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Collembolan communities in shrublands along climatic gradients in Europe and the effect of experimental warming and drought on population density, biomass and diversity

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Abstract

Sampling of arthropods from plants, soil surface and soil was carried out at six sites in shrublands across Europe as part of a multi-disciplinary, EU-sponsored ecosystem research project: 'VULCAN: Vulnerability assessment of shrubland ecosystems in Europe under climatic changes'. Climatic gradients spanned from cold temperate heath- and moorland (Netherlands, Denmark, Wales) to Mediterranean maquis (Catalonia, Sardinia) and from moist moorland (Wales) to dry continental forest-steppe shrubland (Hungary). The experimental setup at each site included three warming plots where radiation during the night was impeded, resulting in an average air temperature increase of 0.3–1.3 °C. (April–June 2003), three drought plots where precipitation was prevented during 1–4 months in the growing season and three control plots.

Collembolan biomass and, less distinctly, population density and average individual weight in the control plots decreased from the northern to the southern sites, suggesting a latitudinal cline controlled by temperature or interaction between temperature and moisture. In contrast, species richness tended to increase from North to South. The extremely dry Hungarian site with low biomass and number of species differed from this pattern and fit into a moisture-controlled cline from humid Atlantic to dry continental climates. These observations may reflect long-term adaptations to climate.

Both warming and drought treatments resulted in significant effects on collembolan density and biomass. More significant effects were observed in the drought treatments than in the warming treatments. The most significant effects for total Collembola and individual collembolan species were found in the Dutch and the Spanish sites, while only few were found in the British, Hungarian and Italian sites. Nearly all significant effects of both warming and drought treatments were negative. Differential responses, i.e. negative, positive or unaffected, of individual species resulted in changes in community structure. The vertical distribution between plants, soil surface and soil showed an increasing proportion of collembolan biomass in the soil layer concurrently with a decreasing proportion in the soil surface layer from the northern to the southern sites. The same change in vertical distribution was observed in several sites as a response to the warming and drought treatments. It is concluded that the effects on collembolan communities resulting from climatic manipulations are very complicated and the result of many direct and indirect factors, partly acting in opposite directions.

Keywords: Collembola, climate, soil, ecosystem, community

1. Introduction

A large number of studies have documented that the present global climatic change has significant consequences for flora, fauna and ecosystem processes worldwide (e.g. Graham & Grimm 1990, Walther et al. 2002, Parmesan & Yohe 2003, Weltzin et al. 2003). Climate change is primarily a global warming correlated with rising atmospheric CO_2 content, but is predicted to involve changes in geographical and temporal precipitation patterns so that some regions will experience increased precipitation while other regions will be subject to drought. Climate models produce the common large-scale prediction that precipitation will increase in the tropical and temperate zones and at high latitudes, whereas the subtropical latitudes will be subject to decreasing precipitation (Walther et al. 2002). However, modelling results for specific geographic regions are ambiguous with discrepancies between the outputs of different models (Weltzin et al. 2003).

The long-term effects of these large-scale physical changes on the biotic communities are highly complex and variable depending on geographical position, ecosystem type, stratum (e.g. above ground plants, litter, soil) and kind of organism. Thus, the same climatic change may have different effect in different climatic zones, biomes and habitats (Hodkinson et al. 1998, Sjursen et al. 2005). The biomes with their flora and fauna, including the Collembola, are to a great extent products of long-term climatic influences. Clines across continents of collembolan density, biomass and biodiversity have been traced and broadly correlated to mean annual temperature and precipitation. Thus, a cline of decreasing population density was suggested from low arctic and cold temperate to tropical climate zones (Petersen & Luxton 1982), while no obvious change in biomass was found at annual mean temperatures between 0 °C and 10 °C (Petersen 1994). Information about changes over time of such large scale biogeographical patterns of distribution related to recent climatic change is not available for small soil animals such as Collembola and Acari, which generally have poor dispersal ability and where general knowledge about geographical distribution and phenology is limited. However, in a few localities monitoring of changes in quantitative population parameters, e.g. abundance, biomass, biodiversity and dominance structure over time, has been correlated with trends in local temperature and precipitation (Irmler 2006, Jucevica & Melicis 2006).

In order to study the effects on field communities of ambient temperature and precipitation (moisture) isolated from other environmental factors, experimental manipulations of field plots using active (Harte et al. 1996) or passive heating (Kennedy 1994, Convey et al. 2002, Dollery et al. 2006, McGeoch et al. 2006, Hågvar & Klanderud 2009) or irrigation and artificial drought (Frampton et al. 2000, Lindberg et al. 2002, Taylor et al. 2004, McGeogh et al. 2006) have been widely used.

The present paper is based on a combination of the biogeographical and the experimental approaches mentioned above with the same experimental setup repeated in six sites along transects from cool to warm and from moist to dry climate in Europe. Biomass and community structure of Collembola along the gradients reflect the long-term adaptation of the communities to climate and other environmental conditions, while the superposed field experiments were intended to yield information on relatively short-term effects of heating and drought and their dependence on local environmental factors. Because this study is part of a multidisciplinary study focused on ecosystem structure and function (Beier et al. 2009), biomass was included as a main measure for quantification of collembolan populations. Based on the scarce literature available it may be expected that collembolan density and biomass will decrease from the northern temperate heathland to the southern subtropical/Mediterranean maquis and from the moist Atlantic heathland to the dry forest steppe of Central Europe.

It was expected that the effect of artificial warming and drought on the collembolan populations caused by the field experiments would differ from site to site depending on ambient climatic and other environmental factors, strength and duration of exposure and the robustness of the collembolan communities to increased temperature and reduced precipitation. Replacement of populations vulnerable to higher temperature and drought by immigration of more resistant species from other localities is unlikely considering the short duration of the experiments. Therefore, the following hypothesis for expected changes of the collembolan communities is proposed: both increased mean annual temperature and decreased precipitation will result in changes of the community structure where some vulnerable species will not be able to maintain the population size of the unexposed habitat while others may benefit from lower competition from the more vulnerable species. However, warming will also tend to shorten the generation time and consequently lead to increased reproduction, which may counteract possible harmful effects of warming. In summary, we may expect quite complicated effects of the warming and drought treatments which will probably differ over the large-scale gradients studied. The present study intended to examine density, biomass and species composition of the collembolan communities as related to the large-scale climatic gradients in Europe and to which extent the effect of climate manipulations on the size and structure of the collembolan communities vary from site to site depending on location on the large-scale gradients.

2. Material and methods

2.1. Site descriptions. The European transects

The transects included six shrubland sites (Beier et al. 2009), i.e. wet *Calluna* moorland (Wales), dry to mesic *Calluna* heathland (Denmark, Netherlands), maquis (Sardinia and Catalonia) and poplar shrubland on inland dunes (Hungary), representing large-scale North-South (cool to warm climate) and West-East (wet to dry climate) gradients in Europe (Tab. 1). Apart from the considerable differences in climatic factors, differences in soil properties also existed between sites, where the top soil of the three northern moor- and heathland sites have a high content of organic matter and low pH while the Central and Southern European sites have very low soil organic matter content and high pH.

2.2. Experimental manipulation of temperature and precipitation

Manipulations of temperature and precipitation were carried out in the same way in all sites, i.e. by covering experimental plots with automatically working curtains, resulting in reduced heat radiation during night and reduced precipitation in the growing season (Beier et al. 2004). In all sites each of the treatments (warming, drought and control) were replicated in three experimental plots, each covering 4 x 5 m^2. In order to avoid lower precipitation as a result of the warming treatment, the reflective curtains were retracted in case of rain during the night. During one or two periods per year critical for plant growth (Tab. 2), the drought plots were automatically covered by transparent polythene curtains at the onset of rain and retracted as soon as the rain stopped. In the Danish, Dutch, British and Spanish sites the climatic manipulations started in 1999, while in the Hungarian and Italian sites the experimental setup was working as of 2002. Thus, at the time of fauna sampling the treatments had been active in ca. 4.5 and 1.5 years in the two groups of sites, respectively.

The experimental passive warming resulted in an increase of mean air temperature ranging from 0.3 to 1.3 °C in April to June 2003 (Tab. 2), while the difference between soil temperatures in warming treatment and control plots varied between -0.1 °C and +2.2 °C. With the exception of the Italian site, drought treatment reduced precipitation between 9.9 and 92.6% during the month of fauna sampling, which resulted in a reduction of soil moisture (Tab. 2).

2.3. Sampling and extraction of arthropods

The fauna samplings were carried out from April to July 2003 in the sequence: Capo Caccia (Sardinia, Italy: Apr. 29–May 4), Garraf (Catalonia, Spain: May 13–17), Kiskun Sag (Hungary: May 27–June 1), Mols (Denmark: June 23–27), Oldebroeck (Netherlands: July 9–13) and Clocaenog (Wales, U.K.: July 19–23). The time schedule was chosen so that the mean temperatures of the sampling months were expected to be relatively similar. Five sample plots (1.25 m^2) were chosen for fauna sampling within each of the experimental plots. The positions of the sample plots were selected to represent the most dominant plant species occurring in all plots of the respective sites. (Tab. 1). In the British and the Dutch sites where the cover of heather *(Calluna vulgaris*) was nearly complete, all sample plots had high cover of heather plants. In the British site the positions of sample plots were selected by distinguishing between dominance of old and young plants and the presence of *Vaccinium myrtillus*, while in the Dutch site distinction between high, low and wiltered *Calluna* was used as criterion for selection of sample plots.

Arthropods from the surface of plant leaves and stems were sampled from the total area of each sample plot by systematic suction of all plant surfaces using a vacuum cleaner powered by a generator. A polythene box with fine-meshed netting over the exit hole connected between the suction mouthpiece and the vacuum cleaner functioned as a fauna trap. Animals dropping to the ground during sampling were caught in small polythene boxes with aqueous benzoic acid placed beneath the plants. The area of the boxes was used to recalculate the number of specimens sampled to numbers per m^2. This estimate was added to the numbers per m^2 calculated from the plant suction samples. After sampling from the plants, the same suction method was used to sample animals occurring on the ground surface from the same area in the Italian site and a smaller area (78.6 cm^2) in the other 5 sites. Suction from the soil surface was not possible in the Welsh site because too much moisture prevented proper function. Instead, sample units (area: 76.6 cm^2) of the surface litter-/moss-layer were collected and brought to the Mols Laboratory in a refrigerated box for high-gradient extraction. In each site, after sampling the surface layer, a 10 cm deep soil core (area: 25 cm^2) was taken in each sample plot and stored in a refrigerated box for 2–8 days until mounting in high-gradient extractors (Gjelstrup & Petersen 1987) at the Mols Laboratory. Extraction to aqueous benzoic acid solution was accomplished through 10 days with surface temperature of inverted soil cores gradually increasing from 25 °C to 60 °C. After extraction and sorting the animals were stored in glycerol. Animals in the suction samples from the plant layer and the soil surface were separated from plant and soil particles by means of glycerol flotation (Gjelstrup & Petersen 1987). Sampling of soil cores was difficult in the Italian site because of the extremely compact surface soil. This may have resulted in slightly smaller area and depth of some soil cores. Identification of Collembola to species was based on Baquero & Jordana (2008), Bretfeld (1999), Carapelli et al. (2001), Fjellberg (1998, 2007), Gisin (1960), Jordana et al.(1997), Mateos (2008), Potapov (2001) and Rusek (2002). Identification of some questionable specimens from the Hungarian site was kindly checked by Dr Lázslo Dányí, Hungarian Natural History Museum, Budapest, Hungary, and some specimens from the Spanish site by Professor Rafael Jordana, University of Navarra, Pamplona, Spain. Specimens of *Lepidocyrtus* from Sardinia were checked by Dr Eduardo Mateos, University of Barcelona, Spain.

Biomass was calculated as numbers per m^2 multiplied by average individual weights. The average individual weights were based on measurements of body lengths of a representative number of specimens, as far as possible specific for species, site, stratum (plant/surface/soil) and treatment and calculated as dry weight using regressions in Petersen (1975). The dry weights were recalculated to estimates of wet weight by multiplication with 3 (approximate fresh weight: dry weight ratio based on Petersen 1975). Because length-weight regressions for several species in the present study are not known, approximations for those species were obtained by using regressions for related species of similar body shape. Thus, the individual weights were calculated using the following original regressions: *Onychiurus armatus* (Tullberg, 1869) juv. (for Poduromorpha excl. Onychiruridae), *Onychiurus armatus* s. l., juv + ad (for *Protaphorura* Absolon, 1901 and *Onychiurus* Gervais, 1841), *Tullbergia krausbaueri* Börner 1901 (for *Mesaphorura* Börner, 1901, Tullbergiinae), *Folsomia quadrioculata* (Tullberg, 1871) s. l. juv. (for *Micranurophorus* Bernard, 1977), *Folsomia quadrioculata* s. l. juv+ad (for *Cryptopygus* Willem, 1901, *Folsomia* Willem, 1902, *Folsomides* Stach, 1922), *Isotoma notabilis* Schäffer, 1896 juv. (for *Pseudisotoma* Handschin, 1924, *Isotoma* Bourlet, 1839; *Isotomurus* Börner, 1903), *Isotoma notabilis* juv+ad (for *Parisotoma* Bagnall, 1940), *Lepidocyrtus lignorum* (Fabricius, 1793) (for Entomobryidae), *Tomocerus flavescens* (Tullberg, 1871) (for Tomoceridae), *Dicyrtoma minuta (*O. Fabricius, 1783), juv+ad. (for Dicyrtomidae and Sminthuridae), *Sminthurinus aureus* (Lubbock, 1862)*/flammeolus* (Gisin, 1957) (for other Symphypeona and Neelipleona).

2.4. Statistical treatment

The overall effect of sites and treatments on total collembolan density, biomass and average individual weight was tested by a mixed model analysis of variance (Littell et al. 2006). The model included site, treatment and interaction between treatment and site. A random factor with block*treatment was used to account for the nested design, i.e. the dependencies between observations in the same block, where treatment was nested within block. This test was calculated using Proc mixed in ©SAS vers. 9.2 (SAS Institute, Cary, NC). An initial analysis of the residuals revealed that, for each of the three variables, one observation for each test proved to be a substantial outlier, which disrupted the fit to normality. After removal of the outliers, the residuals for all tests fulfilled assumptions of normal distribution and homogeneity of variances.

Testing the effect of experimental warming and drought, respectively, on density and biomass of collembolan species and higher taxa was carried out by the non-parametric Mann-Whitney test (©SYSTAT 8.0, 1998). The latter analysis was based on mean values of the data from the 5 sample plots within each plot, i.e. 3 values per treatment considering each of the 9 plots in each site as the smallest independent unit (Peñuelas et al. 2004). The tests were confined to species or species groups with a dominance in abundance above 1%. PCA analysis based on log (n + 1)-transformed mean values of population density in each treatment in each site and Shannons diversity index, evenness and species richness was performed using ©SAS/INSIGHT (SAS Institute 2004).

Tab. 1 Selected site characteristics based on measurements from the control plots of the six VULCAN-sites (Beier et al. 2009). Data in bold print are from 2003, the year of fauna sampling calculated from original data provided by researchers from the individual sites. Soil temperatures and soil moisture are mean values of data measured in the month where fauna sampling was accomplished. Other data are unaltered from Beier et al (2009).

	Clocaenog, Wales U.K.	**Mols Denmark**	**Oldebroek Netherlands**	**Kiskun Sag Hungary**	**Garraf, Catalonia Spain**	**Capo Caccia, Sardinia, Italy**
Location	53° 03' N 3° 28' W	56° 23' N 10° 57' E	2° 24' N 5° 55' E	46° 53' N 19° 23' E	41° 18' N 1° 49' E	40° 36' N 8° 9' E
Altitude	490	58	25	130	210	35
Air temperature: Control (°C)						
Year (mean of 3–5 years, 1999–2004)	8.2	9.0	10.1	10.8	15.6	15.6
April–June 2003	**9.5**	**12.3**	**10.9**	**17.8**	**19,1**	**19,4**
Month of fauna sampling	**13.9 (July)**	**16.8 (June)**	**15.4 (July)**	**19.7 (May)**	**18.2 (May)**	**14.2 (Apr)**
Precipitation. Control (mm)						
Year (mean of 3–5 years, 1999–2004)	1741	644	940	509	580	511
April–June 2003	**593**	**171**	**151**	**45**	**85**	**38**
Month of fauna sampling	**312**	**40**	**64**	**20**	**68**	**11**
Soil temperature: Control (°C)						
Organic soil layer	**13.3**	**15.8**	**15.4**	-	-	-
Mineral soil layer	**10.8**	**14.9**	-	**20.3**	**25.7**	**14.9**
Soil moisture. Control (% of wet soil)						
Organic soil layer	**48.0**	-	**17.5**	-	-	-
Mineral soil layer	-	**9.4**	-	**3.5**	**21.1**	**6.14**
Potential evapotranspiration (mm $^{a-1}$)	302	590	595	1016	1034	1026
Nitrogen deposition (g N m^{-2} a^{-1})	2.1	1.6	4.1	1.2	0.5	1.0
Main growing season(s) (>5°C more than 5 days)	April–Sept	April–Sept	April–Oct	April–Sept	Jan–May Oct–Dec	Jan–May Oct–Dec
Dominant Plant species in fauna sample plots	***Calluna vulgaris, Vaccinium myrtillus***	***Calluna vulgaris, Deschampsia flexuosa, Holcus mollis***	***Calluna vulgaris***	***Populus alba, Festuca vaginata, Cynodon dactylon***	***Erica multiflora, Globularia alypum, Dorychnium pentaphyllum***	***Helichrysum microphyllum, Cistus monspeliensis, Dorychnium pentaphyllum***

Plant cover (%) in control plots	100	100	95	35	69	50
Soil type (FAO standard)	Peaty podzol	Sandy podzol	Haplic arenosol	Calcaric arenosols	Petrocalcic Calcixerepts	Luvi and Litosoils
Top soil						
Depth (cm)	0–6	0–3	0–4	0–10	0–12	0–10
pH	3.9	3.7	3.7	7.9	8.1	8.1
SOM (%)	89	41	65	0.74	7.8	3.1
Deeper soil						
Depth (cm)	6–17	3–20	4–16	10–20	12–37	10–35
pH	4.0	4.1	3.8	8.1	8.3	8.3
SOM (%)	37	1.8	3.3	0.32	3.5	1.8

Tab. 2. Average changes of climatic variables induced by drought and warming treatments in 2003 calculated from original data from the 6 sites (see Tab. 1). When period of the year is not indicated, the calculations are based on mean data from the month of fauna sampling.

	Clocaenog, Wales U.K.	**Mols Denmark**	**Oldebroek Netherlands**	**Kiskun Sag Hungary**	**Garraf, Catalonia Spain**	**Capo Caccia, Sardinia, Italy**
Effects of warming treatment on mean temperatures (°C)						
Air temperature April–June 2003	+1.3	+1.1	+0.8	+0.8	+0.8	+0.9
Air temperature. Month of fauna sampling	+1.4	+1.0	+1.0	+0.9	+0.9	+0.5
Organic soil temperature	+0.2	0.0	+1.0	-	-	-
Mineral soil temperature	+0.8	+0.1	-	+2.2	+2.2	-0.1
Effects of drought treatment on mean temperatures during the month of fauna sampling (°C)						
Air temperature	-0.1	+0.3	0.0	-0.6	+0.2	+0.2
Organic soil temperature	+0.1	-0.2	0.0	-	-	-
Mineral soil temperature	+1.0	+0.1	-	+2.0	-0.6	+0.1
Effects of drought treatment on precipitation and soil moisture. Month of fauna sampling (% of Control)						
Precipitation	-15.8	-9.9	-99.4	-92.6	-92.4	0.0
Organic soil moisture	-36.5	-	-73.1	-	-	-
Mineral soil moisture	-	-31.9	-	-7.8	-38.4	+17.6
Drought treatment period 2003 (dd.mm-dd.mm)	02.06–22.09	16.05–07.06 18.07–01.08	19.05–30.08	01.05–25.06	26.03–04.07 19.09–09.12	08.04–09.06 04.10–02.12

3. Results

3.1. Density and biomass of Collembola across sites

The highest densities of total Collembola in the control plots (sum of all three strata: plants, soil surface and soil) were recorded in the Spanish, Danish and British sites, while the density in the Italian site was less than a fifth of that found in the Spanish site (Fig. 1A, Tabs 3–9). The biomass of total Collembola (Fig. 1C) decreased 4–21 times from the northernmost sites in Denmark and Wales to the southern sites in Hungary, Catalonia and Sardinia with a medium sized biomass in the Dutch site. This trend observed for biomass was partly a result of a similar decrease in population density but, especially for the Hungarian and Spanish sites, was also due to lower average weights of the collembolan specimens (Fig. 1B). Excluding the very low biomass of the Hungarian site, the collembolan biomass correlated negatively (Pearson correlation coefficient = -0.67; $P < 0.01$) with mean annual temperatures spanning from 8.2 °C in the Welsh site to 15.6 °C in the Catalonian and Sardinian sites (Tab. 1). Thus, decreasing latitude and increasing mean temperatures were very generally correlated with decreasing mean collembolan biomass. The precipitation gradient spanning from 1,741 mm a^{-1} in Wales to 509 mm a^{-1} in Hungary (Tab. 1) was attended by an 8-fold reduction of collembolan biomass, but the rank of biomass estimates in the six sites only roughly corresponded to the rank of annual precipitation. However, both for annual precipitation and collembolan biomass, a clear decrease was seen between the three northern and the three southern sites.

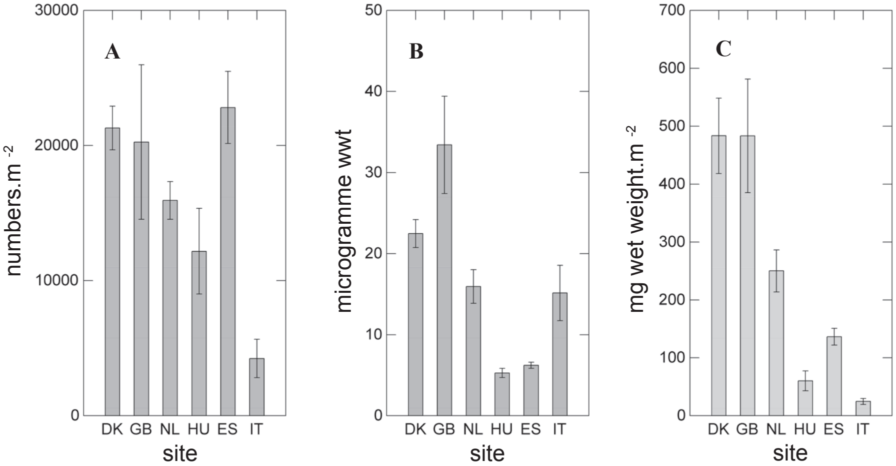

Fig. 1 Population density, average individual weight and biomass of total Collembola in all strata combined (plants above ground, soil surface and soil 0–10 cm depth) in the control plots at six European shrubland sites arranged from north to south: DK (Mols, E. Jutland, Denmark); GB (Clocaenog, Wales, U.K.); NL (Oldebroeck, The Netherlands); HU (Kiskun Sag, Hungary); ES (Garraf, Catalonia, Spain); IT (Capo Caccia, Sardinia, Italy). **A**: Density (numbers m^{-2}); **B**: Average weight per specimen (µg wet weight); **C**: Biomass (mg wet weight m^{-2}). Vertical bars: Standard Error.

Significance of between site comparisons from mixed model analysis of variance shown in Table 3.

3.2. Effects of climatic manipulations on density and biomass

The air temperature in the warming treatment increased 0.3–1.3 °C in April–June 2003 depending on site, while the change in soil temperature in the month of soil fauna sampling varied from -0.1 °C in the Italian site to +2.2 °C in the Hungarian site (Tab. 2). The drought treatment removed only 10 and 16% of the water input during the month of fauna sampling in the Danish and British site, respectively. In the month of fauna sampling, nearly all precipitation was intercepted in the Dutch, Hungarian and Spanish sites, while no interception was observed in the Italian site (Table 2). The result of the decrease in water input was reductions in soil moisture measured during the month of fauna sampling, spanning from 8% in the Hungarian site to 73% in the Dutch site. In the Italian site 18% increment was measured in the mineral soil (Tab. 2).

The drought treatment resulted in a significant reduction of total collembolan density relative to control in the Dutch (Tab. 6) and the Spanish site (Tab. 8), while the effect on total collembolan biomass was significant in the Danish (Tab. 4), Dutch and Spanish sites. The drought treatment also resulted in significant negative effects on density and biomass for several families, species groups and species in the same three sites, while few or no taxa were significantly influenced in the British (Tab. 5), Hungarian (Tab. 7) and Italian (Tab. 9) sites.

The warming treatment resulted in a reduction of total collembolan density and biomass in the Spanish site (Tab. 8). In the Dutch site 7 of 18 species/species groups showed significantly reduced biomass in the warming treatment (Tab. 6). A few significant reductions were found in the warming treatment of the Danish and Spanish sites, while significant negative effects of warming were missing in the British, Hungarian and Italian sites. One species (*Lepidocyrtus* sp. 1) had significantly higher biomass in the warming treatment of the Italian site compared to the control.

Tab. 3 Significances of between-site comparisons of total collembolan density (upper right part of matrix) and biomass (lower left part of matrix) in the control plots based on a mixed model analysis of variance. Type 3 tests for fixed effects gave the following results: for density site and the interaction between site and treatment were significant (Site: $F_{5,245} = 26.03$, $P < 0.001$; Treatment: $F_{2,6} = 3.77$, $P = 0.08$; Site*Treatment: $F_{10,245} = 2.64$, $P = 0.005$). For biomass site was significant ($F_{5,245} = 80.23$, $P < 0.001$), treatment not significant ($F_{2,6} = 4.56$, $P = 0.06$) and interaction between site and treatment considered significant ($F_{10,245} = 1.85$, $P = 0.052$). Site labels as Figure 1.

							Density
	DK	GB	NL	HU	ES	IT	
DK		*	ns	**	ns	***	DK
GB	ns		ns	ns	*	***	GB
NL	*	ns		ns	*	***	NL
HU	***	***	***		***	**	HU
ES	***	**	ns	***		***	ES
IT	***	***	***	ns	***		IT
	DK	GB	NL	HU	ES	IT	
Biomass							

Tab. 4 Density and biomass of Collembola species and larger taxonomic groups in the Danish VULCAN site and results of Mann-Whitney tests comparing control (C) with warming (W) and drought (D) treatments, respectively. Species with a dominance higher than 1% were analysed; significant effects relative to the control at $P < 0.05$ indicated as *.

taxon name	**Density (no. m^{-2})**			**Biomass (mg wwt. m^{-2})**		
	C	**W**	**D**	**C**	**W**	**D**
Mesaphorura macrochaeta [1]	933	1,147	2,372	1.5	1.5	4.4
Isotomiella minor	1,098	415 *	693	3.8	1.7	1.9
Parisotoma notabilis	557	2,965	767	1.7	8.8	5.3
Isotoma viridis group (2 spp)	163	44	313	1.6	0.36	2.2
Entomobrya nicoleti [2]	9,417	10,659	5,030 *	153.0	180.0	76.0 *
Lepidocyrtus lignorum + *L. lanuginosus*	3,412	4,895	2,544	66.6	100.5	45.2
Pogonognathellus flavescens + *P. longicornis*	685	708	154	204.5	246.7	61.7
Megalothorax minimus	560	269	1,126	0.27	0.13	0.54
Sphaeridia pumilis	915	992	978	0.42	0.61	0.66
Sminthurinus niger [3]	753	1,090	1,163	4.2	8.5	2.5
Heterosminthurus claviger [4]	1,823	1,247	1,116	63.8	21.24*	15.8 *
Deuterosminthurus pallipes f. *repanda*	24	124*	5	1.1	2.8	0.12
Sminthurus nigromaculatus [5]	526	346*	193*	24.7	11.8	12.5*
Poduroidea (4 spp)	293	290	89	0.49	0.48	0.15
Onychiuridae (≥1 sp)	933	1,147	2,372	1.5	1.5	4.4
Isotomidae (5 spp)	1,845	3,424	1,773	7.2	10.9	9.3
Entomobryidae (6 spp)	12,883	15,692	7,820 *	220.9	288.8	135.1 *
Tomoceridae (2 spp)	685	708	154	204.5	246.7	61.7
Neelipleona + Symphypleona (9 spp)	4,655	4,112	4,705	101.0	49.7	41.4 *
Collembola sum	**21,294**	**23,372**	**16,913**	**535.5**	**598.1**	**252.1 ***

[1] possibly including a few specimens of other small Tullbergiinae; [2] including high densities of juveniles, some of these may belong to other *Entomobrya* species; [3] including juveniles of Sminthurinus, probably mostly *S. niger*; [4] may include females or juveniles of other *Heterosminthurus* species; [5] including juveniles of *Sminthurus* not identified to species.

Tab. 5 Density and biomass of Collembola species and larger taxonomic groups in the British VULCAN site and results of Mann-Whitney tests comparing control (C) with warming (W) and drought (D) treatments, respectively. Species with a dominance higher than 1% were analysed; significant effects relative to the control at $P < 0.05$ indicated as *.

taxon name	**Density (no. m^{-2})**			**Biomass (mg wwt. m^{-2})**		
	C	**W**	**D**	**C**	**W**	**D**
Micranurida pygmaea	494	614	119*	0.84	1.0	0.21*
Protaphorura armata s. l.	2,027	1,908	2,843	95.9	90.2	134.5
Folsomia brevicauda	10,109	6,559	1,898*	34.4	22.3	6.5*
Folsomia quadrioculata s. str.	1,862	1,250	3,192	21.4	14.3	36.6
Isotomiella minor	1,985	1,257	1,348	6.4	4.1	4.4
Isotoma viridis s. str.	954	259	276	7.6	2.1	2.2
Lepidocyrtus lignorum	1,347	1,474	919	36.8	40.2	25.1
Pogonognathellus longicornis	305	468	184	262.4	403.5	158.7
Entomobrya nicoleti [1]	55	16	101	1.5	0.44	2.8
Megalothorax minimus	413	783	579	0.19	0.37	0.27
Dicyrtomina + Dicyrtoma (2+1spp)	82	69	84	5.1	4.6	4.6
Poduroidea (4 spp)	850	722	230	7.1	2.3	2.9
Onychiuridae (2–3 spp)	2,151	1,943	3,447	96.0	90.2	134.8
Isotomidae (5 spp)	14,918	9,341	6,714	69.8	42.9	49.7
Entomobryidae (2 spp)	1,403	1,489	1,096	38.3	40.7	29.9
Tomoceridae (2 spp)	339	626	184	263.6	408.9	158.7
Symphypleona + Neelipleona (5 spp)	579	963	855	8.5	8.2	13.0
Collembola sum	**20,249**	**15,098**	**12,533**	**483.3**	**593.3**	**389.1**

[1] including juvenile Entomobrya ; some may belong to other Entomobrya species.

Tab. 6 Density and biomass of Collembola species and larger taxonomic groups in the Danish VULCAN site and results of Mann-Whitney tests comparing control (C) with warming (W) and drought (D) treatments, respectively. Species with a dominance higher than 1% were analysed; significant effects relative to the control at $P < 0.05$ indicated as *.

taxon name	**Density (no. m^{-2})**			**Biomass (mg wwt. m^{-2})**		
	C	**W**	**D**	**C**	**W**	**D**
Ceratophysella granulata	702	124*	0*	9.3	1.6*	0.0*
Schoettella ununguiculata	684	0	107	2.5	0.0	0.40
Pseudachorutes parvulus	533	320	240	0.57	0.53	0.77
Micranurida pygmaea	1,973	640*	507*	3.0	1.0*	0.49*
Mesaphorura macrochaeta [1]	3,813	1,253	3,387	3.5	1.8	2.6
Folsomia quadrioculata s. l.	320	53	1,227	1.2	0.24	6.4
Pseudisotoma sensibilis	720	53*	53*	3.9	0.25*	0.44*
Parisotoma notabilis	354	970	0	0.80	2.1	0.0*
Isotoma viridis s. l.	335	97	213	3.4	0.22*	1.6
Entomobrya nivalis	1,043	548	236	34.7	13.4*	7.7*
Orchesella cincta [2]	445	789	309	27.1	82.6	20.8
Lepidocyrtus lignorum /lanuginosus	850	224	244	13.2	4.5	12.2
Lepidocyrtus cyaneus /violaceus	613	180*	421	7.3	1.8*	5.2
Pogonognathellus (2 spp)	187	454	17*	45.0	49.7	2.9*
Megalothorax minimus	987	1,821	0*	0.29	0.43	0.0*
Sminthurinus aureus [3]	648	230	8*	0.11	0.04	0.001
Heterosminthurus cf. *claviger*	137	49	32*	7.01	2.7	1.8*
Sminthurus nigromaculata	837	147*	469*	41.0	12.4*	52.9
Poduroidea (all spp)	4,212	1,545*	1,093*	23.8	7.1*	4.0*
Onychiuridae (all spp)	3,813	1,253	3,387	3.5	1.8	2.6

Isotomidae (all spp)	1,728	1,174	1,547	9.4	2.8*	8.8
Entomobryidae (all spp)	3,084	1,777	1,236*	97.6	107.5	46.3
Tomoceridae (all spp)	187	454	17*	45.0	49.7	2.9*
Neelipleona + Symphypleona (all spp)	2,909	2,405	509*	70.9	19.4*	55.6
Collembola sum	**15,934**	**8,609**	**7,789***	**250.1**	**188.3**	**120.2***

[1] possibly including a few specimens of other small Tullbergiinae; [2] including few unidentified specimens, mostly juveniles; [3] including juvenile *Sminthurinus* which may belong to other species.

Tab. 7 Density and biomass of Collembola species and larger taxonomic groups in the Hungarian VULCAN site and results of Mann-Whitney tests comparing control (C) with warming (W) and drought (D) treatments, respectively. Species with a dominance higher than 1% were analysed; significant effects relative to the control at $P < 0.05$ indicated as *.

taxon name	**Density (no. m^{-2})**			**Biomass (mg wwt. m^{-2})**		
	C	**W**	**D**	**C**	**W**	**D**
Mesaphorura spp. + *Scaphaphorura arenaria*	1,467	880	53	1.3	0.77	0.05*
Micraurophorus musci	1,840	0	0	1.6	0.0	0.0
Folsomides cf. *portulacensis* [1]	8,729	3,955	5,493	50.6	22.9	31.9
Entomobrya handschini + *Entomobrya* sp. [2]	76	0	8	5.1	0.0	0.57
Sminthurus maculatus	6	0	0	0.06	0.0	0.0
Fasciosminthurus angulipunctatus [3]	29	20	20	1.1	0.46	0.30
Poduroidea (1 sp) [4]	27	44	0	0.45	0.74	0.0
Onychiuridae (≥2 spp)	1,467	880	53	1.3	0.77	0.05*
Isotomidae (2–3 spp)	10,569	3,955	5,493	52.2	22.9	31.9
Entomobryidae (2–3 spp)	76	0	35	5.1	0.0	2.4
Symphypleona (2–3 spp)	35	20	20	1.2	0.46	0.30
Collembola sum	**12,173**	**4,898**	**5,602**	**60.3**	**24.9**	**34.6**

[1] may include another *Folsomides* species, not identified at present; [2] an unidentified *Entomobrya* is included in this group; [3] includes juveniles and preadults which may belong to a different species of *Fasciosminthurus*; [4] *Xenylla maritima*.

Tab. 8 Density and biomass of Collembola species and larger taxonomic groups in the Spanish VULCAN site and results of Mann-Whitney tests comparing control (C) with warming (W) and drought (D) treatments, respectively. Species with a dominance higher than 1% were analysed; significant effects relative to the control at P <0.05 indicated as *.

taxon name	**Density (no. m^{-2})**			**Biomass (mg wwt. m^{-2})**		
	C	**W**	**D**	**C**	**W**	**D**
Xenylla maritima + *X. mediterranea*	2,582	1,691	726	8.4	4.8	1.9
Pseudachorudina meridionalis [1]	1,200	1,574	320	2.9	3.7	0.82
Protaphorura cf. *quercetana*	958	364*	160*	4.9	2.2	0.52*
Mesaphorura sp. [2]	3,697	1,385*	3,653	2.4	1.5	1.8
Isotomiella minor	1,120	0*	160	3.1	0.0*	0.44
Folsomides parvulus	3,333	987	293*	14.2	5.1	1.2*
Cryptopygus albaredai	587	987	747	0.97	1.6	1.2
Cryptopygus thermophilus	1,794	1,788	435	8.3	12.0	1.3
Entomobrya cf. *quinquelineata*	1,059	202*	286*	19.1	2.2*	4.5*
Lepidocyrtus sp. (near *L. selvaticus*)	2,631	1,202	535	15.5	7.3	3.3
Lepidocyrtus sp. (abd. III unpigmented)	922	995	168	6.8	7.4	1.2
Heteromurus major	1,276	794	624	20.9	12.9	9.9
Deuterosminthurus cf *pallipes* f *repanda*	155	111	60	3.9	1.9	1.5
Bourletiellini, all species	104	76	39	11.0	9.2	5.1
Poduroidea (all spp)	3,879	3,291	1,099	11.5	8.5	2.8
Onychiuridae (all 5 spp)	4,655	1,776*	3,840	7.3	3.0*	2.5*
Isotomidae (all spp)	7,473	3,954*	1,982*	29.9	19.2	4.3*
Entomobryidae (all spp)	6,169	3,254	1,783*	69.8	32.4*	20.3*
Symphypleona (all spp)	626	422	175*	18.1	11.9	6.2
Collembola sum	**22,810**	**12,697***	**8,907***	**136.6**	**72.7***	**35.4***

[1] may include some specimens of *Pseudachorutes* sp.; [2] may include more than one species of small Tullbergiinae.

Tab. 9 Density and biomass of Collembola species and larger taxonomic groups in the Italian VULCAN site and results of Mann-Whitney tests comparing control (C) with warming (W) and drought (D) treatments, respectively. Species with a dominance higher than 1% were analysed; significant effects relative to the control at $P < 0.05$ indicated as *.

taxon name	**Density (no. m^{-2})**			**Biomass (mg wwt. m^{-2})**		
	C	**W**	**D**	**C**	**W**	**D**
Xenylla maritima [1]	1,789	1,097	722	5.9	3.5	4.7
Protaphorura armata s. l.	133	2,267	747	4.0	31.0	22.2
Mesaphorura sp.	1,360	427	667	0.63	0.20	0.89
Cryptopygus thermophilus	293	1,040	133	0.32	1.7	0.33
Entomobrya multifasciata				2.7	3.8	5.6
Entomobrya, all species	191	232	136	3.3	4.7	6.5
Lepidocyrtus sp. 1 (*curvicollis group*)	68	465	322	0.56	10.4*	5.5
Lepidocyrtus sp. 2 (*pigmented*)	28	6	5	0.34	0.33	0.21
Deuterosminthurus pallipes f. *repanda*	43	168	38	0.79	4.9	2.2
Sminthurus (s. str.) sp.	77	15	66	6.5	3.5	18.8
Poduroidea, all species	1,815	1,177	775	6.0	3.7	5.0
Onychiuridae, all species	1,520	2,720	1,440	5.4	31.6	23.9
Isotomidae, all species	453	1,147	214	1.1	2.5	1.3
Entomobryidae, all species	319	706	653	4.9	15.7	13.2
Symphypleona, all species	126	212	108	7.4	9.2	21.2
Collembola all spp.	**4,234**	**5,962**	**3,190**	**24.8**	**62.7**	**64.7**

[1] May include other *Xenylla* spp.

Although negative effects of warming and drought treatments on density and biomass of total Collembola were only significant in few sites and no examples of significant positive effects were found, individual species showed both lower, higher and similar estimates in warming and drought treatments as compared to the control. As treated above, only very few of the increments were significant while several significant negative effects were found. Nevertheless, the data suggest displacements between individual species and thus changes in the community structure caused by the climate manipulations. For example, the density of the most dominant species in the control of the British site (Tab. 5), *Folsomia brevicauda* Agrell, 1939, was reduced by a factor of 5 in the drought treatment, where it was ranked as the third most numerous collembolan. The rank as the most dominant species in the drought treatment switched to another *Folsomia* species (*F. quadrioculata*), which had a higher density in the drought treatment than in the control.

The PCA-diagram shown in Fig. 2 based on mean population densities illustrates the community structure and the effect of drought- and warming treatments. The first (PC 1) and second axis (PC 2) account for 44% of the variation in the complete dataset. The first axis separates the northern and southern sites, while the second axis reflects collembolan diversity as it groups the sites into lower values in the Hungarian and British sites vs. higher values in the remaining countries. All except the Danish and Dutch sites are well separated and it is demonstrated that differences between treatments are much smaller than differences between sites. The position on the graph of the treatments in relation to the controls within each site does not reveal obvious patterns which can be interpreted as a uniform reaction to the climate manipulations valid for all sites.

3.3. Vertical distribution of collembolan biomass

The distribution of collembolan biomass between above-ground plants, soil surface/litter and soil to 10 cm depth (Fig. 3) shows that the percentage found in soil tended to increase from the northern and the Hungarian sites to the two Mediterranean sites, while the percentage found at the soil surface decreased along the same gradient. The proportion recorded from plants above ground was only a few percent in the Danish site and mostly less than 10% in the other sites. The proportion found in soil increased in the warming treatments and even more so in the drought treatments in all but the Danish and Spanish sites, whereas the opposite was the case for the proportion sampled from the soil surface. The proportion estimated from the plants above ground increased in the drought treated plots of the British, Dutch and Hungarian sites.

3.4. Species diversity

108 different species or species groups were recorded in the material sampled in the six sites (Appendix), which can be considered a minimum because some taxa identified to the genus or subfamily level, e.g. small Tullbergiinae, definitely included more than one species. The species composition differed much between the sites and no species was identified in all sites. However, the three northern sites had nine of 23–33 species in common, while fourteen of 38–40 species were common for the two Mediterranean sites. The Hungarian site only shared three of ten species with other sites.

The species richness in all treatments combined (Appendix) was very low (10) in the Hungarian site. For the other sites the number of species tended to increase from the northernmost sites in Wales and Denmark (23 and 27 species, respectively) through the

Dutch (33 species) to the Mediterranean sites in Catalonia and Sardinia (38 and 40 species, respectively. The number of species found in the control plots (Fig. 4) also increased from the northern to the southern sites except for very low number recorded in the Hungarian site. The effects of the climatic manipulations (Fig. 4) were generally relatively small and appear not to be due to differences in numbers of collected specimens. Reductions in species richness were only observed in the drought treatments of the British, Dutch, Hungarian and Spanish sites.

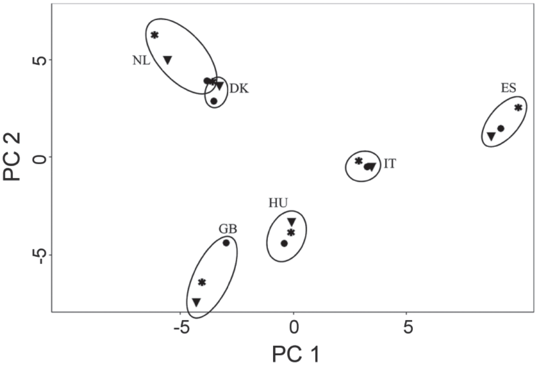

Fig. 2 PCA plot of the 1st (PC 1) and 2nd (PC 2) principal component of log(x+1) transformed collembolan population means for each country and climate treatment. Symbols belonging to each individual site has been encircled. Site labels as Figure 1. Treatment symbols: Control *; Drought ●; Warming ▼.

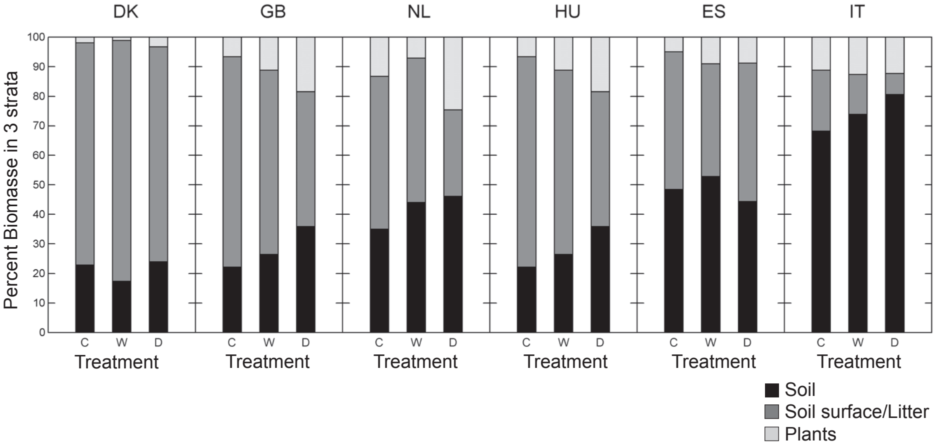

Fig. 3 Distribution of collembolan biomass in three strata (plants above soil, soil surface and soil) depending on climate treatment at each of six European shrubland sites. C = Control; W = Warming treatment; D = Drought treatment. Soil: black; Soil surface/litter: dark grey; Plants: light grey. Site labels as Figure 1.

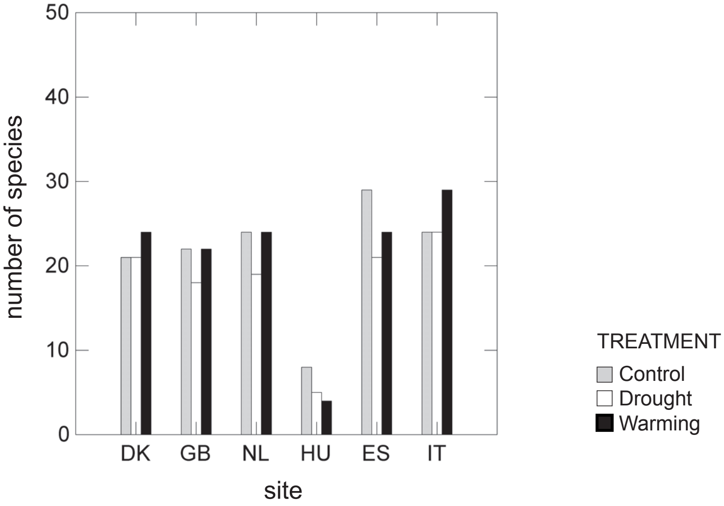

Fig. 4 Species richness of the collembolan communities in each climate treatment at six European shrubland sites. Control: grey columns; Drought treatment: white columns; Warming treatment: black columns. Site labels as Figure 1.

4. Discussion

4.1. Collembolan communities in relation to the long distance temperature- and drought gradients in Europe

The trend observed that biomass and to some degree density and average individual weight of Collembola decreased towards lower latitude and higher annual mean temperature agrees with earlier descriptions of long-distance clines (Petersen & Luxton 1982) and probably is the result of long-term adaptation of the collembolan populations and communities to climate. The strongly reduced biomass associated with continental climate with low precipitation conforms with the vulnerability of many collembolan species to drought. The increasing proportion of biomass estimated in the soil layer from north to south concurrently with the decreasing proportion on the soil surface indicate increasing severity of the environmental conditions in the uppermost layers of the litter/soil profile, probably due to a combination of high temperature and low moisture.

The increase in species richness that, with the exception of the extremely dry site in Hungary, was observed from the northern to the southern sites in Europe agrees with the very general pattern of macro-scale increase of biodiversity from the poles to the tropics (Whittaker et al. 2001, Willig et al. 2003). The latitudinal cline reflects several interacting factors which may influence biodiversity. Thus, interaction between temperature and water availability may be critical (Whittaker et al. 2007).

The low diversity in the Hungarian site may – like the low biomass – be explained by the extreme desert-like environment with a soil consisting of fine sand, poor vegetation cover, low precipitation and high summer temperature. It is not obvious why the Dutch, Spanish and Italian sites have the highest species diversity. The Dutch site is a fairly uniform heathland strongly dominated by *Calluna vulgaris*, a vegetation type that is generally considered to have a poor fauna. The Spanish and the Italian sites have compact, stony soils with a fairly sparse plant cover, low precipitation and high mean temperature. Especially the Italian site was extremely dry at the time of sampling, making sampling of soil cores very difficult. The low collembolan biomass recorded there probably mostly reflects the severe environmental conditions in this site, but it cannot be excluded that the sampling conditions had a negative effect on the density and biomass estimates. Nevertheless, the highest number of species was recorded from this site.

4.2. Effect of climatic manipulations

The warming treatment resulted in relatively modest increments of air and soil temperatures (i.e. mostly below 2 °C), which did not exceed the natural year-to-year differences at the sites and were realistic compared with the temperature increase observed during the last century and predicted for the future (Beier et al. 2004). The drought treatment removed 65–90% of the water input during the drought periods in 1999–2000, i.e. less than 100% according to Beier et al. (2004). The effect of reduced precipitation on soil moisture during the fauna sampling of the present study varied considerably from site to site and was not obviously related to the precipitation measured the same month. This might be due to delayed effects of previous interceptions of precipitation in combination with soil and temperature properties of the particular sites. The reductions in soil moisture are not believed to be more severe than what may be expected as the result of naturally occurring drought periods. Thus, the temperature and moisture conditions that caused the changes observed in density, biomass and diversity of collembolan communities in the manipulated climate experiments were within the range of naturally occurring fluctuations and were in no way extreme.

The significant negative effects on collembolan populations of warming manipulation found in the Danish, Dutch and Spanish sites agree with a few studies from Arctic and sub-Arctic environments (Convey et al. 2002, McGeoch et al. 2006), but in contrast Kennedy (1994) found a significant increase of collembolan density in small tents used for temperature manipulation in fellfield habitats at Signy Island, maritime Antarctica. This was explained by a larger recruitment of juveniles or shorter generation times or by the observed increase of moss and lichen cover inside the experimental cloches, which indirectly may have stimulated microarthropod population growth. Such factors may have been active in the present experiments as well and may in some cases have counteracted negative effects of warming, but generally not enough to result in significant positive reactions to the warming treatment.

The generally lower biomass and slightly reduced number of species found in drought treatments as compared with what was found in control plots agrees with the results of Frampton et al. (2000), Pflug & Wolters (2001) and Lindberg et al. (2002). Lindberg et al. found that eight years of drought treatment decreased the abundance, species richness and, less markedly, dominance structure of the collembolan community in a Swedish spruce forest soil. Long-term drought had larger effect than long-term irrigation.

Hodkinson et al. (1998) warned against a too simplistic view on climate effects on fauna communities. They found that increased temperature led to a significant decline in collembolan population density in a polar semi-desert at Svalbard, while there was no effect of experimental warming in a tundra heath. Between-year and between-site variations were found to exceed the differences resulting from the temperature manipulation experiments. In this as well as other studies (Harte et al. 1996) treating effects of artificial heating, the interaction with soil moisture is emphasized and Hodkinson et al. (op.cit.) concluded that water availability during the summer growing period is probably of greater significance than temperature for many arctic soil fauna groups.

A complication for interpretation of the climate manipulation results is that some changes in soil moisture may have accompanied the warming treatment. Thus, mean annual soil moisture in 1999–2000 were 3–10% higher in the warming treatment than in the control in the British and Danish sites, respectively, but 9–10% lower than the control in the Dutch and Spanish sites (Beier et al. 2004). However, compared to the effects of drought treatments on soil moisture, i.e. reductions between 10 and 33%, this side-effect of the warming treatment was probably less important for the collembolan communities than the effect caused by the drought treatment.

The examples mentioned above show that the outcome of climate manipulations such as those carried out in the present study may be very complex and different from place to place depending of a number of environmental factors and the composition of the non manipulated fauna. Therefore, it is not strange that the effects observed in the six different sites from large-scale transects through Europe differ.

In the British site, where only two species were affected significantly, i.e. reduced in the drought treatment, the very moist or even drenched moss- and litter layer and soil characteristic of this particular site may have improved as habitat for some species as a result of the climate manipulations. In the Hungarian and Italian sites the climate manipulations had relatively small effects. The reason for this might be the relatively short duration of the field experiment, i.e. about 1.5 years, from the start of treatments to sampling compared to 4.5 years in the other four sites.

Analysis of the depth distribution of total Collembola across sites and treatments showed a general agreement between a large scale biogeographical pattern and the effect of climatic manipulations in most of the sites. This indicates that one effect of climate change on collembolan communities will be a displacement of vertical distribution towards deeper soil layers, possibly accompanied by a change in composition of life forms.

McGeoch et al. (2006) emphasize that although the abundance and biomass of total Collembola declined drastically in dry-warm treatments carried out at the sub-Antarctic Marion Island, the responses of individual species were different resulting in marked changes in structure of the microarthropod communities. Similarly, the response of individual species to the warming and drought treatments in the present study differed resulting in altered structure of the collembolan communities with marked, significant reductions for some species and insignificant or exceptionally even positive responses in other species.

While there were clear differences in collembolan biodiversity in terms of species richness along the large-scale European climatic gradients, the effect of warming and drought treatments in the individual sites were relatively small and not possible to test statistically. This may be due to the relatively short experimental period where the possibility of changes in number of species caused by extinction or immigration would be small.

4.3. Conclusions

Estimates from the non-manipulated part of the six sites of collembolan biomass, and to some degree population density and average individual weight, show a tendency to decrease from the northern to the southern sites suggesting a latitudinal cline, which is probably mainly controlled by temperature or temperature interacting with moisture. In contrast, biodiversity in terms of species richness tend to increase from North to South. The low biomass estimates and number of species recorded from the extremely dry Hungarian site may be understood as one extreme of a gradient from the humid Atlantic north-western Europe to the dry continental central Europe. These results are in agreement with expectations and fit to earlier published observations. This large-scale pattern suggests prospective trends of collembolan community development resulting from long-term climatic change.

Significant effects on collembolan density and biomass were shown as results of identical climate manipulation experiments carried out in the six European sites. As expected, the effect varied from site to site, but no general pattern related to the large-scale European transects was apparent. Thus, most significant effects for total Collembola and individual collembolan species were found in the Dutch and the Spanish sites, while only few were found in the British, Hungarian and Italian sites. In agreement with the hypothesis proposed in the introduction, nearly all significant effects of both warming and drought treatments were negative. The expected positive effect on population growth caused by increased mean temperature in the warming treatment could not be demonstrated, but higher reproduction rates may have counteracted possible harmful effects of warming and contributed to the lower number of significant reductions. The negative effects together with increments, also from drought treatments, found for a few species and apparent absence of changes in population size of several individual species indicate that the climate manipulations may primarily have resulted in changes of the collembolan community structure. In summary, the explanation of changes in the collembolan communities caused by climatic manipulations are evidently very complicated and the result of many direct and indirect factors, partly acting in opposite directions.

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Appendix List of species from all sites and treatments. Site labels as Figure 1.

	DK	**GB**	**NL**	**HU**	**ES**	**IT**
Schoettella ununguiculata (Tullberg, 1869)			x			
Ceratophysella denticulata (Bagnall, 1941)			x			
Ceratophysella granulata Stach, 1949			x			
Ceratophysella sp.						x
Xenylla maritima Tullberg, 1869			x	x	x	x
Xenylla mediterranea Gama, 1964 /*X. brevisimilis mediterranea* Gama, 1964					x	x
Xenylla sp. (different from above)						x
Willemia anophthalma Börner, 1901	x	x				
Brachystomella parvula (Schäffer, 1896)	x					
Friesea mirabilis (Tullberg, 1871)		x				
Friesea truncata Cassagnau, 1958			x		x	
Xenyllodes sp.						x
Pseudachorutes parvulus Börner, 1901 / cf. parvulus			x		x	
Pseudachorutes sp. (near *P. subcrassus* Tullberg, 1871)						x
Pseudachorudina meridionalis (Bonet, 1929)					x	
Micranurida pygmaea Börner, 1901	x	x	x			
Neanura muscorum (Templeton, 1835)	x	x	x			
Neanura sp.						x
Protaphorura armata (Tullberg, 1869) s. l.		x				x
Protaphorura cf. *quercetana* Mateos-Frias & Arbea, 1986					x	
Onychiurus sp. (with anal spines)						x
Onychiurus sp. (no anal spines)					x	x
Mesaphorura macrochaeta Rusek, 1976 (+ other small Tullbergiinae ?)	x	x	x			
Mesaphorura sp. / small Tullbergiinae				x	x	x
Scaphaphorura arenaria (Petersen, 1965)				x		
Neotullbergia ramicuspis (Gisin, 1953)					x	
Marcuziella tripartita Rusek, 1975						x
Tullbergiinae gen.sp. (different from species above)			x			
Tetracanthella cf. *hygropetrica* Cassagnau, 1954 (ecomorph)					x	
Tetracanthella sp.						x
Micranurophorus musci Bernard, 1977				x		
Folsomia litsteri Bagnall, 1939 s. Fjellberg, 2007	x					
Folsomia penicula Bagnall, 1939						x
Folsomia brevicauda Agrell, 1939		x				
Folsomia quadrioculata (Tullberg, 1871) s. str.		x	x			
Folsomia manolachei Bagnall, 1939			x			
Isotomodes sp.						x
Isotomiella minor (Schäffer, 1896)	x	x	x		x	

Folsomides parvulus Stach, 1922					x	x
Folsomides cf. *portulacensis* Gama, 1961 [4]				x		
Cryptopygus thermophilus (Axelson, 1900) [1]					x	x
Cryptopygus albaredai Selga, 1962 [1] /*C. delamarei* Poinsot, 1970 [1]					x	x
Cryptopygus sp. [near C. exilis (Gisin,, 1960)] [1]						x
Isotomurus cf. *gallicus* Carapelli et al. 2001					x	
Isotomurus cf. *graminis* Fjellberg, 2007					x	
Isotomurus sp.						x
Pseudisotoma sensibilis (Tullberg, 1876)			x			
*Parisotoma notabilis (*Schäffer, 1896)	x	x	x		x	x
Isotoma viridis Bourlet, 1839 s. str. (may include *I. anglicana* Lubbock, 1862)	x	x	x			x
Isotoma caerulea Bourlet, 1839	x					
Desoria sp.		x				
Isotoma sp. (ecomorph)					x	x
Entomobrya lanuginosa (Nicolet, 1842)						x
Entomobrya marginata (Tullberg, 1871)			x			
Entomobrya cf. *quinquelineata* Börner, 1901 [2]					x	
Entomobrya handschini Stach, 1922 f. *aetiopella* [4]				x		
Entomobrya nivalis (Linné, 1758)			x			
Entomobrya nicoleti (Lubbock, 1867)	x	x				
Entomobrya multifasciata (Tullberg, 1871)			x		x	x
Entomobrya cf. *violaceolineata* Stach, 1963 [4]				x		
Emtomobrya sp. *(muscorum*-group)					x	
Entomobryoides cf. *myrmecophilus* (Reuter, 1886)						x
Lepidocyrtus lanuginosus (Gmelin, 1790)	x				x	
Lepidocyrtus lignorum (Fabricius, 1793)	x	x	x			
Lepidocyrtus cyaneus Tullberg, 1871			x			
Lepidocyrtus sp. *near L. selvaticus* Arbea & Ariza, 2007 [3]					x	
Lepidocyrtus sp. (unpigmented)					x	
Lepidocyrtus sp. (undescribed sp. in *L. curvicollis* group) [5]						x
Lepidocyrtus sp. (blue)					x	x
Pseudosinella sp. (*P. alba* (Packard, 1873) group)						x
Orchesella cincta (Linné, 1758)	x		x			x
Orchesella sp. (different from *O. cincta*)						x
Seira domestica (Nicolet, 1841)					x	x
Heteromurus major (Moniez, 1889)					x	
Cyphoderus albinus Nicolet, 1842	x		x	x	x	
Pogonognathellus flavescens (Tullberg, 1871)	x		x			
Pogonognathellus longicornis (Müller, 1776)	x	x	x			
Tomocerus minor (Lubbock, 1862)		x				

	DK	GB	NL	HU	ES	IT
Oncopodura crassicornis Shoebotham, 1911 /*Oncopodura* sp.					x	
Megalothorax minimus Willem, 1900	x	x	x		x	
Sphaeridia pumilis Krausbauer, 1898	x				x	
Sminthurides parvulus (Krausbauer, 1898)		x				
Stenacidia violacea (Reuter, 1878)					x	
Arrhopalites principalis Stach, 1945			x			
Arrhopalites sericus Gisin, 1947		x	x			
Arrhopalites sp.					x	
Sminthurinus aureus (Lubbock, 1862)			x			x
Sminthurinus niger (Lubbock, 1867)	x					
Sminthurinus sp. (*S. niger* group near *S. alpinus* Gisin, 1953)						x
Sminthurinus elegans (Fitch, 1863)						x
Dicyrtomina ornata (Nicolet, 1841)		x				
Dicyrtomina saundersi (Lubbock, 1862)		x				
Dicyrtoma fusca (Lubbock, 1893)	x	x	x			
Dicyrtoma sp					x	
Heterosminthurus claviger Gisin, 1958/ cf. *claviger*	x		x			
Heterosminthurus bilineatus (Bourlet, 1842)		x				
Deuterosminthurus pallipes (Bourlet, 1843)	x		x		x	x
Bourletiella viridescens Stach, 1920	x					
Bourletiella sp.					x	
Fasciosminthurus angulipunctatus (Loksa & Bogojevic, 1970) [4]				x		
Fasciosminthurus sp. (near *F. cassagnaui* Nayrolles, 1994)					x	
Fasciosminthurus sp. (near *F. bedosae* Nayrolles, 1994)					x	x
Fasciosminthurus sp. (near *F. cugnyi* (Nayrolles, 1987)						x
Sminthurus maculatus Tömösvary, 1883 s. Stach, 1956				x		
Sminthurus nigromaculatus (Tullberg, 1872)	x		x			
Sminthurus (s. str.) sp. (near *S. bourgoisi* Nayrolles, 1995)						x
Sminthurus sp. (near *S. nigromaculatus* or *S. hispanicus* Nayrolles, 1995)						x
Spatulosminthurus flaviceps (Tullberg, 1871)	x					
Number of species	**26**	**23**	**33**	**10**	**38**	**40**

[1] According to Rusek (2002) *Cryptopygus* is not indigenous to Europe, but because of still unsolved taxonomic relationships (Fjellberg, 2007) the genus *Cryptopygus* in a broad sense is maintained here.

[2] Juvenile specimens close to *E. quinquelineata* not possible to identify with certainty. They may be *E. fimbaensis* Baquero & Jordana, 2008 or *E. lawrencei* Baquero & Jordana, 2008 (R. Jordana, pers. comm.).

[3] Juvenile specimens of *L. lusitanicus* Gama, 1964 group. Pale but with characteristic transversal dark 'belt' on abd. 3. Near *L. selvaticus* Arbea & Ariza, 2007 (R. Jordana pers. comm.).

[4] Identifications confirmed by Dr L. Dányi, Hungarian Natural History Museum, Budapest.

[5] Undescribed species according to Dr E. Mateos, University of Barcelona. Manuscript with description in preparation.