










Legacy effects of experimental environmental change on soil micro-arthropod communities

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Citation: Roos, R. E., T. Birkemoe, J. Asplund, P. Luptáčik, N. Raschmanová, J. M. Alatalo, S. L. Olsen, and K. Klanderud. 2020. Legacy effects of experimental environmental change on soil micro-arthropod communities. *Ecosphere* 11(2):e03030. 10.1002/ecs2.3030

Abstract. Global change experiments such as experimental warming and nutrient addition strongly affect the structure and functioning of high latitude and altitude ecosystems. However, it is often unknown to what extent such effects are permanent or whether changes persist after environmental conditions return to pre-treatment levels. In this study, we assess the legacy effects of temperature manipulation and nutrient addition experiments on alpine soil micro-arthropod (i.e., Collembola and Oribatida) communities nine years after the treatments were discontinued. Treatment effects on the vegetation were still detectable six years after cessation, although grazing increased the recovery rate. Because micro-arthropods are often closely associated with vegetation, we expected to find that treatment effects on Collembola and Oribatida abundance and species composition persisted to date, reflecting plant community dynamics. Also, we expected large-bodied, drought-resistant Collembola species that live on top of the soil to show less strong legacy effects. We did not find legacy effects of environmental treatments on Collembola and Mesostigmata in terms of abundance. However, we found persistent changes in community composition of Collembola and Oribatida, suggesting treatment effects persist to date. The generalist *Folsomia quadrioculata* was the most responsive Collembola species to initial treatments, most likely due to its variable life-history strategy. Although its abundance recovered, *F. quadrioculata* remained dominant in Collembola communities after cessation of the treatments. Grazing affected community composition of both Collembola and Oribatida, but we did not find grazing to reduce legacy effects on micro-arthropod as it did for vegetation. We therefore conclude that the environmental treatments had only temporary effects on micro-arthropods in terms of overall abundance, but that effects on individual species and therefore species composition may be long-lasting and less predictable.

Key words: Acari; alpine ecology; Collembola; community recovery; ecological resilience; ecosystem recovery; experimental warming; herbivory; nutrient addition; Oribatida.

Received 20 November 2019; accepted 3 December 2019. Corresponding Editor: Uffe N. Nielsen.

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INTRODUCTION

Over the last decades, ecosystems at high latitude and altitude have experienced a significant

temperature increase (Isaksen et al. 2016, Rizzi et al. 2017) and this is expected to continue in the future (Stocker 2014). Simultaneously, nitrogen availability may increase due to increased

mineralization rates (Nadelhoffer et al. 1991, Hobbie 1996, Rustad et al. 2001, Aerts et al. 2006), and increased atmospheric nitrogen deposition related to increased precipitation (Hole and Engardt 2008) and human practices such as the combustion of fossil fuels and agriculture (Vitousek et al. 1997). To understand the effects of such environmental changes on alpine ecosystems, a substantial number of studies have implemented experimental environmental manipulations. For instance, Elmendorf et al. (2012) show that experimental warming can substantially alter alpine and Arctic tundra vegetation, and such effects can be further amplified when warming is combined with nutrient addition (Klanderud and Totland 2005). Although the responses to such environmental manipulations can be rapid (within a few growing seasons, e.g., Klanderud and Totland 2005), it is often unknown to what extent treatment effects on ecological communities persist after they are discontinued.

While environmental conditions such as temperature and soil nutrient status often return rapidly to pre-treatment levels after cessation of experimental treatments (Boxman et al. 1998, Limpens and Heijmans 2008, O'Sullivan et al. 2011), the effects on community composition may be long-lasting (Strengbom et al. 2001). Very few studies have considered such legacy effects after cessation of environmental manipulations, but Street et al. (2015) found persistent effects on Arctic heathlands up to 18 yr after cessation of nitrogen addition. Similarly, Olsen and Klanderud (2014) found incomplete recovery of alpine vegetation six years after warming and nutrient addition treatments are ceased, but that herbivory increased the recovery rate. In general, alpine plant communities may be slow to respond to environmental changes as the plants are long-lived and growing seasons are short. However, the legacy effects of experimental drought events on alpine grasslands resembled the short-term responses of temperate grasslands, but with persistent changes in community composition (De Boeck et al. 2018). Such persistent legacy of environmental treatments may indicate that the ecosystem has experienced a regime shift (Scheffer et al. 2001, Van Nes and Scheffer 2007), and thus that restoring pre-treatment conditions are not sufficient to allow the ecosystem to recover.

The majority of studies on the responses of Arctic and alpine ecosystems to experimental environmental change, as well as the few studies on their legacy effects, have focused on vegetation. Yet, aboveground vegetation is intricately linked to belowground processes and communities (Wardle et al. 2004). As such, soil faunal communities, in addition to climate and leaf litter quality, play a role in the breakdown of plant litter (García-Palacios et al. 2013, Bradford et al. 2017). In Arctic and alpine ecosystems, where soil macrofauna (e.g., earthworms) is often absent, micro-arthropods, such as Collembola (springtails) and Acari (mites), are a conspicuous and ubiquitous component of soil fauna. The responses of these micro-arthropods to environmental manipulations are complex (Coyle et al. 2017) because micro-arthropod communities are simultaneously linked to vegetation (Coulson et al. 2003, Mitchell et al. 2016, 2017), to food availability (many soil micro-arthropods are fungivorous or bacterivorous species), and to microclimatic conditions (Coulson et al. 1996, Hodkinson et al. 1998, Sjursen et al. 2005). On the species level, responses of micro-arthropods are likely to be trait-dependent. For example, Makkonen et al. (2011) found drought-tolerant, large-bodied, surface-living Collembola to be most tolerant to experimental warming, and Bokhorst et al. (2012) found small bodied fauna to be more sensitive to winter climate change than large-bodied species. For Acari, soft-bodied juvenile mites were found to be more susceptible to environmental changes than hard-bodied adults (Alatalo et al. 2017).

In this study, we revisited an environmental manipulation study in an alpine ecosystem in southern Norway nine years after the cessation of seven-year nutrient addition and warming treatments (Fig. 1a). The treatments, most notably the combination of nutrient addition and warming, substantially altered vegetation from dominance by dwarf shrubs to graminoids (Klanderud and Totland 2005). Six years after cessation of the treatments, Olsen and Klanderud (2014) reported persistent treatment effects on the vegetation composition, but that grazing ameliorated legacy effects compared to when herbivores were fenced out. Similarly, the micro-arthropod communities, in particular Collembola and some Acari, responded strongly to nutrient

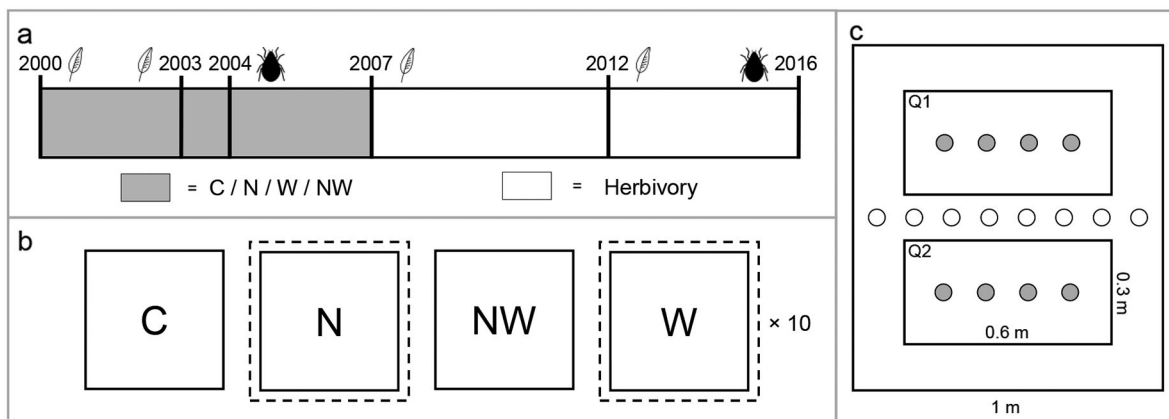


Fig. 1. (a) A timeline of the experiment at Finse and measurements taken. Leaf symbols indicate years of vegetation recording (2000, 2003, 2007, and 2012), and mite symbols indicate arthropod sampling (2004 and 2016). From 2000 to 2007, plots received environmental treatments (nutrient addition and/or warming by open top chambers). In 2007, treatments were discontinued and herbivore excluding fences were erected around half of the plots until sampling for this study in 2016. (b) Each block contained four plots that each received one of the environmental treatments or a control treatment. In 2007, two plots of each block were randomly selected to be fenced, ensuring that, overall, an equal number of plots for each treatments was fenced to exclude herbivores or left unfenced. In total, the study contained 10 blocks and 40 plots. (c) Soil micro-arthropods were sampled in between the two 60 × 30 cm vegetation subplots (open circles) in 2004 and from the middle of each vegetation subplot in 2016 (closed circles).

addition with and without warming (Hågvar and Klanderud 2009). We now use this experiment to test the hypothesis that the environmental treatments have similar legacy effects on micro-arthropod communities as they have on vegetation. We expect treatment effects to persist, but that herbivory will have resulted in ameliorated treatment effects. In addition, we expect that large-bodied, drought-resistant Collembola that live on top of the soil are better equipped to deal with variable environmental conditions. Legacy effects on these animals will therefore be less pronounced, as their populations may already partially be in equilibrium with the new (i.e., similar to pre-treatment) conditions. We assess treatment legacy effects in terms of abundance, species richness, and species composition. For abundance, we consider legacy effects present when increased abundances in treatment plots persist to date. For species composition, we compare treatment communities against those in control plots and interpret persistent differences compared to control plots as treatment legacy effects. The results of this study will help us

understand to what extent micro-arthropods can recover from environmentally induced changes in alpine ecosystems.

MATERIALS AND METHODS

Study system

This study was performed at the southwest-exposed slope of Mt. Sanddalsnuten in Southern Norway (60°36'55" N, 7°31'8" E) at approximately 1500 m a.s.l. The site has calcareous phyllite bedrock and is dominated by *Dryas octopetala* heath (see Klanderud and Totland 2004 for detailed site description and plant species lists). The mean monthly summer temperature (June–August) at the nearest meteorological station (Finse; located 2.5 km from the plots, at 1210 m a.s.l.) is +6.3°C with an average monthly precipitation of 89 mm over 1969–1990 (Aune 1993, Førland 1993). In the month of sampling for this study (June 2016), the average temperature was +6.1°C and 67.6 mm of precipitation (Norwegian Meteorological Institute 2016). The area is moderately grazed by domestic sheep and wild

reindeer (*Rangifer tarandus* Linnaeus, 1758). Lemming (*Lemmus lemmus* Linnaeus, 1758) populations in Finse peaked in 2014, while other rodent species showed low abundances throughout the entire duration of the study (Framstad 2017).

In July 2000, 10 blocks of four 1 × 1 m plots were randomly established in the *Dryas* heath (Klanderud and Totland 2005). Within each block, plots received one of four treatments: warming by open top chambers, nutrient addition (slow-released NPK fertilizer: 10 g N, 2 g P, and 8 g K/m² at the start of each growing season), nutrient addition combined with warming, and control (no treatment). Open top chambers increased –5 cm soil temperatures by ~1°C during growing seasons June–September (Klanderud and Totland 2005). Soil nutrient status showed few responses to nutrient addition treatments (K. Klanderud, *unpublished data*), suggesting that nutrients were rapidly immobilized by the microbial community and/or taken up by the vegetation, as suggested by the increased plant biomass.

Within each plot, two permanent 60 × 30 cm vegetation-sampling subplots were established, separated by a 10 cm wide row. In these subplots, vegetation was recorded in 2000 and 2003 to assess vegetation responses to the treatments (Klanderud and Totland 2005, Klanderud 2008). In 2004, Hågvar and Klanderud (2009) sampled soil micro-arthropods in the row between the subplots. The environmental treatments were discontinued in 2007, after seven years of treatment. In the same year, herbivore fences designed to exclude all mammalian herbivores were randomly erected around half the plots within each block, while ensuring that each treatment had the same number of fenced and unfenced plots overall (see Olsen and Klanderud 2014 for more details). Vegetation was again recorded in 2007 and 2012 to assess vegetation recovery under different grazing regimes (Olsen and Klanderud 2014). The herbivory treatment continued until the sampling for this study in June 2016. Fig. 1 illustrates the study and plot design in more detail.

Arthropod sampling and identification

We sampled micro-arthropods on 28 June 2016 by extracting eight soil cores from each plot (10-cm² surface area, 3 cm deep) which included the vegetation and litter on top of the soil. For

analyses, all samples from one plot were combined. The soils at this site are approximately 5–15 cm deep. Our methodology followed Hågvar and Klanderud (2009), but to avoid sampling from disturbed soil (by the sampling in 2004), we took four soil cores from within each vegetation subplot, approximately 20 cm from the original sampling locations (Fig. 1c). Micro-arthropods were then extracted onto water saturated with benzoic acid with the same high-gradient apparatuses modified after Macfadyen (1961) as used in 2004. Extractions lasted for 10 d with a gradual increase in temperature from 30°C to 70°C during the first five days. After extraction, the animals were transferred into containers with 70% ethanol. Collembola and Acari were sorted under a binocular stereomicroscope and identified under a phase-contrast microscope (Leica DM2500, Leica Microsystems GmbH, Wetzlar, Germany). The identification of Collembola followed Fjellberg (1998), Bretfeld (1999), Potapov (2001), and Dunger and Schlitt (2011). Within Acari, Oribatida were identified to species following Weigmann (2006). The order Oribatida presently also includes the cohort Astigmatina (after Krantz and Walter 2009), which were grouped separately and not identified to species level. Other, non-Oribatid, Acari were grouped into Prostigmata and Mesostigmata (including Gamasina and Uropodina). For analyses, species were grouped in accordance with the study with the lowest taxonomic detail (i.e., this one or Hågvar and Klanderud 2009). See Appendix S1: Table S1 for Collembola and Appendix S1: Table S2 for Acari identifications, abbreviations, and groupings.

Eco-morphological groups

Collembola were grouped into eco-morphological groups that describe their vertical distribution in the soil: Epi-edaphic species live above the surface of the soil, hemi-edaphics live near the soil surface, and eu-edaphic species live in deeper layers of the soil. Classifications were based on Hopkin (1997) and the personal database of Prof. Dr. Matty Berg (*unpublished data*, but see Makkonen et al. 2011). *Isotoma* sp. and other Symphypleona could contain species belonging to more than one eco-morphological group and were therefore excluded from statistical analysis on eco-morphological groups (Appendix S1: Table S1).

Statistical analyses

We examined the effects of environmental treatment, sampling year, and herbivory on Collembola and Acari abundance and species richness with linear mixed-effect models using the lmerTest-package (Kuznetsova et al. 2015), lme4-package (Bates et al. 2014), and output via the sjPlot-package (Lüdtke 2016) in R version 3.4.2 (R Core Team 2017). In these models, environmental treatment (levels: warming, nutrient addition, both warming and nutrient addition, and control) and a combined variable of year and herbivory treatment (year+herbivory levels: 2004 herbivory; 2016 herbivory; 2016 no herbivory) were included as fixed factors and block (numbered 1 through 10) as random factor. To meet assumptions of normality of the residuals, and heteroscedasticity, abundance data were natural log transformed. For species richness, generalized mixed effects models from the Poisson family (log link) were used. Due to very low abundances, the epiedaphic Collembola dataset only allowed for a binomial model on absence or presence in treatments, and Astigmatina were not analyzed separately. To test for a priori differences in abundance for all Collembola and Acari groups between herbivory treatments, we performed separate mixed-model analysis on the 2004 data with environmental treatment and herbivory treatment (future herbivory, no future herbivory) as fixed factors, and block as random effect. To test whether treatment effects remained in 2016 and whether controls differed between years, we performed Tukey pairwise comparisons with the emmeans package (Lenth et al. 2017) for all treatments vs. the control, for both grazed and ungrazed plots.

To examine how the species composition of Collembola and Oribatida in the treatment plots changed over time, we used unconstrained and constrained multivariate ordination techniques. First, we used global non-metric multidimensional scaling (GNMDS) to examine the trajectory of the Collembola and Oribatida species composition of the different environmental treatments from 2004 to 2016. The GNMDS was run as specified in Olsen and Klanderud (2014). Because no sampling prior to the start of the treatments was performed, we consider legacy effects absent if treated communities show a shift towards the composition of control communities. Vice versa, legacy effects are present when

treated communities remain separated from controls in ordination space (Appendix S1: Fig. S1). Second, to test for treatment effects on species composition in 2004 and 2016, we used redundancy analysis (RDA). In this analysis, environmental treatment and herbivore treatment, as well as their interactions, were used as explanatory variables, and block was used as a conditioning variable. To assess variable significances, we used Monte Carlo permutation tests with 999 permutations. Then, to visualize the relative effects of treatments over time and the response of species of different edaphic groups (for Collembola), we used principal response curves (PRC). The environmental treatment with and without grazing enclosure and year were used as explanatory variables in the construction of the PRCs.

RESULTS

Abundance and species richness

Four years of nutrient addition and nutrient addition combined with warming led to an initial increase in the abundance of Collembola in 2004 (Table 1, Fig. 2, and see Hågvar and Klanderud 2009). However, there were no such differences in Collembola abundance between the environmental treatments and controls in 2016 (Appendix S1: Table S3). This shows that Collembola abundances in the treated plots were reduced to pre-treatment levels, and that these treatments thus did not have legacy effects on Collembola abundance nine years after the treatments were discontinued. The decrease in Collembola abundance was strongest for the combined nutrient addition and warming treatments that were grazed ($P = 0.05$). Further, the abundance of Collembola across all treatments was reduced in 2016 compared to 2004, but only significantly so in ungrazed plots ($P < 0.001$). Although Collembola abundances were also lower in the ungrazed control plots in 2016 compared to 2004 (Appendix S1: Table S3), this effect was small compared to the responses in the plots that received environmental treatment, supporting the validity of the responses of Collembola abundance to nutrient addition and warming treatments.

The dynamics of Collembola abundances in response to nutrient addition and warming treatments were mainly driven by the abundance of

Table 1. Model parameter estimates from linear mixed-effect and binomial models examining the effects of treatment, the three year and herbivory treatments (year 2004: herbivory, year 2016: no herbivory, and year 2016: herbivory), and their interactions on Collembola abundance.

Predictors	Estimates	CI	P	df	Odds ratios
All Collembola†					
(Intercept)	3.39	3.12 to 3.67	<0.001	66.00	
N	1.42	1.05 to 1.80	<0.001	59.00	
NW	1.34	0.97 to 1.72	<0.001	59.00	
W	0.03	-0.34 to 0.41	0.880	59.00	
2016 no herbivory	-1.10	-1.57 to -0.64	<0.001	63.00	
2016 herbivory	-0.39	-0.86 to 0.07	0.170	63.00	
N: 2016 no herbivory	-0.66	-1.32 to -0.01	0.102	61.00	
NW: 2016 no herbivory	-0.73	-1.40 to -0.06	0.076	65.00	
W: 2016 no herbivory	0.69	0.02 to 1.36	0.095	66.00	
N: 2016 herbivory	-0.76	-1.42 to -0.11	0.060	61.00	
NW: 2016 herbivory	-0.81	-1.48 to -0.14	0.050	65.00	
W: 2016 herbivory	-0.06	-0.73 to 0.61	0.886	66.00	
Random effects					
σ^2	0.26				
τ_{00}	0.02 _{Block}				
ICC	0.06 _{Block}				
Observations	80				
Marginal R^2 /Conditional R^2	0.679/0.698				
Epi-edaphic Collembola‡					
(Intercept)		1.16–9.22	0.033		3.00
N		0.40–10.50	0.433		1.89
NW		0.23–4.30	1.000		1.00
W		0.40–10.50	0.433		1.89
Random effects					
σ^2					
τ_{00}					
ICC					
Observations	80				
Marginal R^2 /Conditional R^2	0.016/0.025				
Hemi-edaphic Collembola†					
(Intercept)	2.79	2.44 to 3.14	<0.001	67.00	
N	1.71	1.22 to 2.20	<0.001	59.00	
NW	1.64	1.15 to 2.13	<0.001	59.00	
W	-0.36	-0.85 to 0.13	0.227	59.00	
2016 no herbivory	-1.13	-1.74 to -0.52	0.003	63.00	
2016 herbivory	-0.48	-1.09 to 0.12	0.195	63.00	
N: 2016 no herbivory	-0.86	-1.71 to -0.00	0.103	61.00	
NW: 2016 no herbivory	-1.12	-1.98 to -0.25	0.038	65.00	
W: 2016 no herbivory	1.28	0.41 to 2.15	0.018	66.00	
N: 2016 herbivory	-0.54	-1.40 to 0.31	0.298	61.00	
NW: 2016 herbivory	-0.70	-1.56 to 0.17	0.191	65.00	
W: 2016 herbivory	0.58	-0.29 to 1.45	0.278	66.00	
Random effects					
σ^2	0.44				
τ_{00}	0.02 _{Block}				
ICC	0.04 _{Block}				
Observations	80				
Marginal R^2 /Conditional R^2	0.643/0.657				

(Table 1. Continued.)

Predictors	Estimates	CI	<i>P</i>	df	Odds ratios
Eu-edaphic Collembola†					
(Intercept)	2.28	1.85 to 2.71	<0.001	51.00	
N	0.83	0.29 to 1.37	0.014	59.00	
NW	0.27	-0.27 to 0.81	0.412	59.00	
W	0.35	-0.19 to 0.89	0.287	59.00	
2016 no herbivory	-1.15	-1.82 to -0.47	0.007	62.00	
2016 herbivory	-0.71	-1.38 to -0.03	0.090	62.00	
N: 2016 no herbivory	-0.24	-1.18 to 0.70	0.671	60.00	
NW: 2016 no herbivory	0.70	-0.26 to 1.67	0.236	63.00	
W: 2016 no herbivory	0.21	-0.76 to 1.19	0.719	64.00	
N: 2016 herbivory	-1.05	-1.99 to -0.11	0.070	60.00	
NW: 2016 herbivory	0.09	-0.88 to 1.06	0.879	63.00	
W: 2016 herbivory	-0.39	-1.37 to 0.59	0.513	64.00	
Random effects					
σ^2	0.53				
τ_{00}	0.15 _{Block}				
ICC	0.22 _{Block}				
Observations	80				
Marginal R^2 /Conditional R^2	0.335/0.483				

Notes: C, control; W, warming; N, nutrient addition; NW, nutrient addition + warming; CI, confidence interval. Data for all, hemi-, and eu-edaphic Collembola were natural log transformed. The odds of presence of epi-edaphic Collembola were tested for treatments only. Model estimates from mixed-effect models are shown on the transformed scale. *P*-values were computed via Kenward-Roger approximation and significant results ($P < 0.05$) are printed in bold.

† log transformed data.

‡ Model run on binomial data.

hemi-edaphic species (Table 1 and Fig. 2c). Although eu-edaphic Collembola initially also responded to nutrient addition ($P = 0.014$), their tendency to decrease in abundance after cessation of treatments was not significant (grazed $P = 0.090$, ungrazed $P = 0.070$). Hemi-edaphic Collembola were more abundant a priori in grazed than ungrazed plots (est. = 1.06, SE = 0.34, df = 31.92, $t = 3.079$, $P = 0.004$, Appendix S1: Fig. S2). Nevertheless, reductions in abundance were generally stronger in ungrazed plots (Table 1). We found no effects of environmental treatment, year, or herbivory on the species richness of Collembola communities (Appendix S1: Table S4).

The abundance of all Acari, as well as the subgroups Oribatida, and Prostigmata was not affected by the initial environmental treatments (Table 2). In other words, these mites did not respond to environmental manipulations on the short term, nor on the long term. The abundance of Acari overall ($P = 0.001$, Table 2; Appendix S1: Fig. S3) and in the controls (Appendix S1: Table S3) was lower in 2016 compared to 2004, suggesting some inter-annual variability in Acari

abundance. However, Mesostigmata showed a different pattern. These predatory mites initially responded positively to nutrient addition alone and in combination with warming. However, similar to Collembola, Mesostigmata abundance did not differ between control and environmental treatments in 2016, indicating that any treatment effects did not persist nine years after the treatments were discontinued (Table 2; Appendix S1: Fig. S3d, Table S3). We found no effect of environmental treatment, not initially nor after cessation of the treatments, or herbivory on Oribatida species richness (Appendix S1: Table S5). Generally, responses in grazed and ungrazed plots were in similar directions, indicating that the treatments and/or the sampling year had greater effects than herbivory.

Legacy effects on community composition

Initially, the Collembola species composition was strongly affected by treatments with nutrient addition, as shown by a clear separation in ordination space from warming treatments and controls in 2004 (Fig. 3a). This was driven by a shift in dominance structure in favor of certain

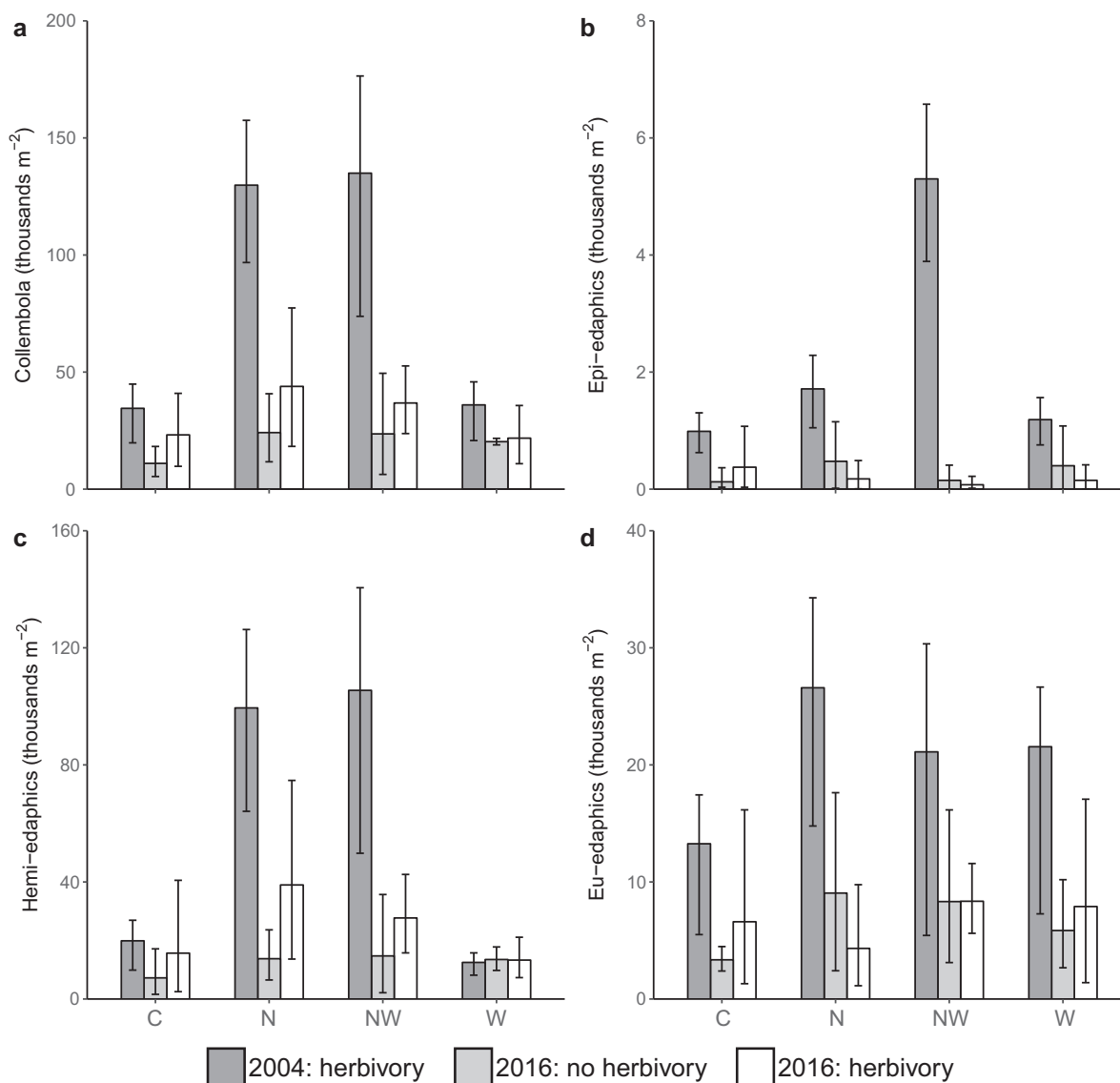


Fig. 2. Mean abundances (in thousands m^{-2}) for (a) all Collembola, (b) epi-edaphic Collembola, (c) hemi-edaphic Collembola, and (d) eu-edaphic Collembola per treatment (C, control; N, nutrient addition; W, warming; NW, nutrient addition + warming) per sampled year in Finse, southern Norway. Data are shown on the non-transformed scale, but error bars indicate exponentiated 95% confidence intervals calculated on natural log transformed data (but on square root data for epi-edaphic Collembola).

Collembola species, most notably the two hemi-edaphic species *Folsomia quadrioculata* and *Parisotoma notabilis* (Appendix S1: Fig. S4; see Hågvar and Klanderud 2009). After cessation of the treatments, species composition in all environmental treatments and the controls was displaced along GNMDS axis 1 and to some extent along GNMDS axis 2. In general, Collembola

composition converged to one point in ordination space, regardless of herbivory treatment. However, control plots remained separated in ordination space from those that received treatments with nutrient addition, indicative of treatment legacy effects. For all environmental treatments except warming, displacement in ordination space was larger for ungrazed plots.

Table 2. Model parameter estimates from linear mixed-effect and binomial models examining the effects of treatment, the three year and herbivory treatments (year 2004: herbivory, year 2016: no herbivory, and year 2016: herbivory), and their interactions on Acari abundance.

Predictors	Estimates	CI	P	df
All Acari†				
(Intercept)	3.67	3.39 to 3.95	<0.001	65.00
N	0.38	0.01 to 0.75	0.100	59.00
NW	0.29	-0.08 to 0.67	0.201	59.00
W	0.18	-0.19 to 0.56	0.429	59.00
2016 no herbivory	-1.34	-1.81 to -0.88	<0.001	63.00
2016 herbivory	-1.56	-2.03 to -1.10	<0.001	63.00
N: 2016 no herbivory	0.51	-0.14 to 1.16	0.206	60.00
NW: 2016 no herbivory	-0.38	-1.04 to 0.29	0.357	65.00
W: 2016 no herbivory	0.27	-0.40 to 0.94	0.509	65.00
N: 2016 herbivory	-0.45	-1.10 to 0.20	0.263	60.00
NW: 2016 herbivory	-0.22	-0.88 to 0.45	0.593	65.00
W: 2016 herbivory	0.39	-0.28 to 1.06	0.346	65.00
Random effects				
σ^2	0.26			
τ_{00}	0.03 _{Block}			
ICC	0.09 _{Block}			
Observations	80			
Marginal R^2 /Conditional R^2	0.681/0.710			
Oribatida†				
(Intercept)	2.66	2.27 to 3.04	<0.001	41.00
N	0.10	-0.35 to 0.55	0.711	59.00
NW	0.00	-0.45 to 0.45	0.991	59.00
W	-0.00	-0.45 to 0.45	0.998	59.00
2016 no herbivory	-0.96	-1.53 to -0.39	0.007	61.00
2016 herbivory	-1.15	-1.71 to -0.58	0.001	61.00
N: 2016 no herbivory	0.29	-0.49 to 1.08	0.540	60.00
NW: 2016 no herbivory	-0.59	-1.40 to 0.23	0.239	62.00
W: 2016 no herbivory	0.49	-0.33 to 1.31	0.328	63.00
N: 2016 herbivory	-0.65	-1.44 to 0.13	0.177	60.00
NW: 2016 herbivory	-0.34	-1.16 to 0.47	0.493	62.00
W: 2016 herbivory	0.45	-0.37 to 1.27	0.371	63.00
Random effects				
σ^2	0.37			
τ_{00}	0.17 _{Block}			
ICC	0.32 _{Block}			
Observations	80			
Marginal R^2 /Conditional R^2	0.424/0.607			
Prostigmata†				
(Intercept)	2.75 to 3.42	<0.001	65.00	
N	-0.08 to 0.82	0.178	59.00	
NW	-0.15 to 0.76	0.270	59.00	
W	-0.15 to 0.75	0.279	59.00	
2016 no herbivory	-2.71 to -1.59	<0.001	63.00	
2016 herbivory	-3.01 to -1.88	<0.001	63.00	
N: 2016 no herbivory	0.51 to 2.09	0.008	60.00	
NW: 2016 no herbivory	-0.63 to 0.98	0.718	65.00	
W: 2016 no herbivory	-0.52 to 1.09	0.563	65.00	
N: 2016 herbivory	-0.88 to 0.69	0.846	60.00	
NW: 2016 herbivory	-0.54 to 1.06	0.596	65.00	
W: 2016 herbivory	-0.04 to 1.57	0.125	65.00	

(Table 2. Continued.)

Predictors	Estimates	CI	<i>P</i>	df
Random effects				
σ^2	0.38			
τ_{00}	0.04 _{Block}			
ICC	0.09 _{Block}			
Observations	80			
Marginal R^2 /Conditional R^2	0.736/0.760			
Mesostigmata†				
(Intercept)	0.81	0.45 to 1.18	0.001	41.00
N	1.05	0.62 to 1.47	<0.001	59.00
NW	0.98	0.55 to 1.40	<0.001	59.00
W	-0.14	-0.56 to 0.29	0.602	59.00
2016 no herbivory	-0.84	-1.38 to -0.31	0.012	61.00
2016 herbivory	-0.77	-1.30 to -0.23	0.022	61.00
N: 2016 no herbivory	-0.35	-1.09 to 0.39	0.443	60.00
NW: 2016 no herbivory	-1.08	-1.84 to -0.31	0.025	62.00
W: 2016 no herbivory	0.49	-0.28 to 1.27	0.299	63.00
N: 2016 herbivory	-0.74	-1.48 to -0.00	0.105	60.00
NW: 2016 herbivory	-0.64	-1.41 to 0.13	0.174	62.00
W: 2016 herbivory	0.11	-0.67 to 0.88	0.821	63.00
Random effects				
σ^2	0.33			
τ_{00}	0.15 _{Block}			
ICC	0.32 _{Block}			
Observations	80			
Marginal R^2 /Conditional R^2	0.494/0.654			

Notes: C, control; W, warming; N, nutrient addition; NW, nutrient addition + warming; CI, confidence interval. Data were natural log transformed and model estimates are shown on the log scale. *P*-values were computed via Kenward-Roger approximation, and significant results ($P < 0.05$) are printed in bold.

† log transformed data.

For Oribatida, the only Acari group identified to species in this study, species compositions were tightly clustered in ordination space in 2004, except for ungrazed nutrient addition and grazed nutrient addition with warming treatments (Fig. 3b). Nine years after cessation of the treatments (i.e., in 2016), all environmental treatments show similar amounts of displacement along GNMDS axis 1, and to some extent along axis 2. In contrast to Collembola, Oribatida species composition of the different environmental treatments diverged into ordination space, suggesting that community dynamics induced by environmental treatments are still ongoing.

In accordance with the GNMDS plot, the RDA analysis showed that the species composition of Collembola communities was significantly affected by all environmental treatments in 2004 (Table 3), but most strongly by treatments with nutrient addition, and that this was mainly driven by the hemi-edaphic *F. quadrioculata* and *P. notabilis* (Fig. 4a). In 2016, the effect of treatments with

nutrient addition on the Collembola community persisted, although less pronounced than in 2004. In 2016, species composition differed significantly between grazed and ungrazed plots overall and for grazed and ungrazed plots within the nutrient addition treatment. This suggests that herbivore grazing affects the Collembola community composition. For Oribatida, the RDA showed that community composition was significantly affected by nutrient addition in 2004, which was reduced to non-significant in 2016. While there was no notable effect of warming in 2004, there was in 2016 (Table 3, Fig. 4b). Similar to Collembola, Oribatida community composition differed between grazed and ungrazed plots, specifically in the nutrient addition treatments.

DISCUSSION

The aim of this study was to assess the legacy effects of environmental manipulations, such as nutrient addition and warming on soil micro-

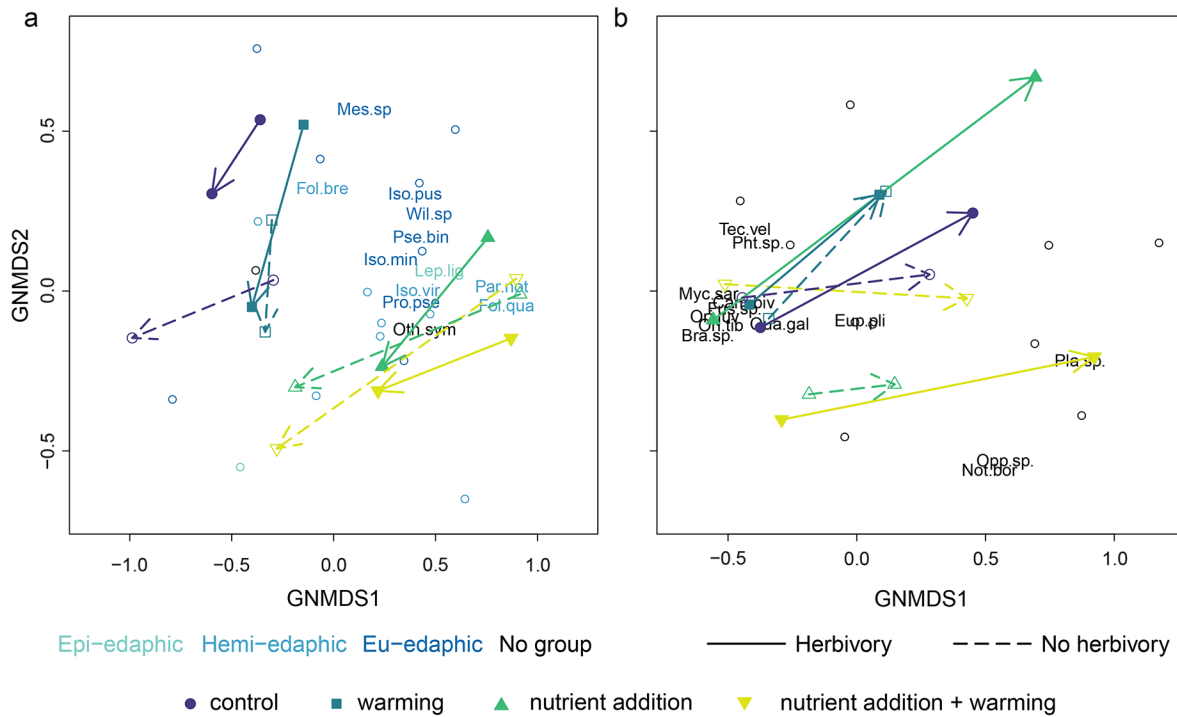


Fig. 3. Global non-metric multidimensional scaling ordination of the trajectories of mean Collembola (a) and Oribatida (b) community composition from 2004 (start of arrow) to 2016 (end of arrow) in control, warming, nutrient addition, and warming combined with nutrient addition treatments with herbivores present (solid line) and herbivores excluded (dashed line) in an alpine heath. Species names are shown only for the 12 most common Collembola and 13 most common Oribatida species, the remaining species are shown as open circles. Collembola species names and circles are colored according to edaphic group, but some species were grouped and therefore not assigned to a specific edaphic group (no group). A few species names were slightly adjusted to avoid overlap. For species abbreviations, see Appendix S1: Tables S1, S2.

Table 3. *F*- and *P*-values of redundancy analysis testing the effects of nutrient addition (N), warming (W), and warming combined with nutrient addition (NW) and herbivore exclusions (E) on species composition of the Collembola and mite communities, in 2004 and 2016.

Treatment	Collembola		Oribatida	
	2004	2016	2004	2016
N	6.03**	3.79*	3.42*	1.39
NW	10.66***	4.70*	1.60	0.30
W	3.96*	0.62	0.54	4.40*
E	0.50	5.25*	0.24	3.48*
N × E	0.94	3.21*	0.84	3.95*
NW × E	1.49	0.57	0.74	0.69
W × E	0.14	0.83	0.45	1.02

Note: Significant effects at $P < 0.05$ are printed in bold.
 $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

arthropod communities (Collembola and Acari) nine years after cessation of the treatments. We hypothesized that dynamics in micro-arthropod communities would match those observed for the vegetation (Olsen and Klanderud 2014), that is, that effects on species abundance and composition would persist to date. However, we found legacy effects on micro-arthropod communities in some respects, while not in others. Specifically, for the abundance of Collembola and Mesostigmata (the groups most responsive to treatments), we found no legacy effects. Contrastingly, for Collembola and Oribatida species composition, we found differences in community composition between treatments and controls to persist nine years after cessation of the treatments. Although mammalian herbivory did influence community

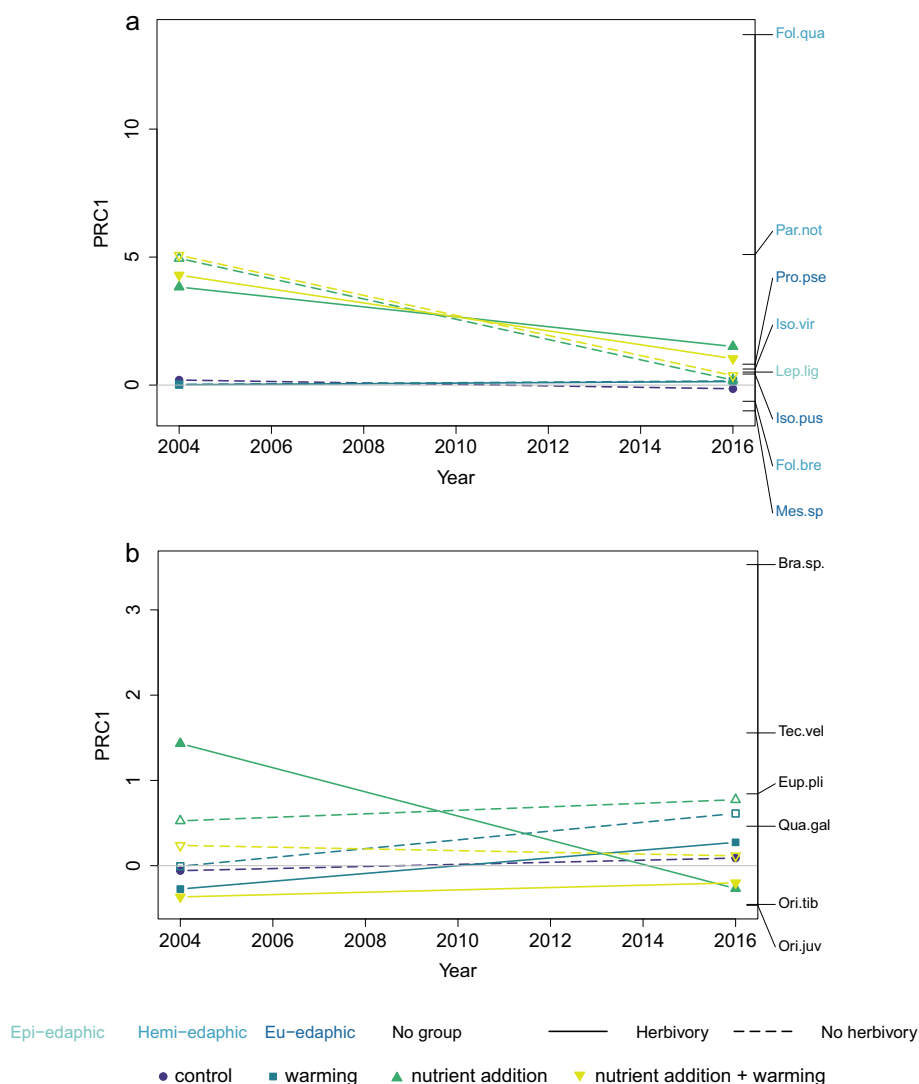


Fig. 4. Principal response curve (PRC) ordination of (a) mean Collembola and (b) mean Oribatida community composition in 2004 and 2016 in control, warming, nutrient addition, and warming combined with nutrient addition treatments with herbivores present (solid line) and herbivores excluded (dashed line) in an alpine heath. The horizontal gray line represents control plots with herbivores present, to which all other treatments are compared. Species names are shown only for the eight most common Collembola, and six most common Oribatida species. Collembola species names are colored according to their eco-morphological group (epi-edaphic, hemi-edaphic, eu-edaphic). For species abbreviations, see Appendix S1: Tables S1, S2.

composition of both Collembola and Oribatida, it did not promote trajectories toward the original community composition as was found for the vegetation (Olsen and Klanderud 2014). Hemi-edaphic Collembola that live near the soil-surface interface, in particular *F. quadrioculata*, were most responsive to environmental treatments

and remained dominant in Collembola communities nine years after treatments were discontinued.

We propose several mechanisms that can explain why Collembola abundances returned to pre-treatment levels, even though treatments are still visible in the vegetation composition (Olsen

and Klanderud 2014; K. Klanderud, S. L. Olsen, and R. E. Roos, *personal observation*). First, nutrient addition may have had a direct, stimulatory effect on the microbial and fungal community, which is an important part of the micro-arthropod diet (Mack et al. 2004, Nemergut et al. 2008, A'Bear et al. 2014). If this effect was reduced shortly after cessation of the treatments, there may not have been sufficient food available to sustain high Collembola abundances. However, the effects of nitrogen addition are reported to be long-lasting and recovery is often incomplete (Street et al. 2015, Bowman et al. 2018), so the availability of food to fungivorous micro-arthropods would have to be tested directly. Second, an increase in the abundance of predators could have controlled Collembola abundance. For example, we found predatory Mesostigmata to initially increase in parallel with Collembola and, together with other predators such as Lycosidae (Lawrence and Wise 2000, Wise 2004), they may have suppressed Collembola populations (Koehler 1997, 1999, Schneider and Maraun 2009). However, we found no legacy effects on Mesostigmata abundance nine years after cessation of the treatments. In case Mesostigmata were indeed responsible for the decrease in Collembola abundance through predation, the temporal resolution of this studies' set-up may have been too coarse to capture such prey-predator dynamics. Further, epi- and hemi-edaphic Collembola are considered to be opportunistic, requiring higher food quality, and having higher fecundity and mobility, but also mortality (Petersen 2002) than eu-edaphic species and Oribatida. These life-history strategies can explain why hemi-edaphic Collembola were most responsive to our treatments as well as why their abundance decreased when conditions became less favorable. Finally, our plots are surrounded by a matrix of untreated terrain, which could have contributed to the formation of a source-sink like system (Bengtsson 2002) where animals move in and out of the plots in accordance to where they find most favorable conditions. For example, in a microcosm experiment, Shackelford et al. (2018) showed that isolated micro-arthropod communities recover at slower rates from a disturbance than those connected to other, disturbed or undisturbed, communities. It is therefore possible that, should we have

subjected the entire alpine landscape to warming and nutrient addition treatments, such as expected under real-world environmental change, legacy effects may have manifested stronger than was observed in our scale-limited experimental study. Such scaling up from experimental plot to landscape scale remains one of the major challenges in ecology (Levin 1992, Dunne et al. 2004, Jackson and Fahrig 2015).

While we found no legacy effects on Collembola and Mesostigmata abundances, we found that differences in Collembola species composition for nutrient addition and nutrient addition with warming treatments compared to the controls, persisted throughout the nine-year recovery period. In contrast, the composition of the Oribatid mite community initially responded to nutrient addition, but this effect did not persist nine years after cessation of the treatment. However, Oribatida community composition was different in previously warmed treatments nine years after the treatment was ceased, although this treatment did not cause any initial responses. This suggest that Oribatida communities may respond to environmental change given sufficiently long time. Similar to our findings, Lindberg and Bengtsson (2005) found persistent effects of summer drought in boreal forests on Collembola and Oribatida community composition, but not on their abundance.

The changes in Collembola community composition in our study were mostly driven by *F. quadrioculata*, which dominated communities that received nutrient addition, and remained dominant after the nine-year recovery period, although its abundance did decrease. *Folsomia quadrioculata* is a common, generalist species that can be found in many different habitats, from forests at mid-latitudes to the high Arctic (Somme and Birkemoe 1999, Sengupta et al. 2016), and is able to colonize glacial forelands approximately 50–70 yr after glacial retreat (Hågvar 2010). In alpine ecosystems in Norway, *F. quadrioculata* has one generation per year compared to species such as *Folsomia brevicauda*, which has a longer, two-year life cycle (Fjellberg 1975). Accordingly, *F. brevicauda* was only abundant in the controls and the warming treatments in our study. Its opportunistic life-history strategy likely makes *F. quadrioculata* highly responsive to short-term environmental changes.

Grazing by herbivores can affect the structure and composition, competitive interactions, and chemistry of Arctic and alpine vegetation, although its impact is often time and site dependent (Bernes et al. 2015 and references therein). In addition, herbivory can act as a buffer against the effects of climatic change (Olofsson et al. 2009) and can decrease legacy effects of environmental manipulations (Olsen and Klanderud 2014, Kaarlejärvi et al. 2015). Although we did find effects of herbivory on Collembola and Oribatida communities, these effects do not directly indicate that grazing shifts communities toward pre-treatment species composition. Further, the control communities showed some shifts in micro-arthropod community composition, which may be due to year-to-year variations in community composition. Alternatively, changes in species compositions in control treatments can be due to ongoing background environmental change, for example, rising temperature and altered dates of snow melt (Høye and Forchhammer 2008), during the twelve years between sampling. Whatever the cause of changes in control community composition, treated communities were still significantly different from control species compositions, indicating that environmental treatment effects persist to date.

In conclusion, our results show that soil micro-arthropods are responsive to environmental treatments in terms of abundance and species composition and that the treatment effects on community composition persist long after the treatments were discontinued. An important next step is to understand how persistent changes in micro-arthropod decomposer communities translate into the functional composition of the decomposer community (Handa et al. 2014) and thereby ecosystem processes such as decomposition, nutrient cycling, and ecosystem respiration.

ACKNOWLEDGMENTS

The study was designed by Johan Asplund, Juha M. Alatalo, and Kari Klanderud. Field work was performed by Ruben Erik Roos, Johan Asplund, Kari Klanderud, and Tone Birkemoe. Peter Luptáčík and Natália Raschmanová identified soil micro-arthropods for 2016. Statistical analyses were performed by Ruben Erik Roos and Siri Lie Olsen. All co-authors contributed to manuscript revisions and agree with the

final version. This study was funded by Carl Tryggers stiftelse för vetenskaplig forskning through a grant to Juha M. Alatalo and a grant from the Research Council of Norway (249902) to Johan Asplund. We thank Sigmund Hågvar for sharing his original data, comments and feedback, Hans Cornelissen and Stef Bokhorst for useful discussions, and Matty Berg for sharing data from his personal Collembola database. Mari Steinert, Ross Wetherbee, Mahdieh Tourani, and Richard Bischof were of great help for discussions on the statistical analyses. We thank the Finse Alpine Research Center and Erika Leslie for hospitality during fieldwork and Kristel van Zuijlen for assistance in the field.

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DATA ACCESSIBILITY

Data associated with this manuscript are deposited in the Dataverse Network Norway (<https://dataverse.no/>) at (<https://doi.org/10.18710/brozeg>).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3030/full>