an eurytopic species with a preference for decaying organic substrates, and *Desoria violacea* is a common inhabitant of dry habitats of Scandinavian mountains, grassland communities of the Tatry, or the Siberian tundra (Potapov 2001). Since these species were not found in normal CO₂ samples (not all reported here), the collembolan community composition within the high CO₂ output areas appears to be not only a subset of the regional species pool, indicating CO₂ as an important controlling factor in species occurrence.

Due to the absence of mofettotoxic species in the high CO₂ samples, species richness was often radically reduced in these samples. Interesting, though, is the strongly increased total abundance at the medium (although still highly elevated) CO₂ concentrations, which was due to large populations of only a few, obviously tolerant species. Strong population increases of a few tolerant species, resulting in large total densities, are often found under environmental stress, both anthropogenic and natural (Kuznetzova 2009). Such species-specific phenomena have been found, for example, after inundation (Russell & Griegel 2006), heavy metal or chemical pollution (i.e., Niklasson et al. 2000, Filser & Holscher 1997, Gillet & Ponge 2003) or salt influence (Rösgen et al. 1993). Further apparent reactions to the elevated CO₂ levels were, i.e., the induction of bisexuality in otherwise parthenogenic *Mesaphorura* species (cf. Chahartaghi et al. 2006). Males have been often observed in these species under various forms of environmental stress, i.e. high alpine sites, sandy seashore habitats (Fjellberg 1998), copper population (Niklasson et al. (2000) or inundation (Russell & Griegel 2006).

The reasons for the existence of mofettotolerant collembolan species cannot be determined through the present studies. Physiological tolerance, however, is an obvious explanation. Zinkler & Platthaus (1996) in one of the few studies on CO₂ tolerance in Collembola found species-specific reactions to heightened CO₂ concentrations, both tolerances of varying degrees and intolerances. On the other hand, the many experimental studies of moderately elevated CO₂ concentrations within climate-change studies can offer some indication of effects that can be expected in mofette fields. For instance, elevated CO₂ concentrations affect many soil-faunistical parameters, such as density, biomass, diversity, activity, consumption rates, life history, migrational abilities etc., however with species-specific responses (i.e., Couteaux & Bolger 2000). Both significant decreases (Hansen et al. 2001) as well as increases on density and species diversity of Collembola have been observed (Maraldo et al. 2010) as well as only minor or no effects (Kardol et al. 2011). These results were dependent on site, species and life-history (Couteaux & Bolger 2000, Kardol et al. 2011, Sticht et al. 2008). Beyond direct effects of increasing CO₂ concentration, important indirect influences on the soil fauna concern elevated CO₂-related changes in food resources, consumption and other factors (Couteaux & Bolger 2000). Especially changes in higher trophic-level groups can trigger top-down effects throughout the entire soil-food web (Niklaus et al. 2003). Increased CO₂ concentration can indirectly influence nutrient supply due to increases in soil C input or changes in organic C dynamics (Cotrufo et al. 1998, Niklaus et al. 2003, Sticht et al. 2008, Drigo et al. 2008). These can occur through altered litter input, plant metabolism or root secretion, which in turn can affect mycorrhiza, soil bacteria and soil fungi (Drigo et al. 2008). All of these indirect effects on nutrient resources and supply can alter bottom-up processes within the food web (Cotrufo et al. 1998), inducing changes in the entire soil food-web structure.

Although the increases in CO₂ levels in these studies are very minor compared to that within mofette fields, such changes in the soil ecosystem due to increased CO₂ concentrations are also known from these areas, which can thus possibly affect the soil fauna. For instance, increased colonisation by mycorrhizal fungi as well as altered mycorrhizal physiology affect plant allocation of photosynthate below-ground in natural CO₂ vents (Ring et al. 2000), thus strongly suggesting changes in rhizosphere processes that can directly or indirectly effect soil fauna. Altered photosynthesis and resulting changes in the chemical composition (i.e., C, N, lignin) of plants and leaf litter due to elevated CO₂ in mofette fields (Körner & Miglietta 1994, Cotrufo et al. 1999, Couteaux et al. 1999, Vodnik et al. 2002) as well as altered litter decomposition and C mineralisation (Cotrufo et al. 1999, Couteaux et al. 1999, Ross et al. 2003) can also lead to changes in the food-resource base of the soil biota. Furthermore, specific CO₂-tolerant strains of microalgae have been identified in experiments and mofette fields (Collins & Bell 2006). All of these factors will most likely lead to changes in the soil nutrient supply and thus on the composition and structure of soil food webs, including soil Collembola (Körner & Miglietta 1994).

Thus, the reasons behind the differences in collembolan community composition and structure due to different CO₂ concentrations as well as a mofette field-specific species composition will be complex and multifactorial. The resolution of these factors was beyond the scope of the present pilot studies and will be investigated in future studies. Nonetheless, although the results cannot be generalised for all mofette fields, these present results indisputably show that Collembola can occur in mofette fields at extremely high soil CO₂ concentrations, that apparent tolerances to these high CO₂ levels are species-specific and that specific (directly or indirectly) CO₂-related distribution and community patterns exist within soil Collembola in at least this mofette area. Although more extensive sampling will indeed reveal more species, probably more varied distribution patterns of some species among the various CO₂ concentrations and more accurate estimates of CO₂-related species richnesses and densities, the general picture will probably remain similar to that found here.

5. References

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