

Effect of simulated environmental change on alpine soil arthropods

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Abstract

The effects of environmental change on soil animal communities are poorly known. Norwegian mountains are subject to both atmospheric nitrogen deposition and increased temperature. In a nutrient poor alpine *Dryas* heath in south Norway, soil arthropods were studied after 4 years of simulated environmental change by warming and/or nutrient addition. Warming alone only affected three low-density Collembola species, while nutrient addition, with or without warming, greatly changed the dominance hierarchy of the microarthropod community. Certain Collembola species with a short (1 year) life cycle and predatory Gamasina mites increased markedly in density. These groups may have been favored by increased litter production, as plant biomass and litter producing graminoids and forbs increased significantly in plots with nutrient addition and nutrient addition combined with warming. Microarthropods with a longer life cycle, such as Oribatida and certain Collembola, were generally unaffected by nutrient addition and probably need more time to respond. The number of Oribatida taxa was, however, reduced in plots with nutrient addition, both with and without warming. A ground-living species of Coccoidea (Homoptera) declined in plots with nutrient addition and warming compared with only warming, probably due to reduced cover of its host plant *Dryas*. The density of Diptera larvae (Sciaridae and Chironomidae) was unaffected by the treatments. Our results show that increased nutrient availability in nutrient poor alpine soils may have large but different effects on different taxa of soil animals. Species with short life cycles reacted first. Nutrient addition and nutrient addition combined with warming resulted in several effects below ground on microarthropods as previously shown above ground on plants: Increased biomass, high dominance of a few rapid-growing species, contrasting responses of closely related species, and a reduction in species numbers. These short-term responses may have profound long-term effects in this alpine ecosystem.

Keywords: Alpine tundra, below-ground changes, nutrient increase, soil-living arthropods, temperature change

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Introduction

The first effects of climate change are likely to be observed in terrestrial habitats at northern latitudes (IPCC, 2007). A marked temperature increase has been noted during the last 2–3 decades in alpine areas of southern Norway where glaciers and snow fields recede (Ytrehus *et al.*, 2008). A key factor for ecosystem responses may be changes in soil processes, which

regulate the availability of plant nutrients (e.g., Dormann & Woodin, 2002). As long as moisture does not become limiting, it is assumed that increased temperature will enhance N mineralization, and thus increase the availability of nutrients for plants (Anderson, 1992; Nadelhoffer *et al.*, 1992; Lloyd & Taylor, 1994; White *et al.*, 1999). Furthermore, Norway and northwestern Europe are influenced by a constant deposition of long-distance transported atmospheric nitrogen (Hole & Engardt, 2008). Fertilization effects are most probable in nutrient-deficient ecosystems, such as alpine habitats with poorly developed soils.

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Environmental change due to warming and/or increased nutrient availability may affect alpine soil organisms in several ways: direct responses to changes in temperature, moisture or food availability, indirect responses due to changes in competitive relationships, or more long-term effects due to permanent changes in root systems and litter quantity and quality following vegetation changes. Among the soil animals participating in decomposition processes is the species-rich group of microarthropods, encompassing various groups of Collembola (springtails) and Acari (mites) (e.g., Seastedt, 1984; Verhoef & de Goede, 1985; Mebes & Filser, 1998).

Experiments with increased temperatures in high arctic soils on Svalbard have shown variable effects on microarthropods. Dollery *et al.* (2006) recorded a reduced abundance of Collembola, while two groups of Acari, Cryptostigmata and predatory mites, increased. A possible explanation was that Collembola were sensitive to drier conditions created by higher temperatures. Other studies on Svalbard have shown either no effect of warming on microarthropods, or a mixture of negative and positive effects on Collembola (Coulson *et al.*, 1996; Hodkinson *et al.*, 1996; Hodkinson *et al.*, 1998; Webb *et al.*, 1998). Hodkinson *et al.* (1998) concluded that the common species of arctic soil mites and Collembola are well adapted to survive enhanced summer temperatures, providing that moisture is not limited. They pointed, however, to increased freeze-thaw events as a possible critical factor in the life history of microarthropods.

Warming experiments in the Antarctic region have given contradictory results on microarthropod groups (Kennedy, 1994; Convey *et al.*, 2002; Sinclair, 2002; McGeoch *et al.*, 2006). In a review, Sinclair & Stevens (2006) concluded that current evidence of climatic change on Antarctic microarthropods is equivocal, but they pointed to reduced soil moisture as a potential problem if temperature increases. They also stressed that to predict effects of climate change on microarthropods, there is a need for increased knowledge in dispersal ability and population and community ecology.

Close connections may exist between vegetation and soil fauna, and soil fauna may respond differently to environmental changes in different vegetation types. For instance, the effect of warming on high arctic Collembola may depend on vegetation type (Coulson *et al.*, 1996; Hodkinson *et al.*, 1998). Coulson *et al.* (2003) showed that under natural conditions on Svalbard, soil microarthropod communities were influenced by plant species within the vegetation mosaic. One possible explanation was that the rhizosphere microflora on which microarthropods feed differed among plant species.

To our knowledge, only one study exists on the effects of both warming and nutrient addition on soil microarthropods. This was under subarctic conditions near Abisko in northern Sweden (Sjursen *et al.*, 2005), where nutrient addition, with or without warming, increased the abundance of most microarthropod groups. Warming alone, on the other hand, favored oribatid mites but reduced Collembola and Gamasina mites.

Our study is from an alpine *Dryas* heath near Finse on Hardangervidda in southern Norway. Alpine habitats have been little studied with respect to soil fauna and climatic change. Furthermore, *Dryas* heaths are widespread in the holarctic and in northern alpine areas. Soil samples were taken in plots where effects of simulated environmental change on the vegetation had been studied (Klanderud & Totland, 2005; Klanderud, 2008). The design included control plots, warming, nutrient addition, and a combination of warming and nutrient addition. Four years of increased temperature at alpine Finse showed only small effects on plant community composition (Klanderud, 2008) and diversity (Klanderud & Totland, 2005). Nutrients, however, changed the previously low stature and species-rich *Dryas* heath to a less diverse community dominated by tall grasses and forbs. Warming combined with nutrient addition resulted in a still taller vegetation canopy consisting mainly of grasses (Klanderud & Totland, 2005; Klanderud, 2008). This situation was a good opportunity to compare above- and below-ground biotic effects of the environmental changes. Thus, soil samples for microarthropods were taken in 2004, when marked changes in vegetation were evident, to examine (1) if warming and/or nutrient addition had any effects on soil arthropod species richness and density, (2) if such effects differed among soil animal taxa (Collembola, Oribatida), and (3) if responses in the soil fauna community below ground reflected the observed plant community responses above ground.

Materials and methods

The study site was a *Dryas octopetala* heath on a southwest exposed slope at about 1500 m elevation near Finse at Hardangervidda, the alpine region of southwestern Norway. During June, July, and August, the mean monthly temperature at 1200 m elevation at Finse is 6.3 °C (Aune, 1993), and the mean monthly precipitation is 89 mm (Førland, 1993). For detailed habitat descriptions and experimental layout, see Klanderud & Totland (2005). Ten randomized blocks contained four treatments each: control (C, no treatment), temperature treatment (T), nutrient addition (N), and temperature plus nutrient addition (TN). The four treatments were

randomly allocated to four randomly positioned 1×1 m plots, ca. 1 m apart from each other, within each block. Hexagonal open-top chambers (OTCs, Marion *et al.*, 1997; Hollister & Webber, 2000) with a diameter of 1 m were used to increase temperature. The yearly addition of slow-released granular NPK fertilizer was 10 g N m^{-2} , 2 g P m^{-2} , and 8 g K m^{-2} . The treatments started in early July 2000, and soil microarthropods were sampled 4 years later (3 and 10 July 2004). The OTCs increased the mean air temperature 5 cm above the ground by 1.5°C , and the mean soil temperature at 5 cm depth by 1.0°C . Changes in vegetation in late August 2003 were described by Klanderud & Totland (2005) and Klanderud (2008).

In the center of each of the 40 experimental plots, eight soil samples were taken, 3 cm deep and with a surface area of 10 cm^2 . They were extracted for microarthropods according to standard procedure in a high-gradient apparatus, modified after Macfadyen (1961). The extraction also gave material of terrestrial Diptera larvae, and of ground-living Coccoidea (Homoptera). In a proglacial area in the high Arctic, Hodkinson *et al.* (2004) found that heat extraction was more efficient than O'Connor's (1962) wet extraction for terrestrial larvae of Chironomidae, but the general value of this comparison is uncertain. The efficiency of heat extraction on other Diptera larvae (Sciaridae) is unknown, and so numbers should be regarded as relative. Similar extraction methods have earlier been used for Coccoidea (Kozár & Miller, 2000). Microarthropods were identified to species as far as possible. Nomenclature of Oribatida is according to Weigmann (2006) and of Collembola according to Fjellberg (1998, 2007).

To examine the treatment effects on the density (individuals m^{-2}) of each of the soil arthropod taxa separately, and on the species richness of Oribatida and Collembola (dependent variables), we used treatment (four levels: C, T, N, and TN) as a fixed factor and block as a random factor in a randomized block design in general linear models (GLMs) ANOVAS. One analysis was done for each of the dependent variables. We used Tukey's HSD *post hoc* test to examine significant differences between treatment means. Response variables were log transformed before analyses to ensure normality and equal variances. Taxa that did not fulfill model assumptions after transformation were analyzed for treatment effects only by nonparametric Kruskal–Wallis tests, and pairwise multiple comparisons were performed by the nonparametric Student–Newman–Keuls method. We used a polynomial regression ($f = y_0 + ax + bx^2$) to examine the relationship between the density of Gamasidae (predictor) and Collembola. All analyses were done in SYSTAT 10.

Results

Table 1 shows treatment and block effects for the density of microarthropods, Coccoidea, and Diptera larvae. Significant response to temperature treatment alone was found in only three low-density Collembola species: an increase in *Micranurida forsslundi* and *Isotoma* sp., and a decrease in *Tetracanthella wahlgreni*. The latter responded negatively to all the treatments. All other responses were due to nutrient addition, usually with similar responses to nutrients alone and nutrients combined with warming. At the group level, nutrients increased densities of Collembola, as well as Gamasina mites, including the subgroups Gamasidae and Zerconidae. The following Collembola species increased in density after nutrient addition: *Folsomia quadrioculata*, *Parisotoma notabilis*, *Isotoma viridis*, *Protaphorura pseudovanderdrifti*, and 'Other Sminthuridae'. *Micranurida pygmaea* increased in fertilized plots without warming. *Desoria tolya*, *Lepidocyrtus lignorum*, and *Ceratophysella scotica* increased in plots with both nutrient addition and warming. Only two oribatid species responded to the treatments: *Oribatula tibialis* increased, while *Fuscozetes* sp. decreased in plots with nutrient addition combined with warming. Other mites, including the abundant group of Actinedida, did not respond to any of the treatments (Table 1).

The species of Coccoidea, *Arctorthezia cataphracta*, decreased in plots with nutrient addition, and in plots with nutrient addition combined with warming, compared with plots with only warming (Table 1). The density of soil-living Diptera larvae (Sciaridae and Chironomidae) was, however, unaffected by the treatments (Table 1).

The mean species number of Oribatida decreased in plots with nutrient addition and in plots with warming combined with nutrient addition ($F_{3,27} = 4.11$, $P = 0.016$). This was due to a reduced number of rare species. However, the number of Collembola species did not change in any of the treatments ($F_{3,27} = 2.00$, $P = 0.138$) (Fig. 1).

There was a nonlinear relationship between the density of Gamasidae mites and Collembola, with an increase in both groups up to a certain level, followed by a flattening of the curve when Gamasidae densities became high (Fig. 2).

Figure 3 illustrates how the dominance structure of the Collembola community was strongly changed by nutrient addition and warming combined with nutrient addition. *F. quadrioculata* increased its dominance five-fold, from about 10% to about 50% of total Collembola numbers. Its close relative, *Folsomia brevicauda*, however, fell in dominance from about 30% to one-fifth of that. This change occurred at the same time as the total

Table 1 Mean density (thousands m⁻² ± SE) of various soil arthropods in control (C), warming (T), nutrient addition (N), and warming combined with nutrient addition (TN) plots at Finse, alpine southern Norway

Taxa	C	T	N	TN	Treatment		Block	
					F/K	P	F/K	P
Oribatida	15.28 ± 2.07	14.79 ± 1.40	19.81 ± 4.29	18.98 ± 4.33	1.01	0.403	3.78	0.003
Brachychthoniidae	6.3 ± 0.94	6.04 ± 1.23	10.48 ± 3.10	6.98 ± 2.03	0.90	0.453	4.98	< 0.001
<i>Tectocepheus velatus</i> ad.	0.79 ± 0.13	0.60 ± 0.18	0.80 ± 0.31	0.66 ± 0.23	0.26	0.853	3.86	0.003
<i>Tectocepheus velatus</i> juv.	1.66 ± 0.23	1.48 ± 0.27	2.20 ± 1.01	1.55 ± 0.66	0.55	0.652	5.17	< 0.001
<i>Tectocepheus velatus</i> tot.	2.37 ± 0.40	2.09 ± 0.41	2.99 ± 1.31	2.20 ± 0.87	0.60	0.619	5.09	< 0.001
<i>Camisia</i> sp. ad.	0.10 ± 0.03	0.12 ± 0.03	0.08 ± 0.05	0.05 ± 0.03	4.14	0.247		
<i>Camisia</i> sp. juv.	0.25 ± 0.10	0.21 ± 0.07	0.09 ± 0.05	0.11 ± 0.04	1.46	0.247	1.41	0.233
<i>Camisia</i> sp. tot.	0.36 ± 0.12	0.33 ± 0.08	0.16 ± 0.10	0.17 ± 0.06	1.90	0.153	2.42	0.037
<i>Platynothrus</i> sp.	0.06 ± 0.04	0.03 ± 0.02	0	0.19 ± 0.13				
<i>Nothrus borussicus</i>	0.04 ± 0.04	0	0.01 ± 0.01	0				
<i>Oppia</i> sp.	0.25 ± 0.12	0.01 ± 0.01	0.10 ± 0.05	0.11 ± 0.07				
<i>Quadroppia quadricarinata</i>	0.93 ± 0.40	1.70 ± 0.28	1.66 ± 0.55	0.84 ± 0.40	2.87	0.055	1.87	0.100
<i>Suctobelba</i> sp.	0.01 ± 0.01	0	0	0				
<i>Belba</i> sp.	0	0	0	0.01 ± 0.01				
Phthiracaridae	0.18 ± 0.09	0.19 ± 0.12	0.11 ± 0.06	0.13 ± 0.04	0.71	0.871		
<i>Carabodes</i> sp.	0.04 ± 0.04	0	0	0				
<i>Mycobates</i> sp.	0.24 ± 0.12	0.09 ± 0.04	0	0.08 ± 0.08				
<i>Oromurcia</i> sp.	0	0.01 ± 0.01	0	0				
<i>Fuscozetes</i> sp.	0.61 ± 0.34 ^a	0.26 ± 0.01 ^{ab}	0.10 ± 0.06 ^{ab}	0 ^b	11.06	0.011		
<i>Oribatula tibialis</i>	0.59 ± 0.13 ^a	1.45 ± 0.37 ^{ab}	0.63 ± 0.17 ^a	2.76 ± 0.77 ^b	4.18	0.015	1.60	0.165
<i>Eupelops</i> sp. ad.	0.35 ± 0.17	0.32 ± 0.10	0.49 ± 0.15	0.28 ± 0.07	2.10	0.552		
<i>Eupelops</i> sp. juv.	0.89 ± 0.39	0.30 ± 0.09	1.05 ± 0.40	0.40 ± 0.14	2.01	0.136	1.94	0.088
<i>Eupelops</i> sp. tot.	1.24 ± 0.54	0.62 ± 0.18	1.54 ± 0.53	0.68 ± 0.20	2.99	0.393		
Oribatida juv.	2.05 ± 0.68	1.97 ± 0.51	2.01 ± 0.70	4.83 ± 1.63	1.03	0.395	2.03	0.075
Gamasina	2.45 ± 0.44 ^a	2.30 ± 0.50 ^a	6.48 ± 0.73 ^b	6.21 ± 0.55 ^b	22.74	< 0.001	1.75	0.126
Gamasidae ad.	0.47 ± 0.10 ^a	0.36 ± 0.08 ^a	1.00 ± 0.21 ^b	0.89 ± 0.09 ^b	8.23	< 0.001	1.86	0.102
Gamasidae juv.	1.24 ± 0.32 ^a	1.03 ± 0.19 ^a	3.28 ± 0.60 ^b	2.60 ± 0.42 ^b	11.38	< 0.001	2.25	0.050
Gamasidae tot.	1.71 ± 0.37 ^a	1.38 ± 0.24 ^a	4.27 ± 0.72 ^b	3.49 ± 0.44 ^b	18.18	< 0.001	3.36	0.007
Zerconidae ad.	0.14 ± 0.06 ^a	0.20 ± 0.08 ^{ab}	0.48 ± 0.11 ^b	0.65 ± 0.28 ^b	9.19	0.027		
Zerconidae juv.	0.60 ± 0.11 ^a	0.71 ± 0.27 ^a	1.74 ± 0.34 ^b	2.07 ± 0.42 ^b	6.40	0.002	0.49	0.870
Zerconidae tot.	0.74 ± 0.10 ^a	0.91 ± 0.31 ^a	2.22 ± 0.38 ^b	2.72 ± 0.58 ^b	7.74	0.001	0.33	0.957
Other mites	24.59 ± 4.16	31.77 ± 4.49	38.95 ± 8.88	33.07 ± 4.81	0.95	0.431	0.58	0.798
Uropodina	0.19 ± 0.17	0.03 ± 0.03	0.23 ± 0.17	0				
Mesostigmata indet.	0.04 ± 0.04	0	0	0				
Scutacaridae	0.01 ± 0.01	0.01 ± 0.01	5.47 ± 5.17	0.63 ± 0.43				
Other Actinedida	24.35 ± 4.11	31.73 ± 4.50	33.13 ± 5.20	32.40 ± 4.67	0.89	0.459	0.684	0.717
<i>Schwiebea</i> sp.	0	0	0.06 ± 0.06	0.01 ± 0.01				
Other Acaridida	0	0	0.06 ± 0.05	0.03 ± 0.03				
Collembola	34.51 ± 6.7 ^a	36.01 ± 6.71 ^a	129.83 ± 13.36 ^b	134.94 ± 26.35 ^b	22.35	< 0.001	1.02	0.446
<i>Ceratophysella scotica</i>	0.06 ± 0.05 ^a	0.13 ± 0.05 ^{ab}	0.32 ± 0.10 ^{ab}	0.62 ± 0.25 ^b	12.15	0.007		
<i>Willemia</i> sp.	0.76 ± 0.26	1.29 ± 0.35	2.37 ± 0.85	3.54 ± 1.86	1.82	0.167	0.82	0.603
<i>Friesea truncata</i>	0.53 ± 0.31	0.19 ± 0.09	0.87 ± 0.58	0.28 ± 0.11	0.66	0.883		
<i>Micranurida forsslundi</i>	0.09 ± 0.04 ^a	0.18 ± 0.05 ^b	0.09 ± 0.06 ^{ab}	0 ^{ab}	8.37	0.039		
<i>Micranurida pygmaea</i>	0 ^a	0 ^a	1.99 ± 1.56 ^b	0.93 ± 0.66 ^{ab}	14.60	0.002		
<i>Neanura muscorum</i>	0	0.01 ± 0.01	0	0				
<i>Protaphorura pseudovanderdrifti</i>	1.25 ± 0.37 ^a	1.27 ± 0.16 ^a	6.55 ± 1.23 ^b	3.35 ± 0.44 ^c	19.83	< 0.001	0.91	0.532
<i>Mesaphorura</i> sp.	6.13 ± 2.58	15.01 ± 8.21	5.96 ± 3.96	5.16 ± 2.26	2.39	0.091	3.55	0.005
<i>Tetracanthella wahlgreni</i>	1.02 ± 0.31 ^a	0.28 ± 0.09 ^b	0.03 ± 0.03 ^b	0 ^b	24.33	< 0.001		
<i>Tetracanthella brachyura</i>	0.76 ± 0.33	0.21 ± 0.10	1.14 ± 0.48	0.44 ± 0.30	3.72	0.293		
<i>Pseudanurophorus binoculatus</i>	0.96 ± 0.29 ^{ab}	0.81 ± 0.30 ^b	2.91 ± 0.74 ^a	2.27 ± 1.09 ^{ab}	3.08	0.044	1.62	0.160
<i>Isotomodella pusilla</i>	1.82 ± 0.57	1.84 ± 0.64	3.43 ± 1.22	4.29 ± 1.68	0.82	0.845		

Continued

Table 1. (Contd.)

Taxa	C	T	N	TN	Treatment		Block	
					F/K	P	F/K	P
<i>Folsomia brevicauda</i>	9.44 ± 2.87	4.90 ± 1.65	7.45 ± 3.45	1.95 ± 0.89	4.61	0.203		
<i>Folsomia palaeartica</i>	0.83 ± 0.79	0.18 ± 0.18	0.68 ± 0.68	0.09 ± 0.06				
<i>Folsomia dovreensis</i>	0	0	0.01 ± 0.01	0				
<i>Folsomia quadrioculata</i>	3.05 ± 1.06 ^a	2.73 ± 0.89 ^a	63.50 ± 13.95 ^b	64.40 ± 18.40 ^b	20.35	<0.001	1.59	0.168
<i>Isotomiella minor</i>	1.25 ± 0.69	0.33 ± 0.13	1.76 ± 0.90	0.32 ± 0.19	4.56	0.207		
<i>Parisotoma ekmani</i>	0.10 ± 0.09	0.17 ± 0.13	0.36 ± 0.35	0.95 ± 0.94				
<i>Parisotoma notabilis</i>	3.82 ± 2.21 ^a	2.37 ± 0.60 ^a	21.91 ± 4.82 ^b	31.02 ± 14.65 ^b	15.26	<0.001	1.46	0.213
<i>Desoria olivacea</i>	0	0	0.01 ± 0.01	1.47 ± 1.31				
<i>Desoria tolya</i>	0.01 ± 0.01 ^a	0 ^a	0.18 ± 0.07 ^{ab}	0.34 ± 0.14 ^b	15.08	0.002		
<i>Isotoma viridis</i>	1.22 ± 0.17 ^a	1.72 ± 0.35 ^a	4.08 ± 0.63 ^b	4.97 ± 1.08 ^b	9.71	<0.001	0.81	0.614
<i>Isotoma</i> sp.	0.06 ± 0.03 ^a	0.20 ± 0.06 ^b	0.01 ± 0.01 ^a	0 ^a	15.69	0.001		
<i>Lepidocyrtus lignorum</i>	1.01 ± 0.15 ^a	1.19 ± 0.20 ^a	1.72 ± 0.24 ^a	5.31 ± 0.62 ^b	35.97	<0.001	1.40	0.238
<i>Megalothorax minimus</i>	0.09 ± 0.05	0.48 ± 0.22	0.46 ± 0.24	0.23 ± 0.11	1.30	0.294	1.31	2.77
Other Sminthuridae	0.27 ± 0.18 ^a	0.51 ± 0.21 ^a	2.05 ± 0.49 ^b	3.02 ± 1.15 ^b	16.05	<0.001	4.59	0.001
Homoptera: Coccoidea	1.10 ± 0.78 ^{ab}	1.43 ± 0.59 ^b	0.08 ± 0.05 ^a	0.05 ± 0.03 ^a	5.22	0.006	2.29	0.047
Diptera larvae	0.36 ± 0.17	0.44 ± 0.20	0.49 ± 0.15	0.73 ± 0.26	0.73	0.546	1.43	0.226
Sciariidae	0.32 ± 0.17	0.36 ± 0.17	0.39 ± 0.17	0.42 ± 0.14	0.18	0.912	1.36	0.254
Chironomidae	0.04 ± 0.02	0.08 ± 0.05	0.10 ± 0.05	0.31 ± 0.15	4.63	0.200		

General linear model (GLM) *F*- and *P*-values are shown for treatment and block effects. When variance was heterogeneous and/or normality test failed, only treatment effect was calculated, with Kruskal–Wallis test statistic (*K*). Degrees of freedom are 3, 27 for the treatment effect and 9, 27 for the block effect. Statistical significant values ($P < 0.05$) are in bold, and differences between treatment means are indicated by different letters (Tukey's HSD or Student–Newman–Keuls method for GLM and Kruskal–Wallis test, respectively). Only taxa that were present in >5 plots of at least one of the treatments were tested.

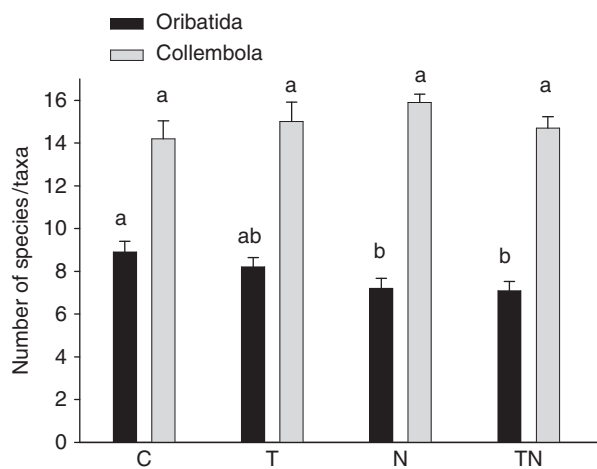


Fig. 1 Species richness of Oribatida and Collembola in control plots (C), plots with warming (T), nutrient addition (N), and warming combined with nutrient addition (TN) at Finse, alpine Norway. Bars with different letters differ significantly ($P < 0.05$, Tukey HSD).

density of Collembola increased fourfold in fertilized plots, with and without warming (Table 1). Among Oribatei, however, neither the abundance nor the dominance structure was significantly affected by nutrient addition (Table 1, Fig. 3).

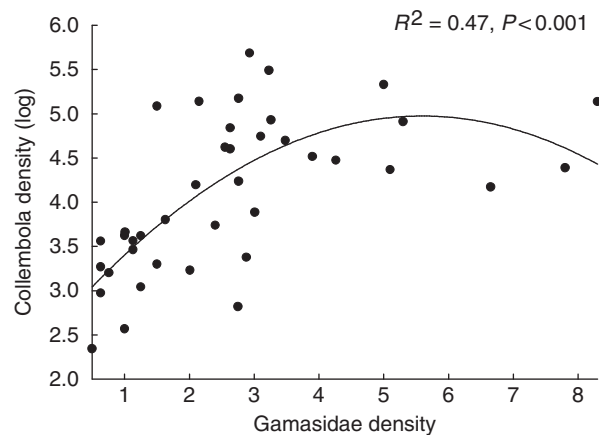


Fig. 2 Polynomial regression of the relationship between the density (1000 m^{-2}) of Collembola and Gamasidae at Finse, alpine Norway.

Block effects were found on the abundance of some taxa (Table 1), indicating differences in soil conditions among blocks. Regarding species richness, there was no block effect for Oribatida ($F_{9,27} = 1.77$, $P = 0.121$), while a clear block effect was seen in the number of Collembola species ($F_{9,27} = 3.60$, $P = 0.005$). This was most likely due to differences in the soil organic layer. The

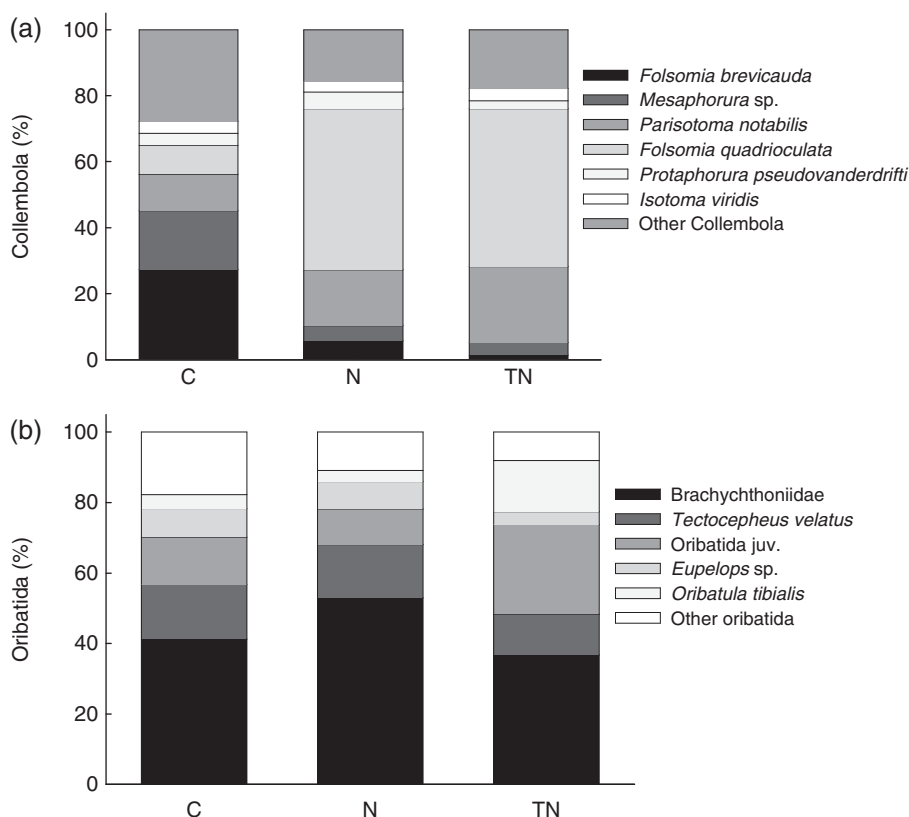


Fig. 3 Dominance structure of the Collembola and the Oribatida community in control plots (C), plots with nutrient addition (N), and warming combined with nutrient addition (TN) at Finse, alpine Norway. Changes between control plots (C) and warmed plots (T) were negligible.

organic content at ca. 5 cm depth, measured as loss on ignition (LOI) was in the range of ca. 12–20%, with no significant difference between treatments (GLM ANOVA; $F_{3,27} = 0.77$, $P = 0.523$), but with a marginally significant difference between blocks (GLM ANOVA; $F_{9,27} = 2.19$, $P = 0.056$). The highest species number of Collembola was found in those blocks with the highest organic content, i.e. in blocks with the thickest organic layer (K. Klanderud, personal observations), and simple linear regressions showed a positive relationship between the number of Collembola species and LOI across all treatments ($R^2 = 0.118$, $P = 0.030$).

Discussion

Nutrient addition, and warming combined with nutrient addition, led to a profound change in the Collembola community, with most pronounced changes in the TN plots for some of the species. The total Collembola density increased fourfold in N and TN plots, mainly due to *F. quadrioculata* and *P. notabilis*. These two relatively large species are habitat generalists (Hågvar, 1982; Fjellberg, 2007) and live in the uppermost part

of the soil profile (Hågvar, 1983). Both species feed partly on fungal hyphae (Bödvarsson, 1970; Hågvar & Kjøndal, 1981; Chen *et al.*, 1996). In particular *F. quadrioculata* is a flexible food generalist (Meibes & Filser, 1998), which in culture eats fungi, green algae, and cyanobacteria (H. P. Leinaas, personal communication). Fertilized plots achieved a completely different vegetation than the C and T plots, being dominated by tall graminoids with more biomass and a higher litter production (Klanderud & Totland, 2005). Thus, a possible explanation for increased collembolan density in fertilized plots is increased food availability due to high fungal activity in decomposing graminoid litter. Also *I. viridis* and 'Other Sminthuridae' represent large, litter-inhabiting species.

Responses among microarthropods to nutrient addition may also be due to changes in soil chemistry and root systems, as well as competition. Competition may be an important ecological factor in microarthropod communities (e.g., Hågvar, 1990). Combined with low reproduction rates in some species, it may take a long time for the microarthropod community to stabilize after environmental change.

Species with a short life cycle may respond rapidly to environmental change. In an Antarctic soil heating experiment, Convey & Wynn-Williams (2002) found a rapid population increase in the microbivorous nematode genus *Plectus*, which has a short life cycle, resulting in changes in the relative abundance of taxa. According to Fjellberg (1974), *F. quadrioculata*, *P. notabilis*, and *I. viridis* have a 1-year life cycle in the present mountain area, which probably explains their rapid response to nutrient addition. *F. brevicauda*, however, which dominated the control plots but remained unaffected by nutrient addition, has a 2-year life cycle and needs more time to respond. That is also the case with the two *Tetracanthella* species. The nearly unchanged Oribatida community after 4 years of nutrient addition is probably due to life cycles spanning 2 or more years. These mites with their low metabolic rates, slow development, and low fecundity cannot respond rapidly to resource flushes (Behan-Pelletier, 1999). Even in a lowland Danish beech forest, Luxton (1981) found that some oribatids developed slowly, with life cycles of 1–2 years. In colder climates, Oribatida often have multiyear life cycles (Walter & Proctor, 1999). In Austrian mountains, *Oromurcia sudetica* has a 2–3 year, or possibly 4-year life cycle (Schatz, 1985). On the Hardangervidda, even the small *Tectocephus velatus* is assumed to use 2 or more years to fulfill the life cycle (Solhøy, 1975), and Tilrem (1994) assumed a development time of 4–6 years for *Ameronothrus lapponicus* living in lichens on erratic boulders at Finse. The significant reduction of species richness of Oribatida in N and TN plots is due to the absence of some rare species and may indicate the beginning of a decline in biodiversity.

The increased abundance of predatory Gamasina mites in fertilized plots is probably due to increased prey abundance. These active mites live high in the soil profile, often in the litter. Gamasidae feed on a variety of animals, including Collembola (Wallwork, 1970). Zerconidae are known to prey on Nematoda (Martikainen & Huhta, 1990). In a similar experiment in two subarctic soils, Ruess *et al.* (1999) found that nematode populations increased in fertilized plots, also in combination with warming, compared with control plots.

Diptera larvae tended to be more abundant on fertilized plots than in the controls, although not significant. *A. cataphracta* (Coccoidea), on the other hand, was reduced by nutrient addition combined with warming, compared with only warming. This holarctic species lives on the ground, feeding on roots of several plants, among them *Dryas* (Kosztarab & Kozár, 1988). *Dryas* abundance decreased significantly in the TN plots (Klanderud & Totland, 2005), which may explain the decline of this species.

Theoretically, soil arthropods may have migrated in or out of the OTCs during the experiment. However, the population increase in species with a short life cycle compared with species with a long life cycle is consistent with a response within the OTC. Furthermore, the soil samples were taken in the central part of each OTC.

Four years of warming may be too short to reveal clear biological effects, both above and below ground. The responses in three low-density Collembola are difficult to interpret. Warming hardly affected vegetation structure, except for a reduced abundance of some bryophyte species (Klanderud & Totland, 2005; Klanderud, 2008), which was most likely due to a drier soil surface (K. Klanderud, unpublished results). Similar warming studies on soil animals have revealed several practical problems. Firstly, increased drought in warmed plots has been a general side effect in these types of experiments, both in Arctic and Antarctic habitats, and Collembola are especially vulnerable to drought stress (summaries by Hodkinson *et al.*, 1998; Sinclair & Stevens, 2006). Secondly, climatic differences between years may mask treatment effects on microarthropods (e.g., Coulson *et al.*, 1996). Moreover, the modifying effect of local soil moisture was shown in a subalpine meadow in the Rocky Mountains, as the effect of warming on soil animals depended on whether the summer was cool and wet, or warm and dry (Harte *et al.*, 1996). The lower number of Collembola species in blocks with a thinner organic layer in the present study may be due to drier surface conditions.

Studies on environmental change are most often limited to above-ground effects. However, both from an ecosystem function and biodiversity point of view, below-ground changes are crucial. In this study, certain effects of nutrient addition were common for below-ground arthropods and above-ground vegetation (Klanderud & Totland, 2005; Klanderud, 2008): increased biomass, high dominance of a few species, reduction in species number, and different responses in closely related species. Further studies in other alpine areas are needed to check the general value of this pattern.

The present study has shown that the soil arthropod community in nutrient poor alpine sites can be sensitive to increased nutrients, likely due to changes in associated vegetation. Microarthropod species with short life cycles can take over the dominance after few years, before species with longer life cycles are able to react. The reduced diversity of slowly reproducing Oribatida may be a result of competition with rapidly expanding Collembola populations. Further community changes may be expected when species with longer life cycles have had the possibility to respond. Nutrient addition in the present ecosystem has triggered processes both above and below ground, which may take many years to stabilize.

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