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2012

### **document version**

Publisher's PDF, also known as Version of record

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### **citation for published version (APA)**

Makkonen, M. A. (2012). *The use of plant litter and soil fauna traits in a mechanistic assessment of litter decomposition under global change*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam]. VU University.

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Chapter II

**Traits explain the responses of a sub-arctic Collembola  
community to climate manipulation**

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Soil Biology & Biochemistry 43 (2011) 377-384

## Abstract

Ecosystems at high northern latitudes are subject to strong climate change. Soil processes, such as carbon and nutrient cycles, which determine the functioning of these ecosystems, are controlled by soil fauna. Thus assessing the responses of soil fauna communities to environmental change will improve the predictability of the climate change impacts on ecosystem functioning. For this purpose, trait assessment is a promising method compared to the traditional taxonomic approach, but it has not been applied earlier.

In this study the response of a sub-arctic soil Collembola community to long-term (16 years) climate manipulation by open top chambers was assessed. The drought-susceptible Collembola community responded strongly to the climate manipulation, which substantially reduced soil moisture and slightly increased soil temperature. The total density of Collembola decreased by 51% and the average number of species was reduced from 14 to 12. Although community assessment showed species-specific responses, taxonomically based community indices, species diversity and evenness, were not affected. However, morphological and ecological trait assessments were more sensitive in revealing community responses. Drought-tolerant, larger-sized, epiedaphic species survived better under the climate manipulation than their counterparts, the meso-hydrophilic, smaller-sized and euedaphic species. Moreover it also explained the significant responses shown by four taxa. This study shows that trait analysis can both reveal responses in a soil fauna community to climate change and improve the understanding of the mechanisms behind them.

## Introduction

High northern latitude ecosystems are predicted to undergo major changes due to both increasing temperature and changing precipitation patterns triggered by global climate change (Christensen *et al.*, 2007; Meehl *et al.*, 2007). The impact of climate warming is already visible at higher latitudes as a greening trend (Lucht *et al.*, 2002). Despite the visible change in the vegetation cover, the mechanisms behind the changes in ecosystems are not fully understood. These mechanisms are complex due to the feedbacks among (1) climate, (2) above and belowground biota and (3) carbon and nutrient cycles. Nevertheless, enhanced understanding of these mechanisms is needed in order to increase the predictability of both the magnitude of climate change and its impacts on ecosystems. As a first step in analysing the mechanisms the focus should be on the responses of both above and below ground biota to climate change. Various meta-analyses have provided a rather good understanding of the northern vegetation responses to climate change (Arft *et al.*, 1999; Rustad *et al.*, 2001; Dormann and Woodin, 2002; Walker *et al.*, 2006). However, our knowledge about the responses of the belowground biota is not as well developed. This is a major omission as soil fauna control various soil processes and is linked with the aboveground vegetation (Wardle, 2002) and therefore is one key component in the above-mentioned feedbacks. Thus, assessing and understanding the responses of soil fauna to climate change increases mechanistic understanding and ultimately the predictability of changes in both communities and ecosystem processes.

The role of microarthropods in controlling soil processes is relatively large in the northern ecosystems, where larger soil macro-fauna are absent or have a low species richness and density (Swift *et al.*, 1979). The community structure and composition of soil microarthropods are strongly controlled by both soil temperature and moisture (Laakso *et al.*, 1995; Huhta and Hänninen, 2001). These factors interact and are thus hard to study independently. Climate manipulations which aim at increasing air and soil temperature by Open Top Chambers (OTCs) or heating cables and lamps have artefacts (Kennedy, 1995; Marion *et al.*, 1997) such as increased evaporation. Soil drying can have a stronger effect than temperature on soil fauna community composition. This has been shown for arctic soil microarthropods (Hodkinson *et al.*, 1998). Within the group of micro-arthropods, the soft bodied Collembola are especially limited by drought. However, Collembola species show different strategies to tolerate drought and this is reflected in their vertical distribution (Vannier, 1983). More specifically, species living in the top soil are more drought tolerant whereas species living in deeper soil layers are more drought susceptible.

Until now, only three longer term (> 2 yr) studies assessing the response of Collembola to soil warming in the north have been conducted (Coulson *et al.*, 1996; Sjursen *et al.*, 2005; Dollery *et al.*, 2006). Temperature increase in these experiments was not reported to affect soil moisture and in general Collembola did not show a strong response to soil warming. Nevertheless, Coulson *et al.* (1996) found in one out of three sampling occasions a significant decrease in total Collembola abundance at their well-drained drier site during a warmer and drier summer suggesting a reinforced role of moisture as a controlling factor of the Collembola community. Long-term experiments in northern latitudes assessing the combined effect of soil warming and drying are urgently needed, because long- and short-term studies conducted in other biomes have shown strong responses of Collembola to drought (Lindberg *et al.*, 2002; Lensing *et al.*, 2005; Shultz *et al.*, 2006). Instead of limiting the Collembola community response assessment to the group level, some of these OTC and drought studies have assessed the community at more detailed taxonomic level and found species-specific responses. Unfortunately these responses were not further assessed to reveal patterns or mechanisms (but see Lindberg *et al.* (2002) and Shultz *et al.* (2006)).

The mechanisms behind the response of species to environmental manipulations are based on a specific combination of traits. In this context, species are not totally independent units with respect to their responses to environmental change. On the contrary species responses are affected by their trait attributes which either differentiate or integrate species in their responses. Using functional traits instead of the traditional taxonomic approach, i.e., strictly species identity, is recommended as a step forward in finding patterns in community responses and the mechanisms underlying them (McGill *et al.*, 2006). Functional traits have been defined as morphological, physiological or phenological traits which impact species fitness via their effects on growth, reproduction and survival (Violle *et al.*, 2007). The functional trait approach has been successfully used to explain the response of different vegetation types to several environmental factors (Keith *et al.*, 2007; Kyle and Leishman, 2009; Wang, 2009), but so far, the use of functional traits in faunal studies has not developed to the same extent. This is mainly due to the low availability of functional trait attributes for fauna although some recent fauna studies have successfully used biological and ecological traits in community assessments (Bêche *et al.*, 2006; Poff *et al.*, 2006; Harrington *et al.*, 2007; Moretti *et al.*, 2009). This trait approach could be fruitful in assessing species-specific responses of a Collembola community to climate change.

The objectives of the present study were to (1) quantify the response of a Collembola community to an altered soil temperature and moisture, and (2) assess if species-specific traits can be used to reveal mechanisms behind the responses. Thereto, we sampled Collembola from a long-term (16 yr) climate manipulation study in sub-arctic Sweden. The manipulation was carried out using OTCs, which slightly increased soil temperature but strongly decreased soil moisture. Collembola traits that have been shown to respond to drought were selected. We hypothesized that in the OTC treatment a decrease in soil moisture would (1) decrease total Collembola density, (2) decrease species richness, diversity and evenness, and (3) have a differential effect on the density of drought-sensitive and drought-tolerant species as revealed by their biological and ecological traits.

## Materials and methods

### *Site description and experimental setup*

The Collembola community assessment was carried out in an experimental area where climate warming has been simulated by Open Top Chambers (OTCs) since 1991. The OTC experiment is located in Abisko, northern Swedish Lapland (68° 21'N, 18° 40'E) at an elevation of 400 m a.s.l. The area has an average annual temperature of -1 °C and annual precipitation of 300 mm (Abisko Scientific Research Station, Meteorological station). The vegetation at the experimental area is described as understorey dwarf shrub heath in an open mountain birch forest of *Betula pubescens* ssp. *czerepanovii* [Orl.] Hämet-Ahti. The dominant understorey species are *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup), *Vaccinium uliginosum* (L.), *Vaccinium vitis-idaea* (L.), *Vaccinium myrtillus* (L.) and *Cladonia* spp. Full details of the vegetation cover and microclimate at the plots are given by Wookey *et al.* (1993). The soil is an iron podsol, with a moderately well-developed raw humus horizon, and the leached A2 or E horizon resting directly on the bedrock (Sonesson and Lundberg, 1974). Soil pH is 4.0 - 4.5 and the depth of the organic horizon ranges from 0 to 9 cm (Robinson *et al.*, 1995).

The experimental setup has been described in detail by Wookey *et al.* (1993). In short, open top polythene tents were used from 1991 until 2000, after which they were replaced by hexagonal ITEX OTCs (Marion *et al.*, 1997). The basic function of the OTCs is to increase the soil temperature by passively trapping the long wavelength solar radiation, which heats both air and soil. As a side-effect, soil moisture can be decreased in the OTCs due to increased evaporation (Kennedy, 1995; Marion *et al.*, 1997), and especially the area close to the edges can be directly sheltered from precipitation as a result of which effective precipitation is lower. These hexagonal chambers were 53 cm high and had a side length of 122 cm at the ground level and 87 cm at the top. The experimental design consisted of eight treatments and a control. The present study assessed only the OTC and the control plots. The minimum distance between these plots was 0.5 m. Earlier measurements in this experiment have shown that the OTC treatment raised the soil temperature at 5 cm depth by circa 1 °C in the period of June-July (Wookey *et al.*, 1993; Richardson, 2000) and decreased the soil moisture by 27-29% compared to the control (Robinson *et al.*, 1995; Richardson *et al.*, 2002). Vegetation composition and structure at the plots have been recorded during four consecutive surveys after the start of the experiment. In the latest assessment (Richardson *et al.*, 2002), carried out nine growing seasons after the start of the experiment, no statistically significant changes in the above-ground biomass of the measured species or plant groups was found. However, there was a trend of bryophyte biomass decrease

in the OTCs. Furthermore, due to the unchanged above-ground biomass, no changes in litter input are assumed. In addition to vegetation surveys decomposition rates and soil nitrogen mineralisation rates (Robinson *et al.*, 1995) have been assessed. Litter decomposition and net nitrification were reduced in the OTCs although net N mineralisation was not affected. No assessments of the belowground biota in the experimental plots had been conducted before the present study.

#### *Collembola sampling and abiotic measurements*

Collembola were sampled in 12 plots, six replicates of control and OTC. Samples were taken in the vicinity of the chamber walls, keeping the central part of the plots intact for future studies. Soil samples were cored circa 20 cm from the OTC chamber walls and control plot edges facing south. Two soil cores (10 cm diameter and 5 cm depth) were cored at circa 40 cm distance from each other in each plot. Sampling was carried out within one day in 2007 (first week of August), 16 years after the start of the experiment. Soil cores were kept cool in a climate room at 4 °C and transported to the VU University Amsterdam for Tullgren extraction (Van Straalen and Rijninks, 1982). This extraction was started one day after the sampling and ran for 16 consecutive days. The Collembola were preserved in a fixative solution (Gisin, 1960), and determined to the species level by using the keys by Fjellberg (1998; 2007) and Hopkin (2007). Partly damaged specimens were pooled into a group named “unknown”. Species richness was calculated as the mean species number and species diversity was calculated using Shannon’s diversity index ( $H$ ) (Begon *et al.*, 2005):

$$H = - \sum_{i=1}^S p_i \ln p_i$$

where  $S$  = total number of species in the community (richness) and  $p_i$  = relative abundance of the  $i$ -th species.

Evenness was calculated using the evenness index ( $J$ ) (Begon *et al.*, 2005):

$$J = H / H_{\max}$$

where  $H$  = diversity and  $H_{\max}$  = the natural logarithm of the species richness in the community.

Measurements of soil temperature and moisture (henceforth “soil microclimate”) in the sampling area were conducted during summer 2008. Soil microclimate was recorded with loggers and sensors at 5 cm depth in 3 randomly assigned control and 3 OTC plots at hourly intervals. Soil temperature was measured by Tinytag Plus soil temperature loggers and Tinytag PB-5002 soil moisture sensors (Gemini Data Loggers, Chichester, UK). HOBO Micro Station moisture loggers (Onset Computer Corporation, Bourne Massachusetts, USA) were used together with ECH2O EC-5 soil moisture sensors (Decagon Devices, Pullman, Washington, USA) to measure soil volumetric water content. Both soil moisture and soil temperature were recorded by two sensors in each measurement plot.

*Collembola traits*

For this study seven morphological and two ecological traits, all listed in Table 1, were selected. The selection was made from the Collembola trait database of M.P. Berg (VU University Amsterdam, unpublished data). This database contains information on the phylogeny, biology, ecology and distribution of 286 species of Collembola that occur throughout Europe. The trait attributes in the database are collected from various literature sources. We concentrated our selection on traits that can be responsive to drought, as earlier studies found that this OTC treatment affected soil moisture more than soil temperature. Selection of the traits was constrained by the availability of trait attributes for all the determined species in the present study.

All the five selected morphological traits (no. of ocelli, body size, body pigmentation level and pattern, presence of modified hairs or scales, furca development and antennae length) define Collembola life form (i.e., vertical distribution groups) (Gisin, 1943). This morphology-based life form grouping has been used in several studies (Detsis, 2000; Kærsgaard *et al.*, 2004; Jucevica and Melecis, 2006) and it expresses habitat and food source requirements simultaneously. The reason for focusing on life form is that Collembola vertical distribution is strongly controlled by soil moisture (Haarløv, 1955) and thus can respond to soil drying. Morphological trait attributes were extracted mainly from Fjellberg (1998; 2007) and Hopkin (2007), except for the no. of ocelli for *Folsomia quadrioculata* (no. of ocelli was 2 as seen on the specimens and did not range from 1 to 3). Body size attributes were taken only from Fjellberg (1998; 2007), where the reported values are sample measurements in Fennoscandia and Denmark by the author (pers. comm.). Body size is the maximum value from the range given by Fjellberg (1998; 2007). The maximum value was used to take into account the seasonal variation. Antenna/body length ratio was determined from the pictures in the articles describing the species.

**Table 1.** Description of the (a) morphological and (b) ecological traits. Data were taken from numerous published literature sources. See section ‘Collembola traits’ for more information.

Traits	Data type	Attribute
a. Morphological traits		
No. of Ocelli	ordinal	0 - 8
Body size	quantitative	in mm, to the nearest 0.1 mm
Body pigmentation level	ordinal	0=white, 1=lightly pigmented, 2=intensely pigmented
Body pigmentation pattern	binary	0=absent, 1=present
Modified hairs or scales	binary	0=absent, 1=present
Furca development	ordinal	0=absent, 1=reduced, 2=fully developed
Antenna/body	quantitative	in mm, to the nearest 0.1mm
b. Ecological traits		
Moisture preference	ordinal	0=xeroresistant, 1=xero-mesophilic, 2=indifferent, 3=mesophilic, 4=meso-hydrophilic
Habitat width	ordinal	0=steno, 1=steno/eury, 2=eury and eury/syn

The two selected ecological traits characterise adaptations to drought. Moisture preference is based on occurrence in habitats differing in soil moisture and can be used as a proxy to express the drought tolerance of the species (Kuznetsova, 2003). This enables the classification of the species into moisture preference groups, ranging from xerophilic to hydrophilic. Also, habitat width has been shown to respond to drought (Lindberg and Bengtsson, 2005). Habitat width expresses the number of habitat types in which a species occurs and thus it classifies the species as stenoeic and euryeic. The trait attributes for moisture preference were taken from Kuznetsova (2003) except for five species, which were not included in that study. Moisture preference attributes of these five species were extrapolated based on the comparison of habitat descriptions for all the determined species. Habitat width was taken from various literature sources. Trait attributes for both eco- and morphological traits are further explained in Table 1.

To determine whether OTC-induced changes in the community composition affect the trait composition, the community-weighted mean trait scores ( $T_m$ ) were calculated according to Garnier *et al.* (2004) as:

$$T_m = \sum_i p_i x_i$$

where  $x$  = the trait attribute of the  $i$ -th species and  $p_i$  = is the relative abundance of the  $i$ -th species. The Collembola species group “unknown” was omitted from the trait assessment (no trait attributes available).

### *Statistical analysis*

All analyses were performed with SPSS for Windows version 17.0 (SPSS Inc., Chicago, IL, USA) unless otherwise stated, and the standard level of significance ( $p \leq 0.05$ ) were used to assert a statistically significant effect.

For the soil microclimate the average value given by the two sensors in a plot was used for the analysis of the treatment effect. Technical problems with soil moisture loggers and sensors decreased the number of replications. Therefore, we used soil moisture data from three control plots and two OTC plots. Furthermore, exceptionally one sensor measurements on soil moisture were used from one of the OTC plots. The effect of the OTC treatment on both soil moisture and temperature was tested by the non-parametric Wilcoxon test for the whole measurement period and for two separate time intervals into which the measurement period was divided according to the first rain event.

Nested ANOVAs were employed to test the effect of the treatment as a fixed factor and plot as a random factor on the Collembola total density, densities of each taxon separately and the community indices. Data of Collembola total density, species richness, diversity and evenness were untransformed. Densities of each taxon were  $\log(x+1)$  transformed to ensure homogeneity of variances and normality at the nested factor level. Densities of the taxa that did not fulfil the model assumptions after log transformation, as assessed by box plots and Q-Q plots, were analysed by nonparametric Kruskal-Wallis tests only at the treatment level (densities of taxa were averaged per plot).



The responsiveness of eco- and morphological traits to the OTC treatment was analyzed first by Principal Component Analysis (PCA) and then by Redundancy Analysis (RDA). PCA and RDA were conducted with Canoco for Windows version 4.5 (ter Braak and Šmilauer, 2002). We used treatment (control and OTC) as an explanatory (environmental) variable, which was recoded into two binary (dummy) variables. The selection of RDA was determined by the data type of the explanatory variables. Community-weighted mean trait scores ( $\Gamma_m$ ) were the response variables (species) assessed in these models. To avoid pseudo replication we used plot level averages of the species values and thus assessed only the level of the treatment. Primary matrix data were centred and standardized by the species prior to ordination to allow different units of measurements in the trait attributes to be incorporated into the same models. For three traits, centred and standardized species data included outliers. Two of these traits, no. of ocelli and body pigmentation level, shared one outlier in the control samples. This outlier was located more towards the OTC samples in both of these traits, and thus the inclusion of the outlier made this model more conservative. The trait habitat width had one OTC sample as an outlier in the opposite direction of control samples. Hence, inclusion made the model less conservative. These outliers were included into the models, as they were not considered true ecological outliers due to the low no. of replication ( $n = 6$ ). However, these statistical outliers were taken into account when discussing the results. The GLM function in Canoco was used to determine the statistical significance of the relationship between the traits (species scores) and the treatment (first constrained axis).

## Results

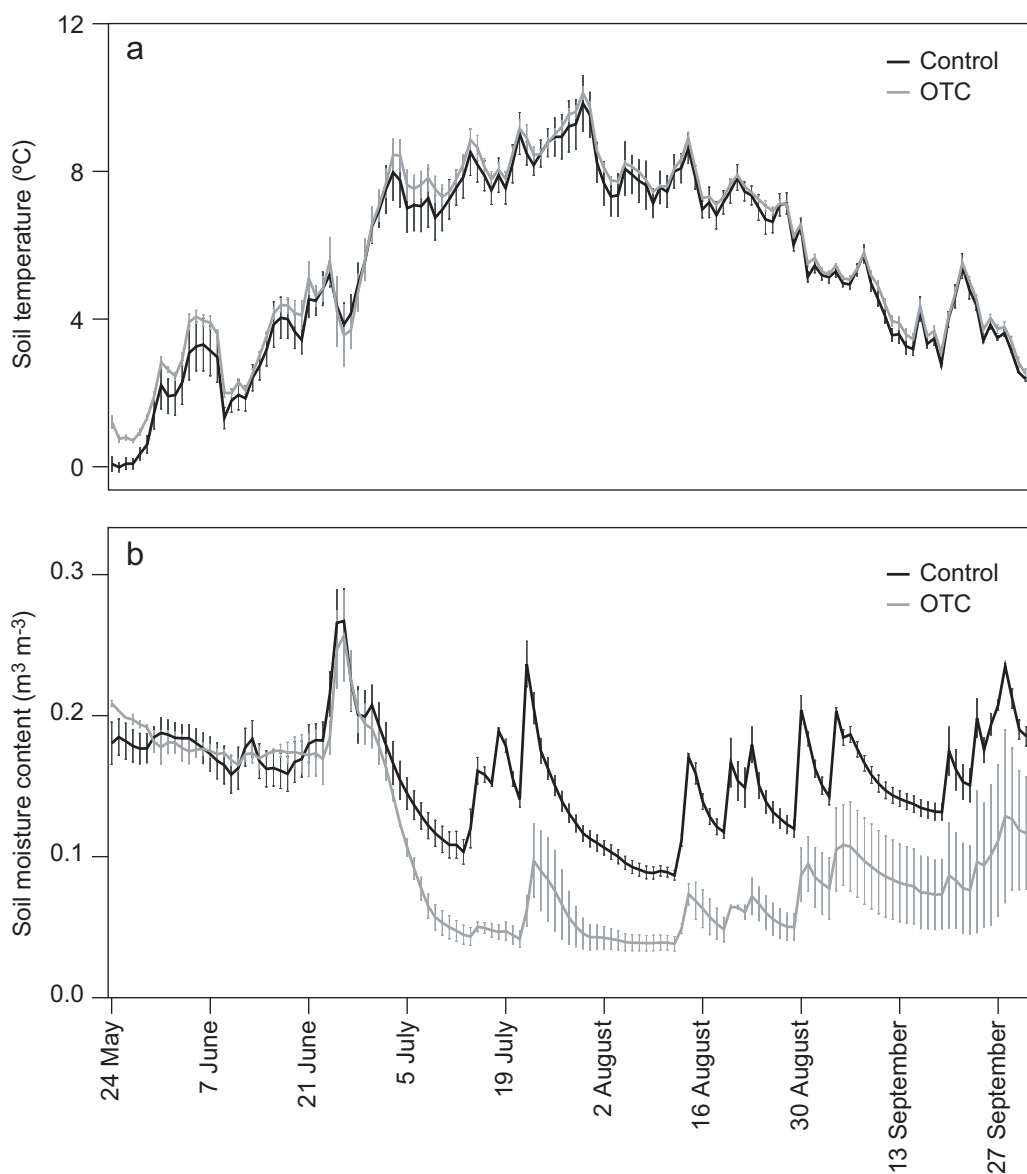
### *Soil microclimate*

The OTCs slightly raised soil temperature, but strongly decreased soil moisture at 5 cm depth (Fig. 1 and Table 2). Soil temperature increased by only 0.3 °C during the whole measurement period. This increase was more profound in the early summer and became more moderate in late summer and early autumn but nevertheless remained significant. Soil volumetric moisture content at 5 cm depth was on average reduced by 0.06 m<sup>3</sup> m<sup>-3</sup> in the OTCs during the measurement period. This reduction in soil moisture content was 33% compared to the control plots. Soil moisture content was not affected by the OTC treatment before the first rain event on 26 June 2008. However, after that and until the end of the measurement period it was reduced by 0.07 m<sup>3</sup> m<sup>-3</sup> (48% decrease compared to control plots). The early season soil moisture measurements probably reflected OTC induced snow accumulation during the winter and thus increased snow water content and prolonged snow melting period in the OTC plots.

### *Collembola community*

Total Collembola density was reduced by 51% as a result of the OTC treatment (Table 3). The OTC treatment not only decreased total density but also average species richness (no. of species) from 14 to 12. Neither species evenness nor the Shannon diversity index were affected by the OTCs. The effect of the plot nested within the treatment was not significant for Collembola total density, species richness, evenness or Shannon diversity index, indicating homogeneous soil conditions among plots.

In total 22 Collembola species were determined of which 21 occurred in the control plots and 19 in the OTC plots. Species that were absent in one of the treatments were observed with low densities in the other treatment. *Isotomiella minor* had the highest density in both treatments. The next three most abundant species were *Willemia anoptbalma*, *Protaphorura pseudovanderdrifti* and *Folsomia quadrioculata* in both control and OTC treatment, although the density rank order differed between the treatments. At the species level, the OTC effect was only significant for four Collembola species. The OTCs decreased the density of *I. minor*, *W. anoptbalma* and *Folsomia sensibilibis*, and increased the density of *Entomobrya nivalis*. Only two species *Megalothorax minimus* and *Pseudanurophorus binoculatus* showed the effect of the plot nested within the treatment, possibly indicating some differences in soil conditions among plots.



**Figure 1.** Average  $\pm$  SE daily soil temperature ( $^{\circ}\text{C}$ ) (a) and soil volumetric moisture content ( $\text{m}^3 \text{m}^{-3}$ ) (b) at -5 cm depth in the control and at the OTC plots. Measurements were performed between 24 May and 1 October 2008;  $n=3$  for both control and OTC plots for soil temperature, but for soil moisture  $n=3$  for control plots and  $n=2$  for OTC plots.

**Table 2.** Difference between OTC and control plots in soil temperature (°C) and soil volumetric moisture content ( $\text{m}^3 \text{m}^{-3}$ ) during the total measurement period (24 May - 1 October: 131 days), before the first rain event (24 May - 26 June: 34 days) and after the first rain event (27 June - 1 October: 97 days) in 2008.

	24 May - 1 October	24 May - 26 June	27 June - 1 October
Soil temperature (°C)			
Average	0.3	0.5	0.2
SEM	0.0	0.1	0.0
Soil moisture content ( $\text{m}^3 \text{m}^{-3}$ )			
Average	-0.052	0.002	-0.071
SEM	0.004	0.002	0.003

P-values of non-parametric Wilcoxon test of the soil temperature and moisture difference between OTC and controls were  $< 0.001$  for both soil temperature and moisture in three time periods 24 May - 1 October (df 130), 24 May - 26 June (df 33) and 27 June - 1 October (df 96), except the  $p$ -value of the difference in soil moisture in 24 May - 26 June was 0.437 (non significant).

### *Collembola traits*

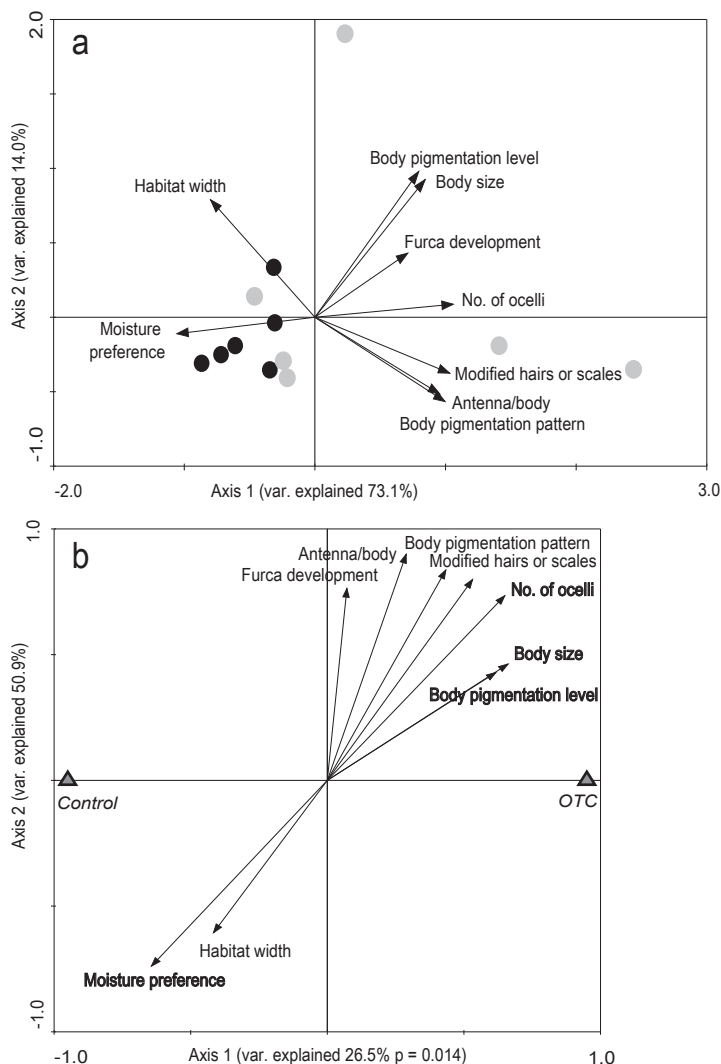
The first two PCA axes explained 87.1% of the variation in the community-weighted mean trait scores ( $T_m$ ) (Fig 2a). The PCA revealed that the traits no. of ocelli and moisture preference were negatively correlated. Strong positive correlation existed between body pigmentation level and body size as well as with the antenna/body ratio and the body pigmentation pattern. The control plots had smaller variance than the OTC plots and these two groups were separated from each other mainly along the first axis. The control plots had higher  $T_m$  values for moisture preference and lower  $T_m$  values for no. of ocelli. The OTC plots were not clearly associated with any single trait or a trait combination. The relationship between traits and the treatment (plots grouped into control and OTC) was further analysed by RDA.

Collembola traits were significantly associated with the first RDA axis (constrained by treatment) (Fig 2b) ( $p = 0.014$ ), which explained 26.5% of the variation in the  $T_m$  data. GLM, ran on the RDA Species scores and the first canonical axis constrained by treatment, showed that four of the traits (no. of ocelli, body size, body pigmentation level and moisture preference) correlated significantly ( $p < 0.05$ ) with the treatment axis (Fig 2b and Table 4). The OTC treatment favoured drought tolerant species (e.g. xeroresistant and xero-mesophilic species), and species with a larger body size, more ocelli and more intense pigmentation. The relationship between the OTC treatment and other traits was not significant. Excluding the outliers would not have affected the number and identity of the significant traits.

**Table 3.** Collembola total and species mean density (thousands  $m^{-2} \pm SE$ ), species richness (mean  $\pm SE$ ), species evenness (mean  $\pm SE$ ), Shannon diversity index (mean  $\pm SE$ ) in control and OTC treatment at the fixed factor level (treatment).

Collembola community	Treatment		Plot	
	Control	OTC	F	P
Total density	67.87 $\pm$ 10.40	33.53 $\pm$ 8.04	<b>6.82</b>	<b>0.026</b>
Species densities				
<i>Isotomiella minor</i> (Schaeffer, 1896)	19.77 $\pm$ 4.31	9.07 $\pm$ 2.57	<b>10.03</b>	<b>0.010</b>
<i>Willemia anophthalma</i> Börner, 1901	11.40 $\pm$ 3.18	2.48 $\pm$ 0.85	<b>6.71</b>	<b>0.027</b>
<i>Protaphorura pseudovanderdrifti</i> (Gisin, 1957)	10.57 $\pm$ 2.17	6.88 $\pm$ 2.31	1.51	0.247
<i>Folsomia quadrioculata</i> (Tullberg, 1871)	7.00 $\pm$ 1.78	5.37 $\pm$ 3.54	4.11	0.070
<i>Folsomia sensibilis</i> Kseneman, 1934	4.30 $\pm$ 0.85	0.71 $\pm$ 0.17	<b>5.78</b>	<b>0.037</b>
<i>Mesaphorura macrochaeta</i> Rusek, 1976	4.14 $\pm$ 1.59	1.20 $\pm$ 0.34	3.83	0.079
<i>Willemia denisi</i> Mills, 1932	2.59 $\pm$ 0.47	1.45 $\pm$ 0.78	0.92	0.337
<i>Parisetotoma notabilis</i> (Schaeffer, 1896)	2.38 $\pm$ 1.62	1.19 $\pm$ 1.04	1.34	0.274
<i>Pseudothorophorus binoculatus</i> Kseneman, 1934	1.87 $\pm$ 0.77	0.16 $\pm$ 0.13	2.04	0.184
<i>Megalothorax minimus</i> Willem, 1900	1.11 $\pm$ 0.48	0.25 $\pm$ 0.12	1.13	0.313
<i>Micranurida pygmaea</i> Börner, 1901	0.91 $\pm$ 0.19	1.77 $\pm$ 1.05	0.41	0.522
<i>Desoria hiemalis</i> (Schoett, 1893)	0.84 $\pm$ 0.31	0.51 $\pm$ 0.21	2.58	0.108
<i>Lepidocyrtus lignorum</i> (Fabricius, 1793)	0.46 $\pm$ 0.13	0.68 $\pm$ 0.18	1.09	0.296
<i>Micranurida forsslundi</i> Gisin, 1949	0.25 $\pm$ 0.06	0.24 $\pm$ 0.06	0.09	0.773
<i>Entomobrya nivalis</i> (Linnaeus, 1758)	0.08 $\pm$ 0.01	0.65 $\pm$ 0.19	<b>10.26</b>	<b>0.009</b>
<i>Neanura muscorum</i> (Templeton, 1835)	0.04 $\pm$ 0.02	0.06 $\pm$ 0.03	0.07	0.796
<i>Pseudachorutes corticicolus</i> (Schaeffer, 1896)	0.04 $\pm$ 0.03	0	2.20	0.138
<i>Dicyrtoma fusca</i> (Luppock, 1873)	0.03 $\pm$ 0.02	0	2.18	0.140
<i>Pseudosinella alba</i> (Packard, 1873)	0.03 $\pm$ 0.02	0.23 $\pm$ 0.16	1.46	0.255
<i>Arthropalites principalis</i> Stach, 1945	0.01 $\pm$ 0.01	0.02 $\pm$ 0.02	0.02	0.902
<i>Sminthurus nigromaculatus</i> Tullberg, 1871	0.01 $\pm$ 0.01	0	1.00	0.317
<i>Entomobrya marginata</i> (Tullberg, 1871)	0	0.49 $\pm$ 0.48	2.18	0.140
unknown	0.04 $\pm$ 0.03	0.11 $\pm$ 0.04	1.95	0.192
Species richness (no. of species)	14.2 $\pm$ 0.6	12.3 $\pm$ 0.5	<b>6.24</b>	<b>0.032</b>
Shannon diversity index	1.90 $\pm$ 0.06	1.79 $\pm$ 0.09	1.00	0.342
Species evenness	0.72 $\pm$ 0.02	0.73 $\pm$ 0.02	0.05	0.824

Nested GLM F- and P-values are shown for treatment and plot effects. When data assumptions for nested ANOVA were not fulfilled, only treatment effect was calculated, with the Kruskal-Wallis test statistic (K). Degrees of freedom are 1 for the treatment effect and 10 for the plot effect. Statistical significant values ( $P < 0.05$ ) are in bold.



**Figure 2.** Ordinations of Collembola community-weighted trait means ( $T_m$ ) in (a.) a Principal Component Analysis (PCA) and (b.) a redundancy analysis (RDA).  $T_m$  scores are presented with plots (control = black circles, OTC = grey circles) in the PCA biplot and with the explanatory variables constrained first axis in the RDA biplot. Axis scaling is (a.) symmetric and (b.) for  $T_m$  scores. Var. explained = variance of the  $T_m$  data explained by the axis in %, bold style in the trait names in (b.) indicates the traits, which are significantly correlated with the treatment. See Table 1 for trait names.

**Table 4.** GLM analysis between mean  $T_m$  scores and the first RDA axis, which is constrained by the treatment. Regression coefficient (Coeff) significance ( $P$ ) and F-value (df = 11 for all the traits).

Traits	First constrained axis		
	Coeff	F	P
No. Of ocelli	1.261	8.0	0.018
Body size	1.285	8.6	0.015
Body pigmentation level	1.198	6.8	0.026
Body pigmentation pattern	0.842		n.s.
Modified hairs or scales	1.032		n.s.
Furca development	0.139		n.s.
Antenna/body	0.560		n.s.
Moisture preference	-1.250	7.8	0.019
Habitat width	-0.809		n.s.

## Discussion

### *OTC treatment and community assessment by traditional methods*

Soil temperature and soil moisture are strongly connected and are hard to tease apart in environmental manipulation studies. It is important to realize that OTC treatment effects can be driven indirectly by soil moisture and much less by temperature (Aerts, 2006). Our continuous soil moisture and temperature measurements at the Collembola sampling area during one summer season showed an increase in soil temperature of only 0.3 °C and a decrease in soil volumetric moisture content of 33% compared to the control plots. These effects are in the range of earlier measurements at these plots (Wookey *et al.*, 1993; Robinson *et al.*, 1995; Richardson, 2000; Richardson *et al.*, 2002), but indicate even stronger OTC effect on soil moisture than on soil temperature. Thus, given the susceptibility of arctic Collembola to drought (Hodkinson *et al.*, 1998) and the observed soil moisture reduction in the OTC plots, we expect that the main driver behind the change in community composition was soil moisture.

The OTC treatment strongly reduced total Collembola density which confirms our first hypothesis that OTC treatment has a negative effect on total Collembola density. However, these findings contrast with the previous OTC studies conducted in mainly moist habitats in northern areas (Coulson *et al.*, 1996; Sjørnsen *et al.*, 2005; Dollery *et al.*, 2006). The previous studies found Collembola to be more resistant to climate manipulation. However, contrary to the previous studies, OTCs in the present study strongly decreased soil moisture, a factor that is more important controlling arctic microarthropods than soil temperature (Hodkinson *et al.*, 1998). As we hypothesised our results are more in line with previous drought experiments (Lindberg *et al.*, 2002; Lensing *et al.*, 2005; Shultz *et al.*, 2006), which found a negative effect on Collembola density.

The OTC treatment decreased species richness from 14 to 12 and thus supported the first part of our second hypothesis that species richness would decrease upon the OTC treatment. However, contrary to our expectation neither species diversity nor evenness was affected by the OTCs, which did not support the other parts of the second hypothesis. Despite the low responsiveness of community indices to the OTC treatment, community taxonomic assessment revealed species-specific responses. Four out of the 22 species in total found in the study, showed a significant response. Densities of *I. minor*, *W. anophthalma* and *F. sensibilis* were decreased by the OTC treatment, whereas the density of *E. nivalis* increased despite the decrease in total Collembola density. These changes can be expected to affect the functioning of the ecosystem considering that *I. minor* was the most dominant species and also *W. anophthalma* and *F. sensibilis* had high densities in both control and OTC treatments. Despite the species-specific changes found in the taxonomic assessment, the diversity indices were not affected by the OTCs, indicating their low sensitivity to reveal changes in the community.

### *Community responses revealed by eco- and morphological traits*

With the trait approach we aimed to find mechanistic explanations for the observed species-specific responses to the OTC treatment. We observed that the community-weighted trait mean scores of traits that relate to drought tolerance, i.e., moisture preference, number of ocelli, body size, and body pigmentation intensity were affected by OTC treatment. Moreover these traits

revealed that the OTC treatment had a differential effect on the density of drought-sensitive and drought-tolerant species which confirms our third hypothesis.

More specifically, four out of the nine selected traits were affected by the OTC treatment. Analysis of the moisture preference trait data revealed that the drought-tolerant Collembola species were more abundant in the OTC treatment than the more hydrophilic species compared to the control. In addition three life form traits (body size, number of ocelli and body pigmentation level) showed an OTC effect. The density of larger-sized Collembola with higher number of ocelli and more intense pigmentation was higher in the OTC treatment. Thus, we found that only three out of the seven traits indicating life form according to Gisin (1943), were affected by the OTC treatment. This raises the question why the other life form traits were not affected. Possible answers are provided by earlier studies or the discrepancy might be due to the differences in the levels of trait attribute classification among the traits used in the present study. Firstly, some earlier studies (Stebajeva, 1970; Petersen, 1980; Hågvar, 1983; Rusek, 1989) have suggested that all morphological traits used by Gisin (1943) as life form indicators might not actually correlate with vertical distribution. These previous studies have also shed doubt on whether the trait 'body size' is a true life form indicator. Nevertheless we found that this trait was affected by the OTC treatment. On the other hand, the observed response can be explained also by a direct influence of moisture. Larger-sized Collembola were more abundant in the OTC treatment. These Collembola have a higher resistance to desiccation due to the smaller surface-to-volume ratio (Kærsgaard *et al.*, 2004) and thus are more tolerant to drought. Clearly, the uncertainty over the traits indicating Collembola life form emphasizes the need for further study. We looked at modern studies assessing the vertical distribution of Collembola species (Ponge, 2000; Lindberg and Bengtsson, 2005) and found that just two traits, number of ocelli and body pigmentation level, can explain the vertical species distribution. This interesting finding suggests that indeed the number of life form indicators could be revised by future research. Secondly, another possible reason for the lack of response of the other life form traits can be the coarse level of classification used in their trait attributes. We expect this to explain especially the low quantitative explanatory power of the two binary traits: presence of scales or modified hairs and pigmentation pattern.

In the present study epiedaphic species, characterized by the number of ocelli and the body pigmentation level traits, were more tolerant to the OTC treatment than euedaphic species. This is a response to the soil drying in the OTC plots. Epiedaphic species are adapted to soil surface conditions, which are generally drier than deeper layers in the profile. They can tolerate drier conditions mainly due to reduced water permeability of their integument, whereas the euedaphic species can not tolerate drier conditions as well (Vannier, 1983). Alternatively, the decrease in euedaphic species found in this study can possibly be explained by their vertical migration to even deeper soil layers (Lindberg and Bengtsson, 2005). However, the organic soil layer is shallow in subarctic birch forest. Thus, a decrease in the density of euedaphic species in the upper 5 cm of the soil (the layer that we sampled) indicates at least their lowered contribution to various soil processes such as plant litter decomposition (which mainly occurs in the upper soil layer) and nutrient mineralization, but most likely also higher mortality compared to the epiedaphic species.

The assessment of the community responses by using ecological and morphological traits provided understanding of the underlying mechanisms. In more detail, community trait assessment can also explain the observed sensitivity of the four Collembola taxa to the OTC

treatment at the absolute density scale. Densities of drought tolerant, larger-sized, epiedaphic species, as *E. nivalis*, better tolerated the OTC treatment and increased, whereas their counterparts, the hydrophilic, smaller-sized and euedaphic species, as *I. minor*, *F. sensibilis* and *W. anophthalma* were more vulnerable and decreased in response to the OTC treatment.

## Conclusions

The OTC treatment, which mainly decreased soil moisture content, reduced the Collembola total density by 51% and average species richness by two species. However, although species-specific responses were observed species diversity and evenness indices did not respond to the treatment. We showed that ecological and morphological trait assessment of the community was more sensitive to not only reveal responses but also provide the underlying mechanisms behind them.

Understanding the species-specific responses to climate manipulation treatment is a key factor in improving the predictability of climate change effects on soil fauna communities and ultimately soil processes. We have shown that a trait based approach helps us to understand that the species-specific responses in climate change studies are not random and helps to unravel the possible mechanisms. In the light of the availability of functional trait attributes for species of many soil fauna groups we encourage the use of eco- and morphological traits. Our study shows that this approach enhances the predictability of soil community changes to climate change.

## Acknowledgements

We thank the staff of the Abisko Scientific Research Station for the maintenance of the experiment. We appreciate advice on the multivariate statistical analysis by Peter van Bodegom, Bob Douma and James Weedon. This research was funded through: the EU Marie Curie host fellowship grant “MULTIARC”, “BioCycle” research project (part of the ESF EUROCORES programme) as financed by the Dutch Organization for Scientific Research (NOW-ALW) and the EU ATANS grant from the Abisko Scientific Research Station.

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