

# Responses of oribatid mite communities to summer drought: The influence of litter type and quality

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## Abstract

A litterbag experiment was used to study the impact of extended periods of summer drought on the structure of oribatid mite communities (Acari, Oribatida) developing in two litter types (beech, spruce) of two qualities (fresh, pre-incubated). Within each litter type, litter quality determined species composition and densities and, in turn, this determined the impact of drought upon the oribatid mite communities. In both litter types, drought had a greater impact on community development in the pre-incubated compared to the fresh litter. In the short-term perspective of the present study, oribatid mite communities in beech litter were less sensitive to summer drought than those in spruce litter. This was partly due to the presence of site-specific, drought-tolerant species but seemed also strongly related to differences in the decomposition patterns between the litter types. Marked changes in densities and composition of oribatid communities after only one period of summer-drought suggest that there is a potential for a significant alteration of oribatid community structure in both litter types if climatic changes persist.

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**Keywords:** Oribatid mite communities; Climate change; Drought; Spruce litter; Beech litter; Decomposition; Litterbag

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## 1. Introduction

The influence of belowground biodiversity on ecosystem functioning and stability has recently received considerable attention (see Hooper et al. (2000) and Wolters et al. (2000)). This interest has been driven by an increasing awareness that soil organisms can have a significant influence on aboveground vegetation dynamics and on ecosystem processes (van der Heijden et al., 1998; Copley, 2000). Among the soil biota, invertebrates have been highlighted as key organisms influencing many basic soil processes (Lavelle et al., 1997). In the organic soil layers in temperate forests, mites (Acari) are the dominant component of invertebrate communities, with the majority being oribatid mites (Walter and Proctor, 1999) within

the Acariformes. Oribatid mites strongly influence decomposition processes and nutrient cycling, both directly via the consumption of detritus and subsequent release of nutrients and, indirectly as a regulatory factor of microorganisms (Verhoef and Brussaard, 1990; Wolters, 1991; Walter and Proctor, 1999).

Climatic conditions, in particular precipitation and temperature, are among the strongest factors regulating oribatid mite communities on a regional scale (Lavelle et al., 1993). Both these factors are expected to undergo considerable alterations during the present century as a result of global climate change (McCarthy et al., 2001). The potential impact of climatic changes on oribatid mites may be considerable, as precipitation and temperature not only influence oribatid mite communities per se, but also determine litter type (e.g. tree species) and quality (e.g. C:N ratio and lignin content). On a local scale, the latter two factors are known to strongly regulate oribatid mite diversity in soil and litter habitats (Hansen and Coleman, 1998). This regulative impact of the litter resource on oribatid mite communities is closely coupled to the process of litter decomposition and may operate via the specialisation of oribatid mites to a particular stage of

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decomposition or through their association with one or more specialised decomposer organisms (Swift et al., 1979).

In view of the anticipated impacts of climate change upon soil biota (Anderson, 1991, 1992; Young et al., 1998) and the potential consequences for ecosystem processes (Groffman and Jones, 2000), the present study aimed to increase our understanding of how the known main regulative forces of oribatid mite biodiversity (precipitation, litter type and quality) operate under a global change scenario. A litterbag experiment investigated the impact of reduced summer precipitation (moisture availability) on oribatid mite communities and, in addition, if organism response could be modified by litter resource type (tree species: European beech (*Fagus sylvatica* L.) or Norway spruce (*Picea abies* [L.] Karst.) and quality (decomposition stage of litter). Summer drought was chosen as a future climate change scenario based on recent predictions of decreases in summer precipitation and increased drought intensities and frequencies for most of Western Europe (Piervitali et al., 1997; Arnell, 1999). Litterbags were filled with either fresh or partly decomposed substrate, enabling a comparison between oribatid mite communities colonising litter at two stages of decomposition. Treatment-induced changes in oribatid mite communities were correlated to modifications in individual abiotic or biotic litter parameters.

## 2. Materials and methods

### 2.1. Site description

The experiment was carried out between 1997 and 1998 at two-forest sites situated ca. 4 km apart in the Vogelsberg area of Hesse, Germany (50°31' N, 9°17' E). One site was a 56-yr-old spruce (*Picea abies* [L.] Karst.) monoculture at 650 m above sea level (a.s.l.). The soil type is a rank cambisol with a loess texture. The organic layer ( $O_1 + O_f$ ) at this site was  $4.5 \pm 0.9$  cm thick and the pH ranged from 3.6 to 3.9. The other site, at 745–764 a.s.l., was dominated by European beech (*Fagus sylvatica* L.) with scattered trees of Scots pine (*Pinus sylvestris* L.) and birch (*Betula* spp.). The age of the trees ranged between 49 and 59 years. The soil type is basalt with loamy loess. The thickness of the organic layer ( $O_1 + O_f$ ) was  $4.3 \pm 0.8$  cm and pH varied from 3.6 to 3.8. The climate of the region is humid continental (subatlantic) with a mean air temperature of 6.4 °C and a mean annual precipitation of 1307 mm. In 1997 and 1998, mean annual temperature was 7.4 and 7.1 °C, respectively. Precipitation in 1997 was 957 and 1505 mm in 1998. Data were obtained from a meteorological station Grebenhain–Herchenhain (50°29'N, 09°16'E), situated 4 km SSE of the experimental sites at a slightly lower altitude (608 m a.s.l.).

### 2.2. Experimental design

At each study site, litterbags containing litter of the main tree species, at two decomposition stages (fresh or pre-incubated), were exposed to two precipitation treatments (control or summer drought). At each site, the experimental design therefore consisted of four precipitation/litter quality treatment combinations. The experiment was replicated within four blocks at each site, with each block consisting of a control and drought plot (size of individual plots: 1.25 m × 3.5 m). The block design was necessary to account for the spatial variation in the occurrence of soil fauna. The blocks were set-up at localities within each site that were as similar as possible to each other to keep site-specific differences in the distribution of the soil fauna to a minimum. There were four litterbag replicates for each treatment combination. Litterbags were moistened with rainwater and afterwards distributed randomly between the L and F organic horizons on each plot. On the drought plots, litterbags were arranged to maximise the distance between the bags and the edge of the roof. The experiment was established in October 1997. After 1 year of exposure the litterbags were retrieved. At the same time, four samples (soil core: diameter 5 cm) comprising the upper organic layers ( $O_1 + O_f$ ) were also taken at random from undisturbed plots that had received ambient rainfall. These samples were used as reference material for the local oribatid mite pool.

#### 2.2.1. Litter quality treatment

Needles and leaves were collected at each site in summer/autumn 1997 using litter traps suspended beneath the beech and spruce canopies. Both litter types were air dried at room temperature for 1 week and then divided into two portions. One portion of these air-dried litters, later referred to as 'fresh' litter, was stored in a cold room at 4 °C until used. The second portion of each air-dried litter was moistened and pre-incubated at 20 °C for a period of 3 months to create the litter quality later referred to as 'pre-incubated' litter. Moisture levels were maintained at field capacity over this period. At the start of this pre-incubation period, a small quantity of freshly collected O-layer ( $O_1 + O_f$ ) was obtained from each site and added to the respective pre-incubation chamber. This procedure was used to ensure that the microbial community normally involved in litter decomposition at each site was present during the pre-incubation period. The aim of this procedure was to degrade labile compounds (mainly C-compounds) in the fresh litter, leaving behind more recalcitrant, partly decomposed litter. When the incubation period was over, the litters were stored in a climate chamber at 20 °C until used to fill the litterbags.

#### 2.2.2. Precipitation treatment

Litterbags on the control plots received ambient precipitation. Roofs covering the drought plots prevented any precipitation reaching the litterbags. Every second week, litter that had accumulated on the roofs was collected

and spread evenly by hand underneath the respective roof. Each roof consisted of a wooden frame (1.25 m × 3.50 m) on six wooden posts (height from ground 80 cm) that was covered with transparent plastic. On top of the plastic foil, a second wooden frame with an opening in one corner prevented water percolation from the edge of the roofs down onto the litterbags. At this corner, the roofs were slightly lower allowing rainwater to be collected for later use. Additionally, a plastic foil was fastened along the sides of each roof. This reached down to 40 cm of the ground and helped to prevent rainfall being blown under the roofs, while at the same time allowing free gas exchange. Horizontal percolation from the surrounding soil into the litterbags was unlikely as the site was relatively flat. The roofs were setup at the start of the experiment in October 1997, removed at the onset of snowfall (middle of December 1997) and replaced after snowmelt (middle of March 1998).

### 2.2.3. Litterbags

The litterbags were made of nylon gauze (25 cm × 25 cm) with a mesh size of 1000 µm; this excluded only macrofauna. Litterbags for the spruce site were filled with ca. 60 g of air-dried material of either fresh or pre-incubated spruce needles. Due to the large volume of 60 g dry mass (DM) beech leaves, two litterbags had to be exposed, each filled with 30 g DM leaves.

### 2.3. Fauna extraction methods and mite identification

Immediately after sampling, the contents of each litterbag was weighed, carefully mixed and stored in sealed plastic bags at 4 °C. Oribatid mites were extracted from subsamples (ca. 3 g DM) by means of a high-gradient-canister method (Wolters, 1983). Extraction started the day of collection and lasted for a period of 14 days. The extracted oribatid mites were counted and separated into adult and juvenile stages. All adult oribatid mites with the exception of the Brachychthoniidae were identified to species level using the keys published by Subias and Arillo (2001), Pérez-Íñigo (1993, 1997), Balogh and Balogh (1992a,b), Balogh and Mahunka (1983), Giljarov and Krivolutsky (1975), Willmann (1931) and Sellnick (1928, 1960). Specific literature was used in many cases; Oppioidea (Moritz, 1970, 1973; Woas, 1986), Carabodes (Sellnick and Forsslund, 1953), Phthiracarus (Berg et al., 1990), and Oribatulidae and Scheloribatulidae (Wunderle et al., 1990). Nomenclature follows that of Subias and Arillo (2001), Krivolutsky (1995) and Balogh and Balogh (1992a,b). Oribatid nymphs and larvae were not identified and were counted separately as 'juvenile oribatid mites' (see Appendix).

### 2.4. Analytical procedures

Subsamples of 3 g FM (fresh mass) litter were dried at 105 °C for 24 h to determine the litter water content (LWC)

of the litter material (expressed as % litter DM; Alef and Nannipieri, 1995). Mass loss in each litterbag was then calculated as % mass loss of initial weight. The pH of the litter was determined after stirring subsamples of air-dried litter for 1 h in de-ionised water (weight (litter): water, 1:10). The organic matter content (loss on ignition: LOI) of the litter was determined by heating to 600 °C. Total carbon and total nitrogen were determined using gas-chromatography (Carlo-Erba NA 1500 Analyser).

Microbial carbon ( $C_{mic}$ ) was measured following the fumigation–extraction method according to Vance et al. (1987) and calculated assuming a  $k_{EC}$ -value of 2.22 (Wu et al., 1990).

### 2.5. Data analyses

#### 2.5.1. Statistical analyses

The effects of the experimental treatments precipitation, litter type and litter quality on the fauna and litter variables from the litterbag data set were evaluated using a three-way ANOVA (STATISTICA<sup>®</sup> software, version 6). Homogeneity of variances was tested using the Levene-test; normality of residuals was checked visually and using the Shapiro-Wilk W test to ensure that the assumptions of the ANOVA were met. When necessary, density data on oribatid taxa, microbial biomass ( $C_{mic}$ ) and litter variables were normalized; density and  $C_{mic}$  data were log transformed ( $\log(x+1)$ ), percentage data (mass loss [% initial DM], LOI [%], C [% DM], N [% DM]) were transformed using arcsin square root and the litter water content [% DM] was transformed using square root prior to statistical analysis. Significant differences between group means were determined by computing Tukey's honestly significant difference test (Tukey's HSD test,  $P < 0.05$ ). Relationships between the microbial biomass and litter parameters were calculated by the Spearman rank correlation coefficient,  $r_s$ .

#### 2.5.2. Community analyses

- Community structure and composition within each sample was recorded as the density of adult and juvenile oribatid mites (number of individuals g<sup>-1</sup> DM) and the total number of taxa present (taxonomic richness) was based upon adult oribatid mites.
- Bray–Curtis' index of similarity. Similarity between the oribatid communities in the different treatment combinations was analysed with single-link cluster analyses based on the calculation of the Bray Curtis index of similarity (Krebs, 1998) for untransformed data (BioDiversity Pro<sup>®</sup> software, version 2).
- Multivariate ordination. A direct canonical ordination in form of a redundancy analysis (RDA) (Jongman et al., 1994) was used to evaluate which of the measured litter parameters had a significant impact on taxonomic composition (density data) of the oribatid mite communities (Canoco for Windows<sup>®</sup> software, version 4;

Ter Braak and Šmilauer, 1998). A partial RDA was conducted with blocks as covariables to remove their effect from the analysis. Due to differences in taxonomic composition between the sites, the two data sets were treated separately. In the RDA, taxonomic data is modelled as a function of ordination axes (Ter Braak, 1994). These are, in turn, restricted to represent linear combinations of a small set of litter parameters, each of which in the present experiment contributed significantly to explaining the variation in the taxonomic data. The statistical significance of the ordination axes was tested by applying Monte Carlo permutation tests (Besag and Clifford, 1989) with 199 permutations (rejection levels:  $P > 0.05$ ). Taxonomic data was log-transformed ( $\log(x+1)$ ) prior to the ordination and taxa with less than two individuals in total or occurring in less than two samples were down-weighted giving them a weight of 0.1 in the analysis (Hill, 1979). The resulting ordination diagrams were scaled to display correlations (standardized and centred by taxon). Sample scores are displayed as points and taxa or litter parameters as vectors (Lepš and Šmilauer, 1999). The vectors point in the direction along which the density of a taxon or the value of a litter parameter increases most rapidly in the diagram and the length of the vector indicates the respective rate of change. For a detailed description on the interpretation of RDA diagrams see Ter Braak (1994).

## 2.6. Methodological evaluation

The results obtained in the present study may be influenced by both methodological shortcomings of

the litterbag approach and site-specific differences. The potential impacts of these confounding variables was examined by averaging community data from both litter qualities of each litter type in the control plots and then comparing this with data from the local pool identified in the  $O_{1+T}$ -layer samples. Averaging over litter quality was necessary to account for the different litter qualities present in the  $O_{1+T}$ -layer samples.

## 3. Results

### 3.1. Litter parameters

The ANOVAs revealed a significant main effect of the factor precipitation on all litter parameters (Table 1). The impact of litter type and litter quality was weaker than that of precipitation, with these two factors only affecting some of the measured parameters (Table 1). The effects of precipitation were independent of litter type and litter quality with no significant interactions between the treatments recorded (Table 1).

The significant main effect of precipitation on litter water content was a result of a large reduction in water content in all litter types and qualities under drought (Tables 1 and 2). The significant main effect of the factor litter type on litter water content was due to the spruce litter tending to be drier than beech litter in the corresponding treatment combinations (Tables 1 and 2). Drought consistently reduced mass loss and N-content, but increased pH, LOI, C content and C/N ratio compared to control conditions. Significant third-order interactions between the three experimental treatments for pH and LOI indicated that the strength of

Table 1

Summary of a three-way ANOVA on litter parameters, microbial biomass and oribatid mite community parameters from 1000  $\mu\text{m}$  litterbags that were exposed at a beech and a spruce forest in Central Germany ( $N=32$ )

Dependent variable	Treatment effects						
	Precipitation (P)	Litter type (LT)	Litter quality (LQ)	P $\times$ LT	P $\times$ LQ	LT $\times$ LQ	P $\times$ LT $\times$ LQ
<i>Litter parameters</i>							
Litter water content [% DM litter]	750.4***	5.4*	2.2 n.s.	0.1 n.s.	1.5 n.s.	0.6 n.s.	0.4 n.s.
PH <sub>H2O</sub>	111.1***	0.0 n.s.	18.6***	0.6 n.s.	2.2 n.s.	97.1***	9.0**
Mass loss [% initial DM]	42.3***	11.6**	0.9 n.s.	2.6 n.s.	2.8 n.s.	72.0***	0.9 n.s.
LOI [%]	96.8***	55.6***	142.3***	0.0 n.s.	2.6 n.s.	107.7***	14.3***
C/N ratio	40.5***	0.0 n.s.	31.8***	3.5 n.s.	4.2 n.s.	0.1 n.s.	0.5 n.s.
C [% DM litter]	6.7*	69.4***	0.5 n.s.	0.1 n.s.	0.0 n.s.	20.0***	0.0 n.s.
N [% DM litter]	42.1***	3.1 n.s.	34.3***	4.2 n.s.	3.5 n.s.	1.5 n.s.	0.3 n.s.
<i>Microbial biomass</i>							
C <sub>mic</sub> [mg C g <sup>-1</sup> DM litter]	77.8***	48.7***	0.1 n.s.	43.8***	24.3***	0.4 n.s.	0.2 n.s.
<i>Oribatid mite community parameters</i>							
Taxonomic richness	57.3***	13.4**	13.4**	4.4*	13.4**	8.3**	3.3 n.s.
Oribatid mites [ind g <sup>-1</sup> DM litter]	101.5***	16.2***	4.7*	13.6**	11.6**	0.7 n.s.	2.3 n.s.
Adults [ind g <sup>-1</sup> DM litter]	47.6***	37.8***	3.3 n.s.	5.2*	14.5**	0.4 n.s.	0.7 n.s.
Juveniles [ind g <sup>-1</sup> DM litter]	88.8***	0.8 n.s.	0.0 n.s.	3.1 n.s.	0.6 n.s.	6.8*	0.4 n.s.

Main effects used in the model were precipitation (ambient precipitation, summer drought), litter type (beech, spruce), and litter quality (fresh, pre-incubated).  $F$ -values and  $P$ -levels of main effects and two- and three-way interactions on each of the dependent variables are presented. Significance level of  $F$ -values: \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$ ;  $P \geq 0.05$  = n.s. (not significant).



Table 2

Mean values of litter parameters, microbial biomass and oribatid mite community parameters derived from litterbags that were exposed at a beech and a spruce forest

Litter type treatments	Litter quality	Beech		Spruce	
		C	D	C	D
<i>Litter parameters</i>					
Litter water content [% DM litter]	F	350.6 b (94.5)	70.3 a (3.6)	337.9 b (16.3)	53.9 a (3.4)
	I	412.9 b (64.5)	73.6 a (18.0)	357.9 b (23.3)	54.8 a (2.9)
PH <sub>H2O</sub>	F	5.0 b (0.4)	5.7 c (0.3)	4.2 a (0.1)	5.2 b (0.1)
	I	4.5 a (0.1)	5.4 bc (0.1)	5.5 bc (0.1)	5.8 c (0.0)
Mass loss [% initial DM]	F	22.3 bc (9.3)	4.4 a (3.3)	27.5 cd (8.0)	15.6 bc (1.6)
	I	37.6 d (2.0)	24.7 cd (3.2)	11.3 ab (4.6)	15.6 bc (1.6)
LOI [%]	F	95.4 cd (0.3)	95.9 e (0.1)	95.0 bc (0.2)	95.9 e (0.1)
	I	93.7 a (0.3)	94.6 b (0.3)	95.2 c (0.1)	95.5 d (0.1)
C:N ratio	F	26.0 ab (2.8)	29.2 bc (2.3)	24.7 a (1.0)	30.7 c (0.9)
	I	23.8 a (0.8)	25.5 a (1.2)	23.0 a (0.9)	25.9 ab (0.5)
C [% DM litter]	F	50.2 ab (0.8)	50.6 b (0.5)	50.8 bc (0.5)	51.3 bc (0.1)
	I	49.2 a (0.7)	49.7 ab (0.3)	51.5 c (0.4)	52.0 cd (0.2)
N [% DM litter]	F	1.9 bc (0.2)	1.7 ab (0.1)	2.1 cd (0.1)	1.7 a (0.0)
	I	2.1 cd (0.1)	1.9 bc (0.1)	2.2 d (0.1)	2.0 cd (0.0)
<i>Microbial biomass</i>					
C <sub>mic</sub> [mg g <sup>-1</sup> DM litter]	F	18.5 c (5.5)	12.3 b (1.3)	17.4 bc (1.2)	5.2 a (0.7)
	I	13.4 bc (3.2)	15.1 bc (2.0)	13.1 bc (1.1)	7.2 a (0.3)
<i>Oribatid mite community parameters</i>					
Mean taxonomic richness	F	5 ab (1.5)	3 ab (1.5)	4 ab (1.7)	3 ab (0.6)
	I	11 c (1.9)	3 ab (1.0)	6 b (1.0)	2 a (1.1)
Oribatid mites [ind g <sup>-1</sup> DM litter]	F	35.7 d (19.4)	27.8 cd (16.4)	43.1 d (11.2)	7.5 ab (4.5)
	I	54.7 d (14.8)	9.8 bc (3.2)	35.8 d (4.8)	2.9 a (1.2)
Adults [ind g <sup>-1</sup> DM litter]	F	25.2 d (14.1)	24.5 d (14.4)	12.0 bcd (3.6)	4.0 ab (2.8)
	I	34.4 d (13.8)	6.3 bc (1.8)	17.0 cd (7.4)	1.5 a (1.0)
Juveniles [ind g <sup>-1</sup> DM litter]	F	10.6 bc (5.5)	3.3 ab (2.9)	31.0 c (9.2)	3.5 ab (2.3)
	I	20.3 c (2.5)	3.5 ab (2.4)	18.8 c (7.1)	1.5 a (0.8)

Litterbags contained fresh litter (F) or pre-incubated litter (I) and were subjected to ambient precipitation (C=Control) or summer drought (D=Drought). Within each site, mean parameter values sharing the same letter are not significantly different at  $P=0.05$  (Tukey's HSD test), [ $n=4$ ; mean (SD)].

the drought effect on these parameters varied among litter types and qualities.

Differential effects of pre-incubation on the different litter types resulted in significant interaction terms for many litter parameters (Table 1). In comparison to the corresponding fresh litter quality, pre-incubated beech litter had a lower pH and C content, but, on the contrary, these parameters had higher values in pre-incubated spruce litter (Table 2). As a consequence, pre-incubation had reversed the order of pH-differences observed between fresh beech and spruce litter (Table 2). Moreover, compared to fresh litter, pre-incubation had stimulated mass loss from beech litter but had slowed down mass loss from spruce litter.

The significant interaction between the factors litter type and litter quality for LOI was a result of greater differences in LOI between litter qualities in beech litter compared to spruce litter (Table 1). In pre-incubated beech litter, LOI values were significantly lower compared to spruce litter in corresponding precipitation treatments while LOI values of fresh beech and spruce litter were similar (Table 2). In general, pre-incubated litter revealed higher N contents and lower C/N ratios compared to fresh litter (Tables 1 and 2).

### 3.2. Microbial biomass

The effects of drought on microbial biomass differed between litter types and qualities (Tables 1 and 2). At the beech site, a reduction in C<sub>mic</sub> values due to drought was only observed in fresh litter, whereas the microbial community in spruce litter was drought-sensitive in both litter qualities (Table 2). This resulted in a positive correlation between litter water content and C<sub>mic</sub> values (Spearman rank correlation coefficient:  $r_s^2=0.52$ ,  $P=0.002$ ) in the spruce litter. In addition, C<sub>mic</sub> values were also positively related to increasing litter N content ( $r_s^2=0.41$ ,  $P=0.008$ ), but negatively related to increasing litter C/N ratio ( $r_s^2=0.49$ ,  $P=0.002$ ) and LOI ( $r_s^2=0.92$ ,  $P<0.0001$ ). In contrast, microbial biomass in beech litter was not correlated with any measured beech litter parameter.

### 3.3. Oribatid community parameters

Average density of oribatids in the litterbags ranged between 2.9 and 54.7 ind g<sup>-1</sup> DM litter. The total number of oribatid taxa extracted from the litterbags was 20, but average taxonomic richness per litterbag sample varied

between 2 and 11 taxa. ANOVA results indicated specific and interactive effects of the experimental treatments on oribatid mite communities (Table 1). In general, drought conditions reduced both taxonomic richness and densities of adult oribatid mites but these effects were considerably influenced by the factors litter type and quality (Tables 1 and 2). Densities of adult oribatid mites under drought conditions were significantly higher in beech litter than in the corresponding litter quality in spruce litter. However, in both types the negative impact of drought was much more pronounced in the pre-incubated litter than in fresh litter suggesting a greater sensitivity of oribatid mites colonising pre-incubated litter (Table 2; Fig. 1).

No differences were found in overall densities of adult oribatid mites between fresh and pre-incubated litter in either litter type (Table 1). However, there were effects of litter quality on taxonomic richness and this differed between litter types (Table 1). In spruce litter, taxonomic richness was very similar in both litter qualities under ambient precipitation. In contrast, pre-incubated beech litter under ambient precipitation contained twice as many taxa as fresh beech litter

and also pre-incubated spruce litter (Table 2). This greater diversity occurred despite the number of potential colonizer taxa (i.e. the number of taxa in the local pool) being similar at both sites (one-way ANOVA,  $F=3.11$ ,  $P=0.13$ ; average taxonomic richness: spruce =  $9 \pm 2$ , beech =  $12 \pm 3$ ).

Juvenile oribatid mites, in contrast to adult oribatid mites, appeared to be unaffected by litter type and quality, but they were particularly sensitive to drought (Tables 1 and 2; Fig. 1).

### 3.4. Taxonomic composition of oribatid communities in litterbags

The results of a cluster analysis on the taxonomic similarity of the litterbag communities in the different treatments indicated distinct differences in composition between the two litter types (Fig. 2). Litterbag communities in beech and spruce litter shared a total of 11 taxa, while 8 taxa (including three abundant taxa) were restricted to beech litter and only one rare taxon was unique to spruce litter (Appendix). Despite these differences in taxonomic composition, the communities in droughted, pre-incubated litter were the most dissimilar from the other communities in both litter types (Fig. 2). A comparison of the remaining treatment combinations indicated litter type-specific differences in the effect of environmental conditions on community similarity. While beech litter communities appeared less sensitive to drought conditions but sensitive to changes in litter quality, spruce litter communities reacted drought sensitive and showed only a limited response to changes in litter quality (Fig. 2).

Analysis of the community density data sets using RDA clearly demonstrated the significant relationships between taxonomic composition and litter parameters (Fig. 3). In the beech data set, the parameters litter water content (LWC), pH and LOI explained 44% of the total variation in the taxa

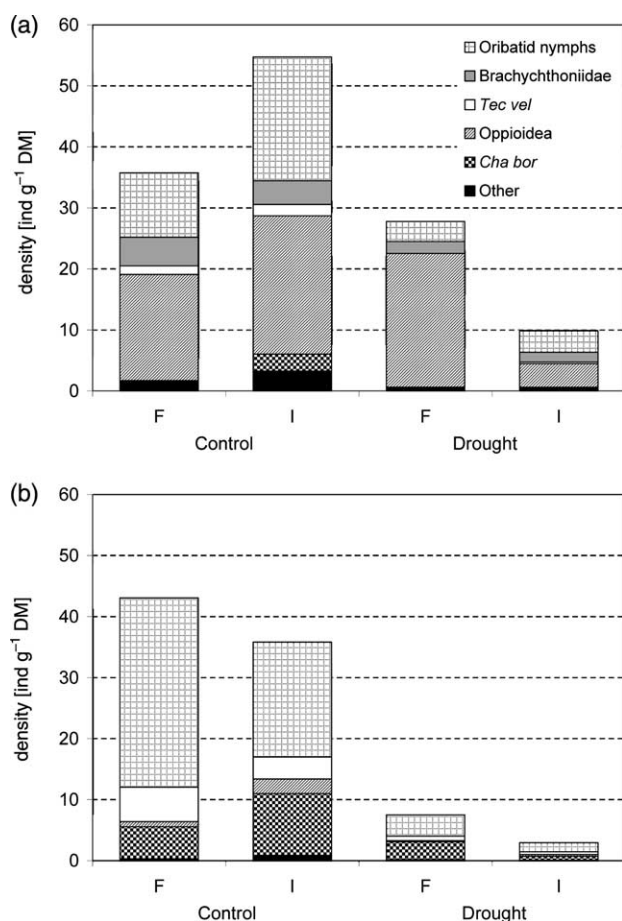


Fig. 1. Mean densities [ind g<sup>-1</sup> DM] of oribatid mite taxa extracted from litterbags that were exposed at a beech (a) and a spruce (b) forest. Litterbags contained fresh litter (F) or pre-incubated litter (I) and were subjected to ambient precipitation (Control) or summer drought (Drought),  $n=4$ . [For taxa abbreviations see Table Appendix].

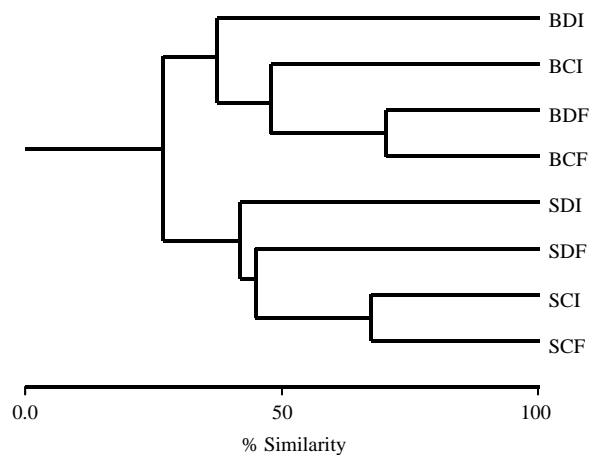


Fig. 2. Cluster Analysis (single-linkage) on the similarity of oribatid mite communities in litterbags based on Bray Curtis' similarity indices. Litterbags contained fresh (F) or pre-incubated (I) beech (B) or spruce (S) litter and were subjected to ambient precipitation (C) or summer drought (D),  $n=4$  (Data not transformed).

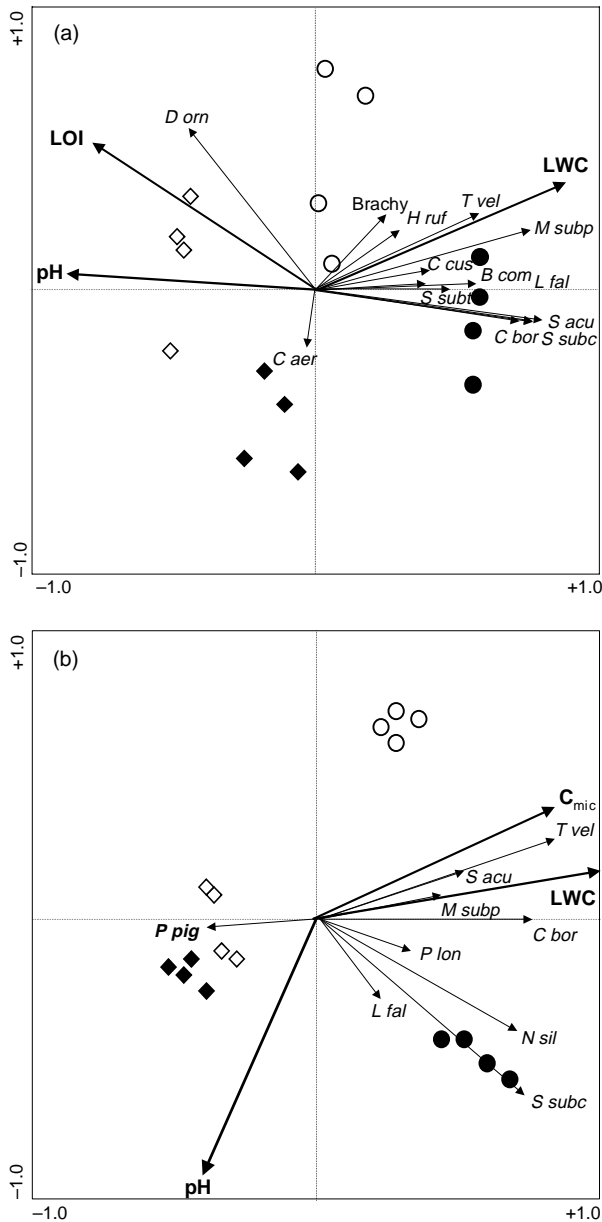


Fig. 3. Correlation triplots based on a partial redundancy analysis (RDA) of the oribatid mite communities in litterbags exposed at a beech (a) and a spruce (b) forest. Vectors indicate quantitative litter parameters (LWC=litter water content;  $C_{mic}$ ; LOI; pH) and taxa (taxa abbreviations: Brachychthoniidae=Brachy; *H.rufulus*=*H ruf*; *P. longulus*=*P lon*; *P. piger* group=*P pig*; *C. spinifer*=*C spi*; *P. peltifer*=*P pel*; *N. silvestris*=*N sil*; *N. sellnicki*=*N sel*; *B. compta*=*B com*; *C. aerolatus*=*C aer*; *T. velatus*=*T vel*; *D. ornata*=*D orn*; *L. falcata*=*L fal*; *M. subpectinata*=*M sub*; *A. grandis europaea*=*A gra*; *S. acutidens* group=*S acu*; *S. subcornigera* group=*S subc*; *S. subtrigona*=*S subtr*; *C. borealis*=*C bor*; *C. cuspidatus*=*C cus*; only taxa that were not down-weighted in the analysis are displayed). Symbols represent samples (○, Fresh litter, Control; ●, Pre-incubated litter, Control; ■, Fresh litter, Drought; ◆, Pre-incubated litter, Drought). For legend details see Fig. 1,  $n=4$ .

data (Fig. 3a). The eigenvalues are 0.31 (axis 1) and 0.04 (axis 2), respectively. Most variation in beech litter was accounted for by the first RDA axis (38%), which was a function of all three-litter parameters (correlation coefficients with axis one: LWC:  $r=0.89$ , pH:  $r=0.9$ ,

LOI:  $r=-0.81$ ). Due to the strong negative correlation of litter water content and pH (pH×LWC:  $r=-0.81$ ), the effects of both parameters need to be interpreted jointly.

The majority of taxa in beech litter were positively related to litter water content and negatively to pH (Fig. 3a). These taxa occurred at either lower than average densities or were absent under drought conditions (cf. Appendix). However, in contrast to this general trend, the species *Disshorina ornata* appeared unaffected by moisture conditions having similar densities within each litter quality under control and drought. Taxa that exhibited preferences for one litter quality (see also Fig. 1; Appendix) were either positively (preference for fresh litter: *D. ornata*) or negatively (preference for pre-incubated litter: mainly Suctobelbidae, Chamobatidae, *Medioppia subpectinata*, *Lauroppia falcata*) correlated to the parameter LOI (Fig. 3a). The latter group was also positively related to more acidic conditions. The clear preference by this large group of taxa for lower LOI and pH values explains the significantly higher taxonomic richness observed in pre-incubated compared to fresh control litter (Table 2).

In spruce litter, variations in the densities of the majority of taxa were significantly correlated to changes in the parameters litter water content,  $C_{mic}$  and pH (Fig. 3b). The eigenvalues are 0.36 (axis 1) and 0.08 (axis 2), respectively. The first two RDA axes explained 52% of the total variation in the data set. Litter water content and  $C_{mic}$  were strongly correlated with the first axis (LWC:  $r=0.97$ ;  $C_{mic}$ :  $r=0.82$ ) that explained most variation (43%). The effects of these two factors upon the oribatid mite communities have to be interpreted jointly due to the strong positive correlation between the two parameters ( $C_{mic} \times LWC$ :  $r=0.92$ ). Litter pH was additionally negatively correlated with the second axis ( $r=-0.89$ ). The majority of oribatid mite taxa in spruce litter had either low densities or were absent from the drought plots (cf. Appendix). Effects of litter quality on oribatid taxa were less distinct than in beech litter (Fig. 3a and b). The most abundant and dominant taxa in spruce litter reacted mainly to changes in litter water content and  $C_{mic}$  (*Tectocepheus velatus*, *Chamobates borealis*, *Suctobelbella acutidens* group, *M. subpectinata*, *Camisia spinifer*) and therefore exhibited no litter quality preferences (Fig. 3b). As a result mean densities of adult oribatid mites were similar in fresh and pre-incubated control litter (Table 2; Fig. 1). However, some differences in taxonomic composition between litter qualities were evident. A group of less abundant taxa (*Suctobelbella subcornigera* group, *Nothrus silvestris*, *Phthiracarus longulus*, *L. falcata*) mainly occurred in pre-incubated control litter (Fig. 3b). The drought-sensitive reaction of these taxa was primarily responsible for the significantly reduced taxonomic richness in the pre-incubated litter under drought conditions (Table 2). Short species vectors indicate a very limited influence of the three litter parameters on population densities of the remaining taxa (Brachychthoniidae,

*Suctobelbella subtrigona*, *Phthiracarus piger* group, *Carabodes aerolatus*).

### 3.5. Methodological evaluation

Prior to the final statistical analysis, which is presented in Table 1, block effects were analysed separately at each site by means of a three-way ANOVA on the effects of block, precipitation and litter type for the fauna and litter variables. At both sites, there was a significant block effect on the mean densities of adult oribatid mites (Beech:  $F=5.02$ ,  $P=0.045$ ; Spruce:  $F=5.14$ ,  $P=0.043$ ) with significantly lower numbers found in one of the four blocks. At the beech site, the block effect was due to the comparatively low numbers of Oppioidea recovered from the control plots (for both fresh and pre-incubated litter) on block four. At the spruce site, the comparatively low numbers of *T. velatus* and *C. borealis* on the control plots in block two resulted in the significant block effect. In no case was there a significant interaction between the block effect and one of the other factors. Therefore, we do not consider the block effect to have significantly influenced the overall results of the experiment.

At the beech site, mean densities of adult oribatid mites in the litterbags ( $30 \pm 14$  ind  $g^{-1}$  DM) were significantly higher (Tukey's HSD test,  $P=0.041$ ) than in the  $O_{1+}$ -layer community ( $8 \pm 3$  ind  $g^{-1}$  DM). However, taxonomic richness in the  $O_{1+}$ -layer and the litterbag communities was similar (Appendix), but the local community was more evenly structured. Litterbag communities were characterised by a large step between the most dominant taxon, *D. ornata* (40%), and the next most abundant taxon, *M. subpectinata* (19%). The most dominant local taxa were the Brachychthoniidae (23%), followed by *S. subcornigera* group (16%) and *Oppiella nova*. The latter species accounted for 15% of the adult oribatid mites in the  $O_{1+}$ -layer but was not found in the control litterbags (Appendix).

At the spruce site, mean densities of adult oribatid mites in the litterbag samples ( $14.5 \pm 5.0$  ind  $g^{-1}$  DM) were similar to those in the  $O_{1+}$ -layer ( $12.5 \pm 12.9$  ind  $g^{-1}$  DM; Tukey's HSD test,  $P>0.05$ ). Total taxonomic richness was lower in the litterbags than in the  $O_{1+}$ -layer (Appendix) and there were some pronounced differences in the dominance structure. The litterbag community was dominated by *T. velatus* and *C. borealis* (Appendix), which together represented, on average, 83% of the adult oribatid mites. The  $O_{1+}$ -layer community was strongly dominated by species of the family Oppiidae, but which accounted for only 4.7% of the adult oribatid mites in the litterbag samples.

Within each site, similarity between litterbag and local communities, estimated using the Bray Curtis index (BCI) using either density data (ind  $g^{-1}$  DM; Beech, BCI: 0.54; Spruce, BCI: 0.56) or relative abundance (%; Beech, BCI: 0.45; Spruce, BCI: 0.54) were moderately high. Litterbag

communities contained the majority of taxa present in the local pools and, with the exception of *O. nova*, it was mainly the very rare taxa from the local pool at both sites that were not found in the litterbags (Appendix). In turn, at both sites, a number of rare taxa extracted from the litterbag material were not found in the local pool (Appendix).

## 4. Discussion

The present study demonstrated that the response of oribatid mite communities to drought was directly determined by differences in taxon-specific drought sensitivity and indirectly, as a consequence of this, by the effects of litter type and quality upon taxonomic composition. The following discussion will focus first on the litter quality-induced changes in species composition of oribatid communities and will then, in turn, use those to explain why oribatid communities in the two litter qualities differed in their response to summer drought. Finally, the response of oribatid communities in the two litter types to the factors precipitation and litter quality will be discussed with respect to the decompositional patterns of broadleaved and needle litter.

### 4.1. Effect of litter quality on oribatid mite communities under control conditions

In forest habitats, decomposing litter appears to gradually move down the soil profile due to the constant input of fresh litter from above. This process results in a layering of the organic horizons with each layer composed of litter at a certain decompositional stage. Each litter layer is characterised by a distinctive oribatid mite community (Anderson, 1975; Hågvar and Kjøndal, 1981). Oribatida communities found in litterbags often closely resemble these communities found in the litter layer that correspond to the decomposition stage of the litterbags material (for beech litter see Woas et al. (1989); for pine see Berg et al. (1998)). These successional stages of oribatid mite communities during litter decomposition also show characteristics that correspond to those observed for oribatid communities in different stages of secondary plant succession (Scheu and Schulz, 1996).

Surface dwellers are usually the primary colonisers of litterbags containing fresh beech litter. *Disshorina ornata* is often very abundant in beech forests (Skubala, 1999) and, as such, is typically the most important species during the early colonisation of litterbags (Woas et al., 1989). As succession continues, further Oppiidae species appear, until they are finally replaced by members of the family Suctobelbidae (Woas et al., 1989). The high dominance of *D. ornata* (61%) in the present study together with the fact that, apart from *M. subpectinata*, no other Oppiidae species were found therefore suggests a relatively early stage of succession in the fresh beech



control litter. This pioneer character of the oribatid community is further supported by the observation that the additional oribatid mite species were restricted to surface dwellers, e.g. *P. peltifer* and *C. aerolatus* (Krivolutsky, 1995), species commonly known as early coloniser species, like *T. velatus* (Maraun and Scheu, 2000) or generalists, as *Hypochthonius rufulus* (Wunderle, 1992). The latter two species are known to be similarly abundant in different beech litter layers (Woas et al., 1989; Krivolutsky, 1995) and in the present study also occurred in similar densities in both litter qualities.

Oribatid mite communities in litter at later stages of decomposition are commonly characterised by greater species richness (Scheu and Schulz, 1996), including more species of less common oribatid mites, and greater numbers of individuals (e.g. Anderson, 1975). This was clearly the case at the beech site, where the effects of litter quality were very pronounced under control conditions as the incubated beech litter hosted more taxa and the community structure was more even than in the fresh litter. In particular, the higher densities and dominance of the genus *Suctobelbella* and the presence of species from the family Phthiracaridae suggested that oribatid mite communities in incubated litter had reached a more advanced successional stage than in fresh litter. These taxa—for the Phthiracaridae the adult stages—are known to occur in more decomposed litter material (Pande and Berthet, 1973; Ponge, 1991; Hansen, 2000). Suctobelbidae species are generally described as late colonisers, mainly inhabiting the F- or H-layer (Märkel, 1958; Hasegawa, 1997; Berg et al., 1998; Lindberg, 2003).

In contrast to beech litter, oribatid mite communities in fresh and pre-incubated spruce litter were rather similar under control conditions. This was mainly due to both communities being dominated by two cosmopolitan and early coloniser species, *T. velatus* and *C. borealis*. Both of these species have a wide ecological range (Rajski, 1970; Scheu and Schulz, 1996) and demonstrate no preference for any particular litter layer (Krivolutsky, 1995). Other species of the genus *Chamobates* have also been found to be early colonisers of litterbags (Crossley Jr. and Hoglund, 1962; Lebrun and Mignolet, 1979). However, greater densities of taxa that either were comparatively rare or did not occur in fresh spruce litter also suggested a later successional stage of oribatid mite communities in pre-incubated spruce litter. The respective taxa are either known as late colonisers (*S. subcornigera* group) or are reported to preferentially feed on decomposing needles, often in the H-layer (Pande and Berthet, 1973; Beck and Woas, 1991).

In both spruce and beech, the abundance of individual taxa that showed a preference for either fresh litter (e.g. *D. ornata*) or pre-incubated litter (e.g. Suctobelbidae species) were strongly correlated to litter parameters e.g. the C:N ratio, litter N content and loss on ignition (LOI). These parameters are often used to characterise the degradation

stage of a substrate (see Chapin III et al. (2000) and references therein) as they undergo significant (usually non-reversible) changes during litter decomposition (Berg and Staaf, 1981). The results from the present study and from Hasegawa (1997), who found a negative correlation between Suctobelbidae species and C:N ratios in litter, support the idea that these parameters may determine when, on a temporal scale, certain mite taxa colonise a decaying substrate. In beech litter, the relationship between taxa densities and changes in LOI was sufficiently common to be significant even at the community level.

The species richness of oribatid mite communities, especially that of late colonisers, in litter is strongly correlated to the rate of litter decomposition, with rapidly decomposing litter types usually hosting more species at higher densities (Anderson, 1975). In general, broadleaved litter, including beech, decomposes faster than needle litter, at least initially (Prescott et al., 2000; Albers et al., 2004). The litter parameters measured in the pre-incubated litter in the present study (Table 2) also indicate greater decomposition of beech compared to needle litter. It seems likely that the higher taxonomic richness in pre-incubated beech compared to pre-incubated spruce litter under control conditions reflects these differences in decomposition patterns between leaf and needle litter. Specifically, the earlier availability of resources and a greater microhabitat heterogeneity at an earlier decomposition stage, with potentially more favourable feeding or oviposition sites (Hansen, 1999) in the beech litter could have facilitated the development of a more diverse community. This idea would support the findings of Sulkava and Huhta (1998), which showed that the heterogeneity at the small scale of an individual soil organism can be an important determinant of soil community diversity.

#### 4.2. Effect of drought on oribatid mite communities in different litter types and qualities

Litter water content was the parameter most strongly affected by the drought treatment and, in turn, was the factor that most strongly affected the abundance patterns of individual oribatid mite taxa. In general, adult oribatid mites seem to be able to tolerate a wide range of moisture conditions (Walter and Proctor, 1999; Taylor et al., 2002), but unfavourable conditions such as extended summer drought can have a strong negative effect on oribatid mites (Lindberg et al., 2002). Direct effects of low moisture availability on mites are probably expressed via the biology of individual species. In the present study, low population densities under drought conditions may reflect direct moisture effects on species with short life cycles and high reproduction rates such as *T. velatus* (Lebrun, 1965; Luxton, 1981). Under favourable moisture conditions, like those in the control, these taxa have the potential to quickly establish populations of considerable size.

For the soft-bodied nymphal stages of the oribatid mites, desiccation is a major problem as their unsclerotised cuticle renders them more susceptible to low moisture conditions than adult mites. In the present study, the generally low densities of juvenile oribatid mites under drought conditions would support this.

The reaction of oribatid mite communities to drought was largely determined by the sensitivity of individual taxa and, since taxonomic composition was related to litter type and litter quality (decomposition stage), both these factors indirectly influenced community response to drought. *Chamobates borealis* and *T. velatus* dominated the community in fresh spruce litter in both control and drought but the abundance of both species in the latter was only 50% of that in the control. Both these species have previously been found to be drought sensitive (Siepel, 1996; Lindberg, 2003). In the fresh beech litter, *D. ornata* was the dominant taxon but, unlike the dominant taxa at the spruce site, this species was tolerant of drought. Niche specialisation by *D. ornata* for drier habitats may be reflected in its greater tolerance for the drought conditions in the present experiment. The fact that taxa colonizing pre-incubated litter were particularly sensitive to drought confirms the finding that later colonisers tend to be drought-sensitive (e.g. Riha, 1951; Lindberg et al., 2002). This may be due to an adaptation of these taxa to the relatively more stable environmental conditions of deeper organic layers.

The physical characteristics of a decaying litter can strongly influence moisture conditions experienced by associated organisms (Dix, 1984). Leaf litter generally exhibits greater surface area and moisture retention compared to needle litter that often forms a relatively dry litter with low surface area (Hansen, 1999; Prescott et al., 2000). A combination of higher moisture retention and a greater microhabitat heterogeneity at an earlier decomposition stage in beech compared to spruce litter (see Section 4.1) might not only explain the observed tendency for higher litter water content in beech litter but, also the absence of an effect of low moisture conditions on microbial biomass in beech in contrast to spruce litter. Both factors could also have contributed to the significantly higher densities of oribatids in pre-incubated beech litter than in pre-incubated spruce litter under drought. Anderson (1975) suggested that there was a strong relationship between structural and nutritional (i.e. the microbial biomass) properties of a substrate and the structure of the mite community present. It may therefore be critical to not only consider the chemical but also the structural aspects of litter decomposition when examining factors controlling the development of oribatid mite communities.

In the present study, as in other studies (e.g. Paul and Clark, 1989), litter moisture was correlated with a number of other litter parameters (pH,  $C_{mic}$ ). In turn, the occurrence and density of some of the oribatid mite taxa were related to these parameters. In parallel with the present results at the beech site, field studies using litterbags and artificial soil pH

gradients in forests have found higher densities of oribatid mites associated with lower soil pH (Hågvar, 1984; Huhta et al., 1986). Data on the reaction of individual oribatid mite species to soil pH is, however, sparse. Ecological studies often emphasise that direct effects of pH on oribatid mites are small (Hågvar, 1984; Huhta et al., 1986; Maraun and Scheu, 2000). The relatively short length of the pH gradients between litter types and qualities (Table 2) in the present study supports the assumption that any effect of pH was primarily due to the strong correlation between litter water content and pH.

In spruce litter, moisture conditions not only influenced the densities of most oribatid mite taxa, but also strongly affected microbial biomass. Microorganisms, in particular fungi, are included in the diet of the majority of adult oribatid mites (Luxton, 1972; Siepel and de Ruiter-Dijkman, 1993; Klironomos and Kendrick, 1995; Schneider et al., 2004). Oribatid mites are commonly considered generalist feeders (Usher et al., 1982; Visser, 1985; Hasegawa, 1997; Maraun et al., 1998) and are often ascribed to one trophic group; the microbe-detritivores (Berg et al., 1998; Scheu et al., 2003). As generalist feeders are unlikely to be food-limited (Takeda, 1987), it may not be surprising that bottom-up effects often seem to be of only limited importance for oribatid mites (Maraun et al., 2001). Nevertheless, it has been shown that the quantity and quality of food resources can influence population growth rates of some oribatid mite species (Bhattacharya, 1962; Stamou and Asikidis, 1993; Hågvar, 1998). It therefore also seems reasonable to assume that, in particular under extreme conditions like drought, the quantity and quality of food resources could affect the colonisation rate of litterbags (Hasegawa and Takeda, 1996). The strong correlation between microbial biomass and densities of the most abundant, drought-sensitive taxa (*T. velatus*, *C. borealis*, *S. acutidens* group, *O. subpectinata*), may therefore indicate that under drought conditions food resources became a limiting factor in spruce litter. Low oribatid mite densities may reflect a drought-specific response to differences in the nutritional quality of both litter and associated microorganisms compared to control conditions.

#### 4.3. Methodological evaluation

According to the literature, species-specific responses to litter type do not appear to be strongly developed within oribatid mites (e.g. Hansen, 2000). However, certain taxa may show preferences for certain habitats as mentioned by Migge et al. (1998). These authors observed a preference by the species *H. rufulus* and genus *Nanhermannia* for beech litter. This was also apparent in the present study. In addition in the present study, a number of other taxa (*D. ornata*, *M. subpectinata*, *C. cuspidatus*, Brachychthoniidae) also showed a preference for beech litter since they were found only or in higher densities in beech litter. The fact that

the Brachychthoniidae mainly occur in beech litter is surprising. This result is contrary to the literature where the group is reported from both beech and spruce sites (Migge et al., 1998; Maraun and Scheu, 2000; Zeitsev et al., 2002).

It could be argued that the difference in the number of litterbags representing a single experimental unit, two in beech and one in spruce (see Section 2), may have influenced any comparison between the litter types. The comparability of both datasets would indeed be problematic if the whole litter material of each litterbag had been used for extraction. The combined species richness of the two beech litterbags would be expected to be higher than for a single litterbag because of the spatial heterogeneity in the distribution of mites in the soil. However, the community estimate in this study was based upon a sample of fixed mass taken from the combined, mixed litter from both beech bags. In order to have an effect of using two litterbags upon either species richness and/or abundance, the abundance in the sample (of fixed mass) from the mixed litter from two litterbags would have to be either greater or less than that from a single litterbag. There is no reason to suppose that this was the case.

Mean densities of adult oribatid mites in litterbags recorded in the present study were typical of communities found in other litterbags studies in temperate forests after 1 year of litterbag exposure (Anderson, 1975; Seastedt et al., 1983; Hasegawa, 1997; Berg et al., 1998). In accordance with litterbag-colonisation studies, in which most ambient species were present in a new substrate after 12 months (e.g. Hasegawa, 1997), the present litterbag communities were, at both sites, similar in composition to the local species pool. However, abundant local late coloniser species not represented in the litterbags (e.g. *O. nova*) may require a longer period of time to colonise litterbags (Hasegawa, 1997).

To conclude, the present study found significant changes in densities and composition of oribatid mite communities in broadleaved and needle litter after only one period of

summer-drought. According to the results there is a potential for permanent alterations of oribatid community structure under persistent periods of summer drought. This is especially likely due to the slow recovery rate of oribatid mite communities after drought disturbance (Lindberg, 2003) and the high drought-sensitivity of juvenile oribatid mites. The consequences of these alterations on ecosystem processes and food web interactions is unclear, particularly since potential effects could be amplified by similar drought-sensitive responses by other soil fauna groups such as Collembola or Enchytraeidae (see Pflug (2001)).

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## Appendix

Mean densities of oribatid mite taxa extracted from litterbags and from soil core samples. Litterbags were exposed at a beech and a spruce forest and contained fresh litter (F) or pre-incubated litter (I). Soil core samples were taken from the O<sub>1+2</sub>-layer (O) at the respective site. Soil core samples received ambient precipitation (A) while litterbags were subjected to ambient precipitation (Control = C) or summer drought (D). [*n* = 4; mean (SD)].

Litter type	Beech					Spruce				
	Precipitation		D		A	C		D		A
Litter quality	F	I	F	I	O	F	I	F	I	O
Total taxonomic richness	8	17	5	8	19	8	5	5	4	15
Mean density [ind 100 g <sup>-1</sup> DM]										
Juvenile oribatid mites	1055 (552)	2029 (254)	327 (292)	350 (245)	147 (77)	3103 (934)	1883 (709)	349 (226)	148 (83)	922 (933)
Brachychthoniidae (Thor, 1934)	468 (440)	387 (383)	195 (193)	159 (227)	232 (210)	0	0	8 (17)	0	49 (42)
<i>Hypochthonius rufulus</i> (C.L. Koch, 1835)	112 (179)	109 (110)	46 (93)	14 (28)	17 (25)	0	0	0	0	0
<i>Phthiracarus longulus</i> (C.L. Koch, 1941)	0	14 (28)	0	0	0	11 (22)	39 (79)	0	0	0
<i>Phthiracarus piger</i> (Scopoli, 1763) group	0	12 (25)	0	0	0	0	0	9 (18)	9 (18)	0
<i>Atropacarus striculus</i> (C.L. Koch, 1935)	0	0	0	0	0	0	0	0	0	1 (3)
<i>Camisia spinifer</i> (C.L. Koch, 1835)	0	0	0	0	0	11 (22)	0	0	0	0

(continued on next page)

Litter type	Beech					Spruce				
	C		D		A	C		D		A
Precipitation	F	I	F	I	O	F	I	F	I	O
Litter quality	F	I	F	I	O	F	I	F	I	O
<i>Plathynothrus peltifer</i> (C.L. Koch, 1839)	14 (28)	0	0	0	0	0	0	0	0	2 (3)
<i>Nothrus silvestris</i> (Nicolet, 1855)	0	12 (25)	0	0	8 (6)	8 (16)	47 (37)	0	0	2 (5)
<i>Nanhermannia elegantula</i> (Berlese, 1913)	0	0	0	0	13 (26)	0	0	0	0	0
<i>Nanhermannia sellnicki</i> (Forsslund, 1958)	0	14 (28)	0	0	2 (5)	0	0	0	0	0
<i>Belba compta</i> (Kulczynski, 1902)	31 (37)	62 (124)	0	15 (30)	0	0	0	0	0	0
<i>Carabodes aerolatus</i> (Berlese, 1916)	13 (27)	0	0	18 (36)	0	0	0	0	0	0
<i>Tectocephus velatus</i> (Michael, 1880)	143 (239)	188 (190)	0	27 (31)	2 (4)	563 (424)	361 (144)	72 (51)	47 (57)	324 (293)
<i>Autogneta spec.</i>	0	0	0	0	1 (2)	0	0	0	0	0
<i>Berniniella sigma</i> (Strenze, 1951)	0	0	0	0	4 (5)	0	0	0	0	11 (8)
<i>Disshorina ornata</i> (Oudemans, 1900)	1459 (884)	510 (194)	2142 (1439)	372 (111)	73 (59)	0	0	0	0	0
<i>Lauroppia falcata</i> (Paoli, 1908)	0	28 (33)	0	0	0	0	10 (20)	0	0	0
<i>Medioppia obsoleta</i> (Paoli, 1908)	0	0	0	0	1 (2)	0	0	0	0	0
<i>Medioppia subpectinata</i> (Oudemans, 1901)	278 (175)	970 (690)	50 (61)	0	31 (24)	47 (38)	55 (62)	0	29 (58)	29 (59)
<i>Oppiella nova</i> (Oudemans, 1902)	0	0	0	0	136 (94)	0	0	0	0	606 (1004)
<i>Allosuctobelba grandis europaea</i> (Paoli, 1908)	0	12 (25)	0	0	0	0	0	0	0	0
<i>Suctobelbella acutidens</i> (Forsslund, 1941) group	0	206 (96)	0	0	87 (36)	38 (31)	45 (68)	0	0	29 (35)
<i>Suctobelbella falcata</i> (Forsslund, 1941)	0	0	0	0	0	0	0	0	0	7 (15)
<i>Suctobelbella perforata</i> (Strenze, 1950)	0	0	0	0	0	0	0	0	0	1 (3)
<i>Suctobelbella similis</i> (Forsslund, 1941)	0	0	0	0	47 (29)	0	0	0	0	6 (8)
<i>Suctobelbella subcornigera</i> (Forsslund, 1941) group	0	461 (274)	0	15 (30)	125 (19)	0	130 (72)	0	0	17 (25)
<i>Suctobelbella subtrigona</i> (Oudemans, 1900)	0	78 (133)	0	0	25 (17)	0	0	20	0	11 (16)
<i>Chamobates borealis</i> (Trägårdh, 1902)	0	278 (238)	0	13 (26)	16 (27)	525 (298)	1012 (684)	291 (262)	61 (24)	155 (73)
<i>Chamobates cuspidatus</i> (Michael, 1884)	0	102 (169)	15 (31)	0	16 (11)	0	0	0	0	0
<i>Ophidiotrichus connexus</i> (Berlese, 1904)	0	0	0	0	2 (5)	0	0	0	0	0

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