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Long-term effects of clear-cutting on Collembola and Oribatida communities in Norwegian boreal spruce forests

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Ecology

ABSTRACT

Norway's boreal forests have a long history of extensive forestry, and today, clear-cutting is the most common forest management practice. The long-term effects of such forestry practices on forest ecosystems and structures are poorly understood, including how this impacts soil fauna. Soil organisms like springtails (Collembola) and oribatid mites (Oribatida) play vital roles in nutrient cycling and carbon storage. To assess the long-term effects of clear-cutting on these groups' taxonomical and functional structure, communities of Collembola and Oribatida in mature previously clear-cut forest stands harvested around 1950, and near-natural forest stands, were compared. This was performed by taking soil samples from 12 such pairs of previously clear-cut and near-natural bilberry-spruce forest stands in southeastern Norway, and extracting the soil microarthropods through the Berlese-Tullgren method. Overall, the results indicate no significant difference in species richness or abundance of Collembola or Oribatida between the two forest management types, and show that the overall species metrics have recovered after the disturbance of clear-cutting over 70 years ago. However, Canonical Correspondence Analysis (CCA) reveals significant differences in community composition, and several species display an apparent affinity for either the near-natural forests or the previously clear-cut forests. Environmental factors, like soil pH, moisture, and temperature, influenced community composition, and soil pH had varying responses for Collembola richness depending on forest management type. These findings highlight the importance of not only looking at overall diversity metrics but also incorporating species-level data and environmental context in ecological assessments of long-term forest recovery.

ACKNOWLEDGMENTS

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This thesis is conducted under the framework of the interdisciplinary EcoForest project, funded by the Research Council of Norway, which aims to enhance our understanding of how modern forestry impacts carbon storage, ecological functions, and biodiversity in the boreal spruce forests of Norway. The project brings together researchers from NMBU, NINA, UiO, and NIBIO, alongside partners from the forest industry (Oslo municipal forests, NORSKOG, The Norwegian Forest Owners’ Federation) and nature conservation organizations (SABIMA, WWF). I am very grateful for the opportunity to collaborate with experts in the field and to contribute to expanding our knowledge as part of the EcoForest team.

I want to express my sincere thanks to my supervisors for their invaluable guidance throughout this journey. In particular, I want to thank my main supervisor, Johan Asplund, for his continuous feedback, patience, and support, and my co-supervisors, Tone Birkemoe and Lea-Rebekka Tonjer, for their insightful feedback throughout the process. I also want to thank Dr. Peter L'uptáčik and Dr. Natália Raschmanová at the Pavol Jozef Šafárik University in Košice for identifying the Oribatida and Collembola species I collected. Lastly, I am incredibly thankful to my dad for his assistance in the field, especially with carrying my soil samples, and all his encouragement meant a great deal to me during this project.

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1. Introduction

Fennoscandia’s cultural, economic, and ecological landscape has historically been deeply intertwined with forest and forestry practices (Josefsson et al., 2010). Norway, in particular, has a rich history of timber production, with its vast forest cover comprising 37.6% of its land area, predominantly consisting of boreal forests dominated by coniferous species like spruce and pine (SSB, 2022). These forests provide diverse habitats for numerous species and house one of the largest carbon stores on land, with approximately 80% of their forest carbon stored below ground (Baldrian, 2017; Bartlett, 2020). Over the last century, this extensive growth in forestry has fundamentally shaped the forest landscape we see today, with far-reaching consequences on the forests’ structural composition, spatial patterns, biodiversity, and biomass dynamics (Esseen et al., 1997). While Norway’s forestry roots extend back over 5000 years, the landscape shifted dramatically by the 1940s, when the forestry transitioned from selective cuttings to widespread clear-cutting (Aasetre & Bele, 2009). Forestry activities have affected clear-cutting in around 70% of the remaining forest areas (Storaunet & Rolstad, 2020). Surviving natural old-growth forests remain limited, with only 1.7% of Norwegian forests remaining mostly unaffected by forestry activities. Forests considered near-natural, with less intensive forest management practices like selective logging resulting in more heterogeneous and natural-looking forests, are also increasingly rare within Norway’s forested expanse. With the areas of both such more “intact” forests, including old-growth and near-natural forests, declining, this results in losses of environmental values and biodiversity (Watson et al., 2018).

Soil biodiversity holds a significant fraction of life on Earth, as it represents the most species-rich terrestrial ecosystem habitats, accounting for high ecological and economic importance (Decaëns et al., 2006). Soil fauna plays a crucial role in influencing carbon storage by regulating microbial communities, decomposing organic material, impacting elemental cycles, and contributing to the overall ecological and evolutionary responses of terrestrial ecosystems to environmental changes (Potapov et al., 2022; Weston & Whittaker, 2004). The most numerically dominant arthropods in boreal soil are typically Collembola (springtails) and Acari (mites), which have their highest biomass in the litter and humus layer (Persson et al., 1980). Collembola, found in soils from the Arctic to the Antarctic, belong to one of the richest taxa in the basal lineage of Hexapoda. They comprise ~32% of the global terrestrial arthropod abundance and global biomass of an estimated ~27.5 Mt carbon (Potapov et al., 2024). Collembola are often found in large quantities in the uppermost soil layers, affecting the nitrogen and carbon cycle, decomposition processes, and microstructure in the soil (Filser, 2002; Siddiky et al., 2012). Research has shown that higher Collembola activity directly increases C-transport into the litter-soil environment (Cassagne et al., 2003). Acari are a diverse group of microarthropods within the Arachnida, occupying many different niches, but with the greatest amount living in soil as predators, scavengers, or primary consumers (Arribas et al., 2019). Among them, Oribatida is a major order of mites that inhabits most terrestrial habitats, such as plant litter, soil, mosses, and lichens (Schatz & Behan-Pelletier, 2008). Similarly to Collembola, oribatid mites exist in high densities in the topsoil layers (Hoy, 2008). Researchers have found more than 200,000 individuals per square meter in boreal forests (Maraun & Scheu, 2000). Oribatid mites affect mineral turnover, vegetation succession, and organic matter decomposition (Hoy, 2008). Identification of soil fauna such as Collembola and Oribatida has been used as bio-indicators for national soil surveys and can be a valuable tool for studying the effects of different forms of anthropogenic land use (George et al., 2017; Vandewalle et al., 2010). Soil communities have dynamic interactions between many species, and changes in the species composition and abundance can reflect changes in soil quality or function, making such biodiversity measures significant indicators of soil health (Bengtsson, 2002).

Forestry practices impact soil development stages and associated fauna dynamics and significantly impact soil ecology (Marshall, 2000). Clear-cutting can reduce the number of organisms involved in biological processes. Other factors, such as soil disturbance and moisture conditions, can influence the extent to which soil animals decrease and soil bacteria increase. Soil organisms, food web structure, and soil fertility are negatively affected by clear-cutting, and soil communities seemingly take a long time to reorganize, as macrofauna abundance can be substantially lowered for over ten years compared to mature forests (Bengtsson et al., 1998). Changes in forest ecosystem processes, such as decomposition and N mineralization, could also be linked to the composition and activity of soil biota following clear-cut harvesting. Furthermore, forestry practices and introductions of coniferous monocultures can reduce the richness and abundance of certain oribatid mite species (Kamczyc et al., 2018). Changes in soil quality resulting from deforestation might significantly reduce the density of soil mites and can affect both abundance and diversity, especially those of oribatid mites (Loskova et al., 2013; Bagheri-Kordeshami et al., 2021). After seven years, a previously clear-cut site in Finland showed mite population densities returning to the original level, except for Oribatida (Huiita et al., 1969*).* Clear-cutting is also a major disturbance affecting Collembola abundance, species richness, and activity (Cuchta et al., 2019). Researchers have shown that clear-cutting in Canadian forests causes a decline in the abundance of Collembola, which takes 60-100 years to return to pre-disturbance levels (Addison et al., 2003). Nevertheless, other studies have had opposite effects, with Collembola abundance either unchanged or increasing after a clear-cut (Huhta et al., 1969; Malmström et al., 2009; Marshall, 2000).

The variations of effects of forestry on soil fauna can be attributed to factors such as morphology and niche, as well as be context-dependent on the forest in the form of tree species, root biomass, type of soil, and what level of disturbance happened in line with the forestry (Kudrin et al., 2023; Mayer et al., 2020; Siira-Pietikäinen & Haimi, 2009). Therefore, trait-based approaches help predict how soil organisms respond to environmental stress by filtering communities based on different functional traits influencing soil fauna distribution (Ellers et al., 2018). Soil-living oribatid mites, for example, exhibit diverse trophic guilds, reflecting their role as phytophages, primary decomposers, secondary decomposers, or predators and scavengers (Potapov et al., 2022). Some oribatid mite groups recover within ten years, but primary consumers like fungivores remain low, possibly due to reduced ectomycorrhizal colonization and changes in soil fungal communities post-clear-cutting (Huhta et al., 1969; Marshall, 2000; Rähn et al., 2023). Different groups of Collembola also react differently to clear-cutting (Siira-Pietikäinen & Haimi, 2009). Collembola, predominantly microbivores and detritivores, exhibit diverse feeding habits based on their depth in the soil profile (Potapov et al., 2022). Species living near the surface predominantly feed on fungi and living vascular and non-vascular plants, and species in deeper soil layers feed on decomposed organic matter. This difference in feeding and depth of living in the soil horizon separates the Collembola into different groups. The 'surface guild' (epigeic) dwells near the surface or on ground vegetation, stone, and bark, while the 'soil guild' (hemiedaphic and euedaphic) inhabits the mineral or litter layer. Euedaphic and hemiedaphic Collembola are seemingly site-dependent, with their abundance sometimes decreasing, remaining stable, or increasing depending on the time since harvest and soil moisture (Kudrin et al., 2023; Siira-Pietikäinen & Haimi, 2009). Larger microbivore Collembola are negatively impacted by clear-cutting, and both Collembola and Oribatida in the upper layers are particularly susceptible to disturbance (Siira-Pietikäinen & Haimi, 2009).

Understanding how species and community structures survive in disturbed areas is crucial, and knowledge about the resilience of soil animal communities is vital to developing strategies to manage and protect their habitats (Bengtsson, 2002). Thus, it is essential to understand how a disturbance process like logging affects soil fauna directly and indirectly. While previous studies point to the fact that forestry can lead to a decrease in diversity and abundance for both Oribatida and Collembola, recent clear-cutting will affect these factors, for example, by raising the average soil temperature and increasing rainfall disturbance, thus impacting the soil fauna in the short term (Hashimoto & Suzuki, 2004). Generally, changes in soil organism communities are strongly affected in the short term by clear-cutting (Marshall, 2000). At the same time, long-term responses are less evident because of the gradual recovery of most biological components with time and transient, natural changes in communities. In addition, the long-term response can also be very complex, even within a taxon. Long-term effects and recovery of soil fauna communities have hardly been investigated, and studies over more extended periods are essential to understand resilience because reorganization usually takes a long time and involves complex interactions between many species (Bengtsson, 2002). Moreover, focusing on the species level is imperative for studying the impacts of forestry on soil biota and function (Siira-Pietikäinen & Haimi, 2009).

The main object of this thesis is to explore the long-term effects of forestry on Oribatida and Collembola communities in southeastern Norway. To do this, I utilized an already established study system with mature, previously clear-cut stands paired with near-natural, not previously clear-cut stands with equivalent soil characteristics. Soil samples were collected from both types of forest stands for comparison.

Specifically, I aim to test the following hypothesis:

1. Near-natural forests will exhibit higher species richness and abundance of Oribatida and Collembola than previously clear-cut forests.
2. The composition of functional groups within Oribatida and Collembola communities will differ significantly between near-natural and previously clear-cut forests.
3. Previously clear-cut forests will show significant changes in the community composition of Oribatida and Collembola, with different species assemblages compared to near-natural forests.

By testing these hypotheses, I seek to understand how forestry practices influence underground biodiversity. This knowledge is essential for comprehending the broader ecological dynamics within forest ecosystems, offering insights into soil ecosystems and enhancing our understanding of soil biodiversity.

2. Materials and Methods

2.1 Site description

This study is conducted within the framework of the existing “EcoForest” project, which established 12 study sites in Southeastern Norway to investigate the long-term impact of modern forestry practices on boreal forest ecosystems (Figure 1). Each study site comprises one plot of near-natural forest (NN) and one plot of mature but former clear-cut forest (CC), selected based on their historical logging regimes. The sites span the boreal zone from 59.8 to 60.9 degrees north and 9.7 to 12.5

degrees east, with elevations ranging from 178 to 668 meters above sea level (m.a.s.l.). There are notable variations in macroscale bioclimatic variables, including different degrees of growing seasons, rainfall patterns, and mean annual temperatures (see Table 2). The dominant vegetation at the study sites consists of Norway spruce (*Picea abies*) forests classified within the site index H40 (G14-G17). The forest understory is mainly occupied by bilberry (*Vaccinium myrtillus*). The selected plots lack small streams or areas with standing water throughout the year, contributing to relatively homogeneous soil conditions.

The site selection criteria for the study sites focused on identifying forests with similar edaphic factors but different historical logging regimes, specifically targeting mature clear-cut forests and areas where forest management had been absent for comparison. This approach aimed to assess the impacts of varying logging histories on forest ecosystems. Additional criteria for site selection focused on achieving approximately equal vegetation type, productivity, soil depth, and slope across the NN and CC plots. The CC plots were cut approximately 70 years ago, with spruce subsequently planted post-logging, and are now classified as mature forests. NN sites were characterized by the absence of recent human activity or removal of dead wood, although selective cutting has historically occurred to varying degrees. Neither NN nor CC sites underwent thinning, ditching, or significant pest attacks. The distance between plots within each site was less than five kilometers. Studies on forest structure and dead wood content indicate that NN sites contain a more considerable amount of dead wood, including a greater volume of wood in later stages of decay and more significant heterogeneity in tree size compared to the previous clear-cut sites (Asplund et al., 2024).

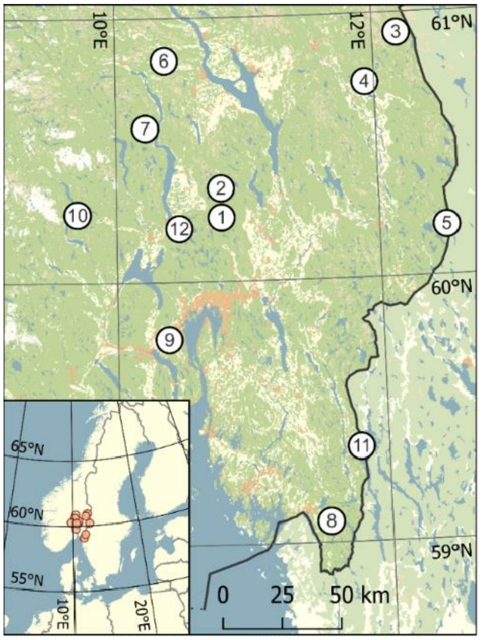

Figure 1: The location of the 12 study sites in southeastern Norway, after Asplund et al. (2024)

Table 1: Overview of study sites, including coordinates, elevation (m.a.s.l.), temperature, precipitation, and snow days for each site. The mean annual temperature is for 2023. Precipitation and days with snow are from 2022 (snow depth >2 cm) (seNorge).

Site no.	Plot name (abbr.)	Forest management type	Mean annual temperature (˚C)	Precipitation (mm)	Days with snow	Elevation (m.a.s.l.)	Latitude (°N)	Longitude (°E)
1	Skotjern (SKO)	NN	2.9	1134	147	610	60.24224	10.795997
	Skotjern (SKO)	CC	2.5	1136	145	571	60.241347	10.808372
2	Gullenhaugen (GUL)	NN	1.8	943	158	668	60.352613	10.796628
	Gullenhaugen (GUL)	CC	2.7	903	151	591	60.369963	10.787187
3	Hemberget (HEM)	NN	2.4	890	161	581	60.915115	12.206472
	Hemberget (HEM)	CC	2.5	890	161	584	60.921114	12.188859
4	Braskreidfoss (BRA)	NN	3.1	787	152	427	60.73977197	11.92845999
	Braskreidfoss (BRA)	CC	3.4	800	147	332	60.74758901	11.92636502
5	Särkilampi (SAR)	NN	3.4	704	151	368	60.187711	12.508022
	Särkilampi (SAR)	CC	3.3	701	151	388	60.200486	12.528086
6	Øytjern (OYT)	NN	2.0	894	128	640	60.838906	10.38122
	Øytjern (OYT)	CC	2.0	902	133	663	60.843198	10.408981
7	Tretjerna (TRE)	NN	2.6	759	151	472	60.583648	10.226522
	Tretjerna (TRE)	CC	2.6	759	151	520	60.577289	10.228499
8	Halden (HAL)	NN	5.7	998	70	211	59.079766	11.546541
	Halden (HAL)	CC	5.7	998	70	197	59.079808	11.55948
9	Blåfjell (BLA)	NN	5.5	845	104	264	59.783114	10.381255
	Blåfjell (BLA)	CC	4.7	837	132	322	59.788026	10.386507
10	Storås (STR)	NN	3.6	752	114	483	60.25914	9.700663
	Storås (STR)	CC	3.3	737	120	432	60.261514	9.709084
11	Marker (MRK)	NN	5.8	746	42	187	59.36014	11.79003
	Marker (MRK)	CC	6.0	761	42	178	59.38347	11.75902
12	Langvassbrann (LAN)	NN	2.8	912	143	607	60.201837	10.473849
	Langvassbrann (LAN)	CC	2.8	959	144	548	60.200996	10.497976

2.2 Sampling procedure

Each of the twelve sites has a pre-established 15 × 15 m main plot per management type (i.e., CC vs NN) (Figure 1a). Within are six randomly positioned subplots, see Figure 1b, with pre-existing data on microclimate, light availability, and vegetation community composition (see details in section 2.4). In cases where trees, rocks, or other obstacles were in this predefined position, the subplot was moved to the closest relative location. I collected soil samples at each subplot between July 5 and July 19, 2023, using a hand-held soil corer (3.6 cm diameter) at a depth of 10 cm. These samples were collected to compare Oribatida and Collembola populations. The soil samples were taken along the vegetation plots in each subplot marked in the field with yellow rods, primarily on the side closest to the subplot center (Figure 2c). If ground conditions such as large, exposed roots or shallow bedrock did not allow soil sampling near the primary chosen position, I moved the soil sampling to another side of the vegetation plot.

Four soil samples were collected from each subplot within every site to ensure that the samples were representative. This resulted in 288 soil samples from both CC and NN, for a total of 576 soil samples. Each soil sample was covered with plastic-coated aluminum foil to avoid heat damage and the spread of microarthropods between the samples. The soil samples were transported in a portable cooler and then stored in a cooling room at NMBU (<10°C) until the extraction procedure was conducted.

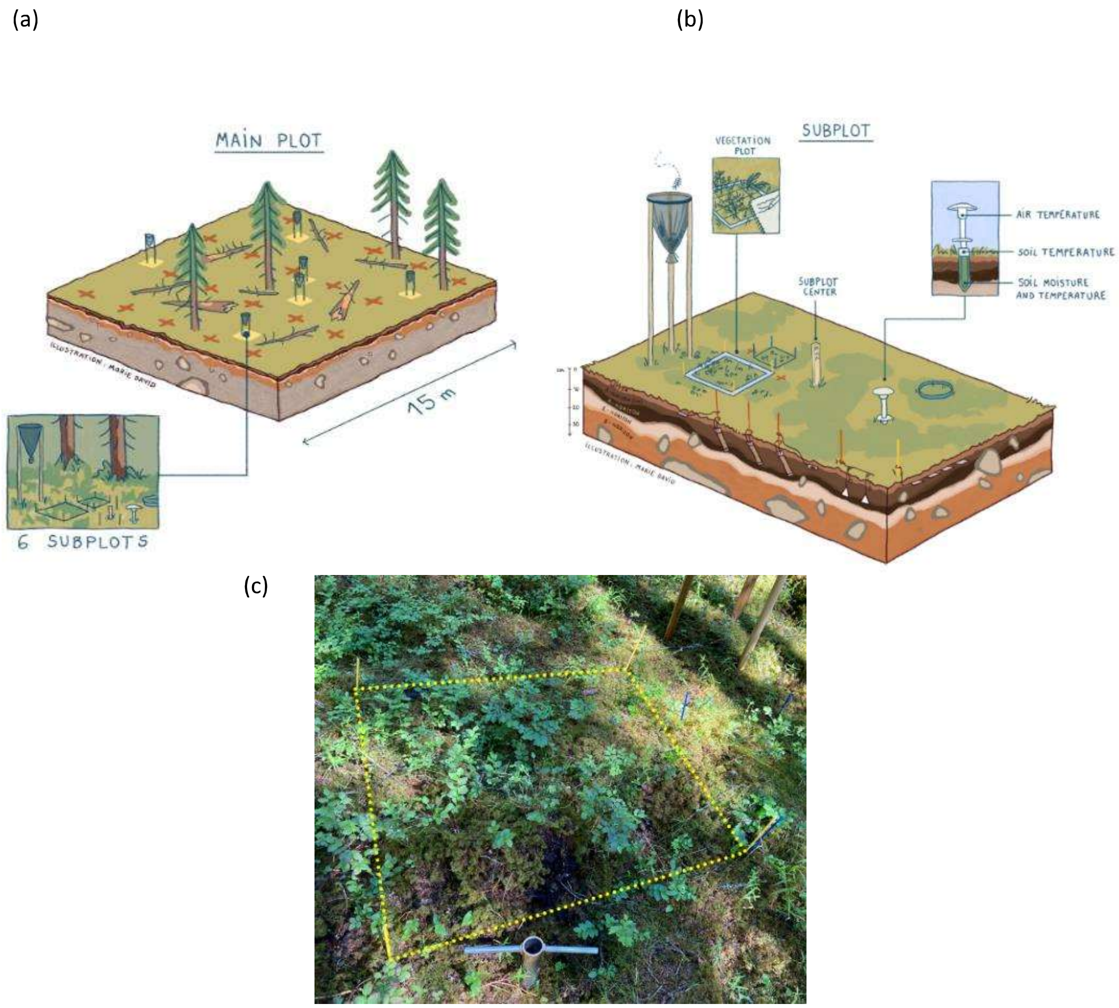

Figure 2: a) 15x15 m main plot of each study site with six randomly placed subplots, b) Overview of subplot setup, c) Photo from the field showing approximately where soil samples are taken, with the soil corer positioned in relation to the vegetation plot (marked with yellow lines). Illustrations: Marie David. Photo: Mina Baklien.

2.3 Laboratory processing

I extracted the microarthropods from the soil using a heating procedure known as the Berlese or Tullgren method, which effectively captures tiny soil-dwelling organisms while minimizing disturbance to the soil structure. The soil cores were dried under controlled and slow heating from lightbulbs above, with running cold water underneath. This gradient creates a vertical gradient from warm and dry to moist and cool conditions in the soil profile, inducing microarthropod movement downwards. The extraction temperature begins at 30°C and increases by four degrees each morning and evening over five days until reaching 60°C, increasing the strength of the vertical gradient during the extraction. The microarthropods exit the soil at the bottom through a mesh into the collector beakers positioned underneath the soil samples. The collection beakers contained a small amount of benzoic acid to kill and preserve the fauna. Before extraction, a few drops of dishwashing soap were added to the benzoic acid in the collection beakers to break the surface tension. After extraction, I combined the material from the collection beakers containing soil extracted from each subplot's four soil samples into one, resulting in a total of 144 samples. After extraction, 70% ethanol was added to the samples to ensure long-term conservation of the Collembola and Oribatida. All the soil samples were weighed before and after the extraction process to measure the water content in each sample.

Samples were kept in the cooling room until further transfer in August. Experts then received the extracted microarthropod samples and identified the Collembola and Oribatida at the species level.

2.4 Environmental variables

Data from the EcoForest project for environmental and bioclimatic factors, including temperature and vegetation, are used as variables explaining the response of microarthropods to forestry. A microclimate and vegetation survey had been performed at each of the six subplots within the plots under the 'Ecoforest' project, providing bioclimatic variables. Among the variables was the tree influence factor (TIF), which refers to nearby trees' influence on a given subplot, related to canopy cover and root presence. At the center of every subplot, temperatures at ~8cm (within the soil), +2 cm (soil surface), and +15 cm (air) were measured every 15 minutes using TMS-4 (TOMST s.r.o, Praha, Czech Republic). The temperature data utilized was for the period spanning three weeks before sampling through to the final collection day (2023-05-24 – 2023-07-19). I used the within-soil temperature range for species richness and abundance analysis, calculated as the maximum minus minimum temperature. Macroclimatic information, such as monthly temperature, precipitation, and snow depth datasets on a 1-km grid, was derived from seNorge and produced by the Norwegian Meteorological Institute (MET). To obtain comparative soil moisture data, each soil sample's measured water content was calculated as gravimetric water content (GWC). See Appendix 1 for full environmental data.

2.5 Data analysis

To examine the impacts of clear-cutting on species richness and abundance in NN and CC forests, I utilized a linear mixed-effect model (LMM)(Niku et al., 2019). This model considers both within-group and between-group variability by analyzing fixed and random effects. The random effects account for pseudoreplicates in the subplots. The comparison of collected data on species richness and abundance in near-natural and clear-cut forests was juxtaposed with relevant environmental data. The aim of interpreting the model results was to determine the impact of clear-cutting on species richness and abundance. The goal was to identify whether variables such as temperature, pH, or others significantly influence species richness and abundance, or have no effect at all.

I used non-metric dimensional scaling (NMDS) to visualize and compare collected data on soil fauna communities in NN and CC forests, based on Bray-Curtis dissimilarity calculated from species abundance data. The NMDS was run using four dimensions (k = 4), and the analysis was conducted at the sub-plot level using the metaMDS function in the vegan package in R (Oksanen et al., 2015). The scatter plots represent the similarities and differences between the communities of Collembola and Oribatida, with each point representing a community of the chosen soil fauna and the distance between the points representing the dissimilarity between the communities. Environmental factors are added as variables.

Constrained correspondence analysis (CCA) examines the effect of forest management type on Collembola and Oribatida community composition. The model included forest management type (CC and NN) as the main explanatory variable, while climatic and edaphic factors such as temperature, soil pH, and gravimetric water content (GWC) were included as covariates.

Figures in R were made using ggplot2 (Wickham, 2016). All statistical tests and figures were conducted using RStudio, R version 4.3.2.

3. Results

3.1 Species richness, abundance, and evenness

In total, 47 Collembola taxa and 106 Oribatida taxa were found across the site (See Appendix 3 for Collembola species and Appendix 4 for Oribatida species). The highest species richness of Collembola was recorded in the near-natural forest of Storås (24), and the lowest species richness was recorded in previously clear-cut Langvassbrenna (13). The near-natural forest in Blåfjell had the highest species richness (41) of Oribatida, while the lowest value was in the previously clear-cut forest in Langvassbrenna (17).

There was no evidence of a difference in species richness for Collembola or Oribatida or the combined total between the two forest management types (Table 2; Figure 3a-c). The mean richness was nearly identical, indicating a negligible observed difference.

In total, 25085 Collembola and 40576 Oribatida were found across the sites. The highest and lowest abundance of Collembola were both found in near-natural forests, with the highest being in Halden (2567) and the lowest in Tretjerna (352). For Oribatida, the highest abundance was in the near-natural forest of Halden (5312), with the lowest abundance in the previously clear-cut forest Langvassbrenna (145). The abundance of Collembola, Oribatida, and the total combined abundance was unaffected by forest management type (Table 2; Figure 3d-f). For Collembola and Oribatida, the difference in mean abundance between forest management types was minimal and could easily be due to random variation.

Species evenness did not differ significantly between the forest management types for Collembola, Oribatida, or the combined community (Table 2; Figure 3g-i). However, Oribatida evenness showed a trend toward lower values in clear-cut forests than near-natural forests.

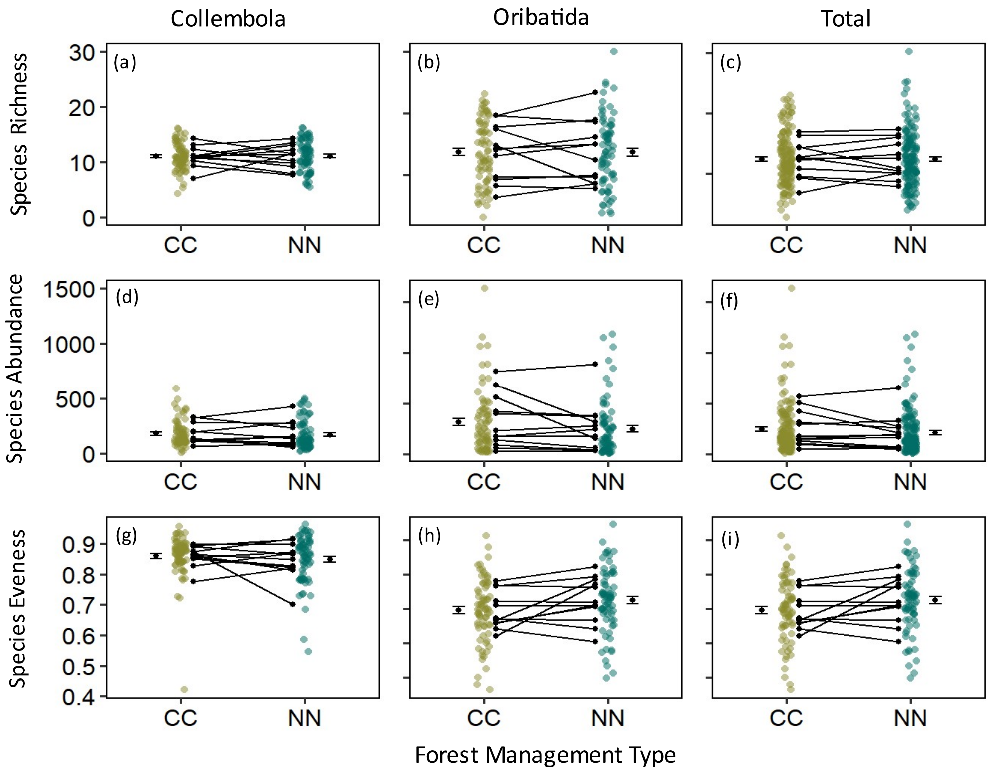

Figure 3: A 3x3 grid of plots displaying species richness (a-c), abundance (d-f), and evenness (g-i), for Collembola and Oribatida across the different forest management types (CC and NN), along with the combined total for both species.

Table 2: Result of the Welch Two Sample t-test for statistical comparison of species richness, abundance, and evenness between forest management types (CC and NN), based on subplot-level data.

	Mean (CC)	**Mean (NN)**	**t-value**	**p-value**
Species Richness (Collembola)	10.96	10.99	-0.06	0.949
Species Richness (Oribatida)	13.75	13.71	0.045	0.964

Species Richness (Total)	12.35	12.35	0.013	0.990
Abundance (Collembola)	177.9	170.5	0.36	0.722
Abundance (Oribatida)	315.3	248.3	1.35	0.179
Abundance (Total)	246.6	209.4	1.35	0.179
Evenness (Collembola)	0.860	0.847	1.01	0.315
Evenness (Oribatida)	0.696	0.725	-1.89	0.061
Evenness (Total)	0.778	0.786	-0.64	0.523

3.2 Functional groups

There were generally no substantial differences in the relative abundance of functional groups of Collembola between NN and CC forest management types (Figure 4a). In CC forests, the Collembola community was dominated by euedaphic species (52.1%), followed by hemiedaphic species (43.5%), whereas in NN forests, hemiedaphic species were most dominant (48%), followed by euedaphic species (44.9%). Epigeic species comprised the smallest proportion in both forest management types (4.4% in CC, 7% in NN) (Appendix 2).

For Oribatida, the relative abundance of functional groups was similar across forest management types (Figure 4b). Secondary decomposers represented approximately half of the community in both CC (45%) and NN forests (48.2%). The second largest group was primary decomposers (38.2% in CC, 38.6% in NN), followed by phytophages (16.2% in CC, 11.9% in NN). Predators/scavengers formed a minor component in both forest management types (0.64% in CC, 1.28% in NN) (Appendix 3).

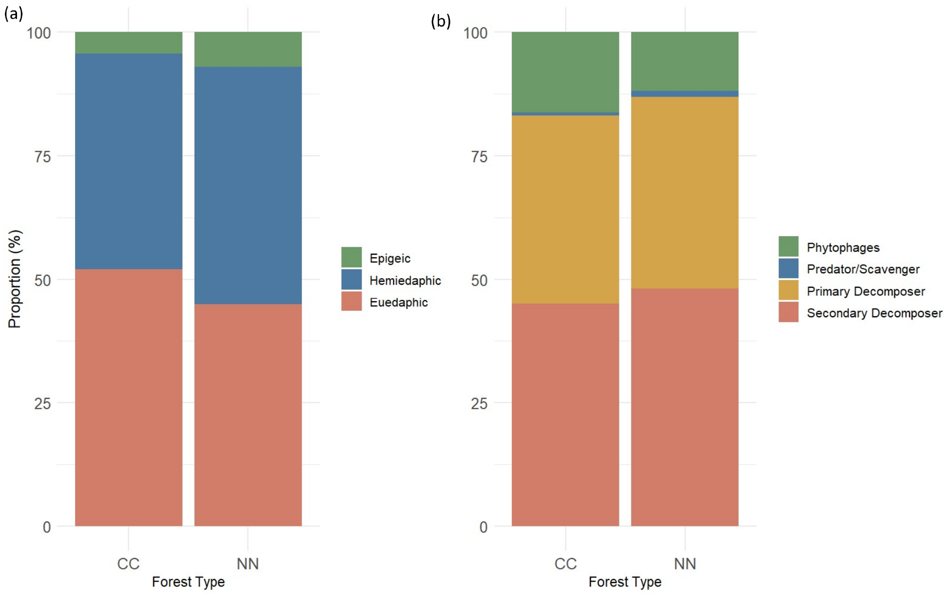

Figure 4: Proportions of functional groups of Collembola (figure a) and Oribatida (figure b) in CC and NN forests. The stacked bars represent the relative abundance of each functional group within the two forest management types (CC and NN).

3.3 Species abundance and environmental factors

Forest management type did not significantly affect the Collembola abundance (Table 3; Figure 5a). However, there was weak evidence for a positive effect of Tree Influence Factor (TIF) on Collembola abundance. The interaction between forest management type and TIF was not statistically significant.

Similarly, forest management type did not significantly affect Oribatida abundance (Table 4; Figure 5b). However, TIF had a significantly positive effect on Oribatida abundance. As with Collembola, the interaction between TIF and forest management type was not statistically significant, suggesting that the effect of TIF on Oribatida abundance does not differ across forest management types.

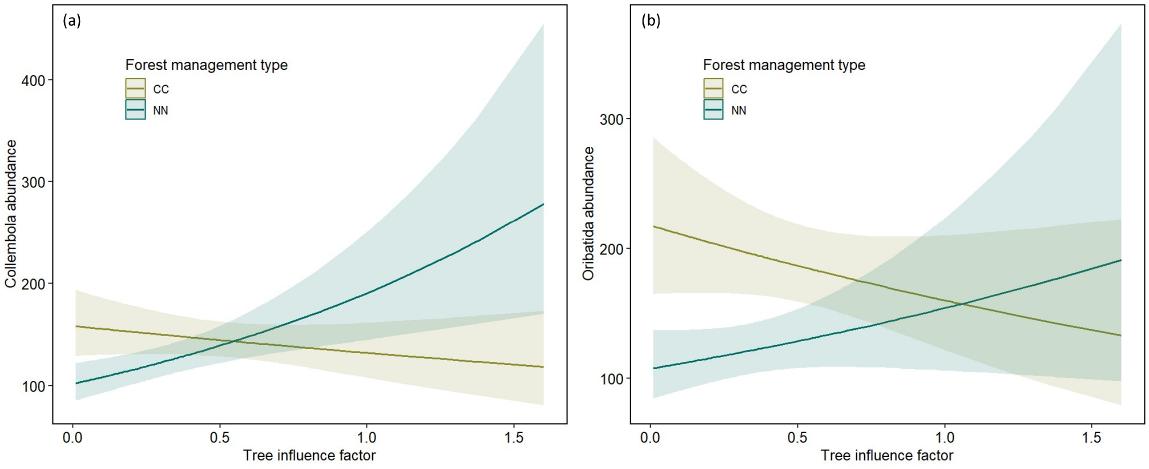

Figure 5: Difference in Collembola (figure a) and Oribatida (figure b) species abundance with changing tree influence factor (TIF) in both forest management types (CC and NN).

Table 3: Analysis of deviance for Collembola abundance

Predictor	Chi-square	Df	p-value
Forest Management Type	0.507	1	0.476
Tree Influence Factor (TIF)	2.762	1	0.097
Forest Management Type x TIF	2.623	1	0.104

Table 4: Analysis of deviance for Oribatida species abundance

Predictor	Chi-square	Df	p-value
Forest Management Type	2.691	1	0.101
Tree Influence Factor (TIF)	3.899	1	**0.048***
Temperature	2.781	1	0.095
Forest Management Type x TIF	1.965	1	0.161

3.4 Species richness and environmental factors

Forest management type did not significantly affect Collembola species richness (Table 5; Figure 6). However, the interaction between forest management type and soil pH affects species richness. At a low pH, Collembola species richness is higher in CC than in NN, but with increased pH, the species richness of Collembola increases in NN, giving the opposite scenario under conditions of increasing alkalinity.

Forest management type had no significant effect on the species richness of Oribatida (Table 6). In addition, soil temperature, pH, and moisture (GWC) do not considerably affect species richness.

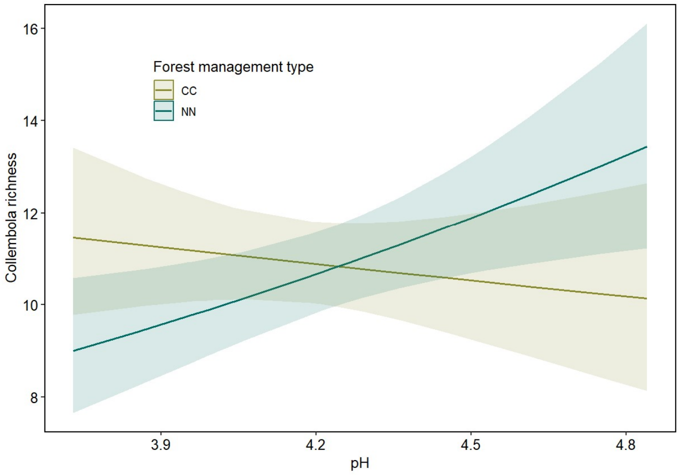

Figure 6: Difference in Collembola species richness with changing pH in both forest management types (CC and NN).

Table 5: Analysis of deviance for Collembola species richness.

Predictor	**Chi-square**	**Df**	**p-value**
Forest Management Type	0.102	1	0.749
Gravimetric Water Content (GWC)	2.439	1	0.118
Soil pH	2.192	1	0.138
Forest Management Type x Soil pH	5.311	1	**0.021***

Table 6: Analysis of deviance for Oribatida species richness.

Predictor	**Chi-square**	**Df**	**p-value**
Forest Management Type	0.804	1	0.370
Gravimetric Water Content (GWC)	3.154	1	0.076
Soil pH	2.656	1	0.103
Soil temperature	3.017	1	0.082

3.5 Community composition

The Collembola community's non-metric multidimensional scaling (NMDS) did not reveal any pattern related to forest management (Figure 7). However, several other environmental variables correlated with the NMDS orientation (Table 7). Temperature is a major factor influencing the Collembola community composition along the first dimension, and GWC had a positive correlation with the second dimension, suggesting that moisture plays a role in shaping community distribution. Similarly, soil pH significantly correlated with the second dimension, indicating that soil acidity influences the Collembola community.

While the two management types did not form distinct clusters in the NMDS, the near-natural sites consistently exhibited lower scores on the second dimension compared to their previously clear-cut counterparts, except for BRA and LAN. A Canonical Correspondence Analysis (CCA) incorporating soil pH, soil moisture (GWC), and temperature revealed a significant difference in Collembola community composition between forest management types (Table 9). These differences appear to be driven by species occurring more commonly in near-natural forests which were *Lepidocyrtus violaceus*, *Orchesella bifasciata*, *Karlstejnia norvegica*, *Lipotrix lubbocki,* and *Micranurida granulate,* as well as species showing high affinity for previously clear-cut plots such as *Mesaphorura yosii, Sminthurinus aureus, Hymenaphorura polonica, Isotoma angelicana, Ceratophysella granulate, Frisea mirabilis, Folsomia sensibilis, Mesaphorura critica,* and *Megalothorax minimus* (Figure 9). However, it should be noted that some of these indicator species were found in only one plot each, such as *K. norvegica* (two individuals found in a single near-natural plot), as well as *M. yosii, H. polonica, I. angelica,* and *C. granulate.* While *M. yosii* was only found in Blåfjell CC, it was found at a high frequency. These findings suggest caution in overinterpreting their distribution.

Figure 7: Non-metric multidimensional scaling (NMDS) ordination of Collembola communities across forest management types. Each point represents one study plot, with data averaged from the associated subplots.

Table 7: Results from testing how well environmental factors explain patterns in the NMDS ordination for Collembola, based on Bray-Curtis dissimilarity.

Variable	R^2	p-value
Soil pH	0.288	**0.001****
Temperature	0.589	**0.001****
Tree Influence Factor (TIF)	0.012	0.427
Gravimetric Water Content (GWC)	0.270	**0.001****

The Oribatida community's non-metric multidimensional scaling (NMDS) did not reveal any apparent clustering related to forest management (Figure 8). Nevertheless, several environmental variables significantly correlated with the NMDS configuration (Table 8). Temperature is a key factor influencing the Oribatida community composition along the first NMDS dimension. Gravimetric water content (GWC) also positively correlated with the first dimension, suggesting that soil moisture contributes to the distribution of Oribatida species. Additionally, soil pH is significantly related to the NMDS structure, indicating that acidity levels affect community composition. In addition, Tree Influence Factor (TIF) also displayed a significant correlation, albeit weaker.

When environmental variables such as temperature, moisture (GWC), and soil pH were included in a Canonical Correspondence Analysis (CCA), the difference in Oribatida community composition between the two forest management types became more pronounced (Table 10). These differences appear to be driven by species with either a high affinity for near-natural forests or high affinity for previously clear-cut forests. A total of 19 species showed high affinity for near-natural forests, while 21 species were more commonly associated with previously clear-cut plots (Figure 10). However, several of these indicator species were found in only one plot, and some were exclusive to the near-natural plot of Blåfjell, such as *Sellnickochthonius furcatus, Eueremaeus valkanovi, Liochthonius tuxeni,* and *Sellnickochthonius immaculatus.* Only two near-natural associated species, *Suctobelbella sarekensis* and *Suctobelbella falcata,* appeared in more than one plot. This warrants caution in overinterpreting the indicator species distribution.

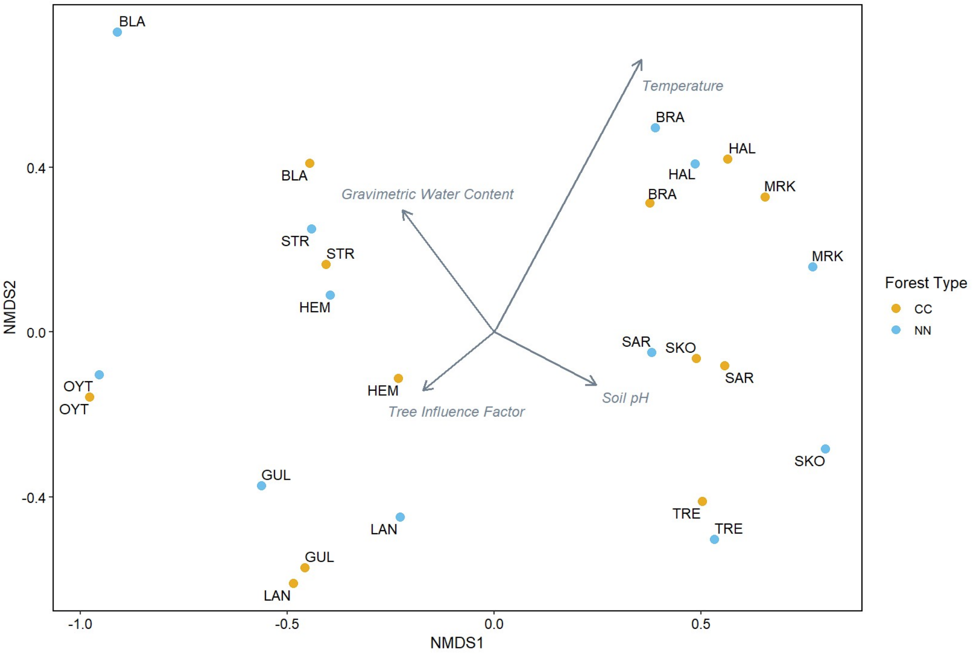

Figure 8: Non-metric multidimensional scaling (NMDS) ordination of Oribatida communities across forest management types. Each point represents one study plot, with data averaged from the associated subplots.

Table 8: Results from testing how well environmental factors explain patterns in the NMDS ordination for Oribatida, based on Bray-Curtis dissimilarity.

Variable	R^2	p-value
Soil pH	0.076	**0.001*****
Temperature (GDD)	0.564	**0.034***
Tree Influence Factor (TIF)	0.051	**0.001*****
Gravimetric water content (GWC)	0.136	**0.005****

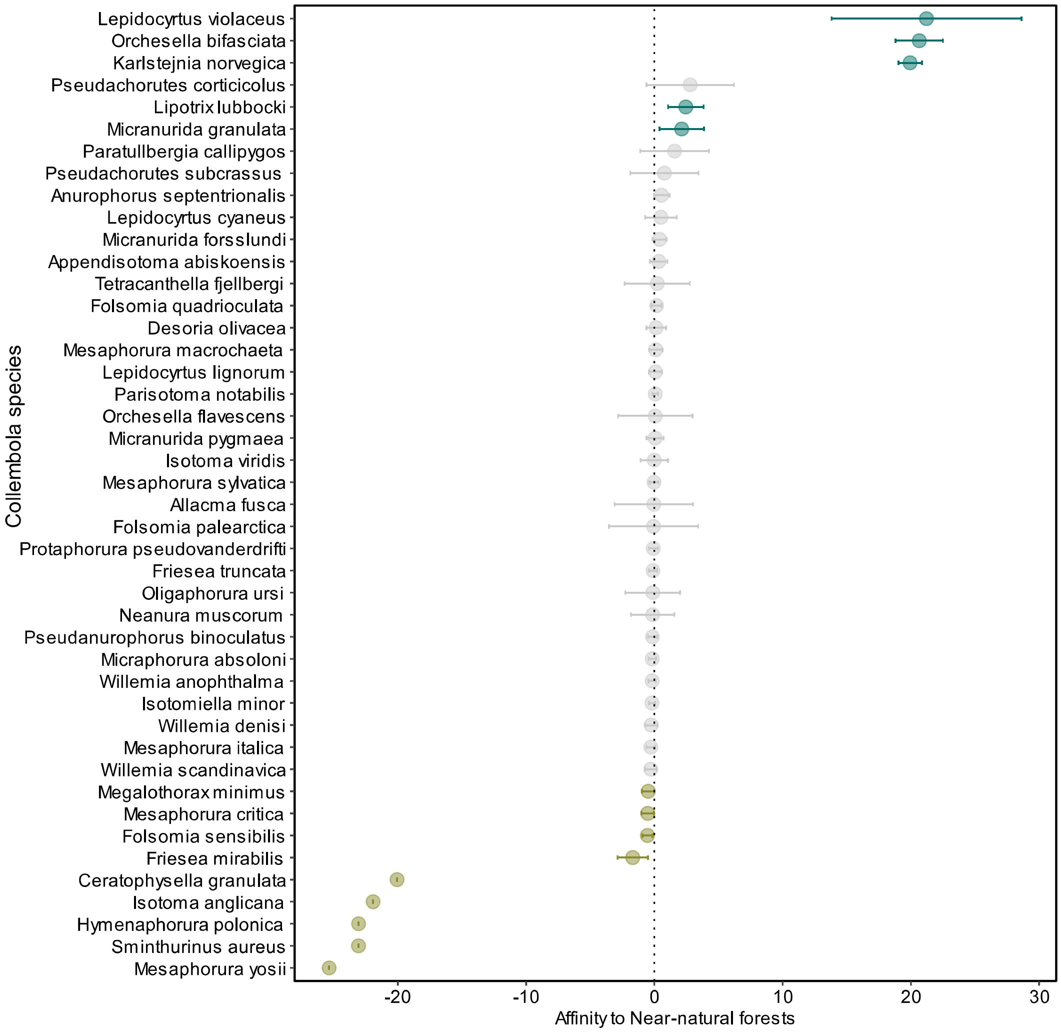

Figure 9: CCA of Collembola species in relation to forest management types (CC and NN).

Table 9: Permutation test for CCA on Collembola species constrained by forest management type and conditioned on environmental variables (999 permutations).

	Df	**Chi-square**	**F**	**p-value**
Model	1	0.030	2.033	**0.032***
Residual	140	2.071		

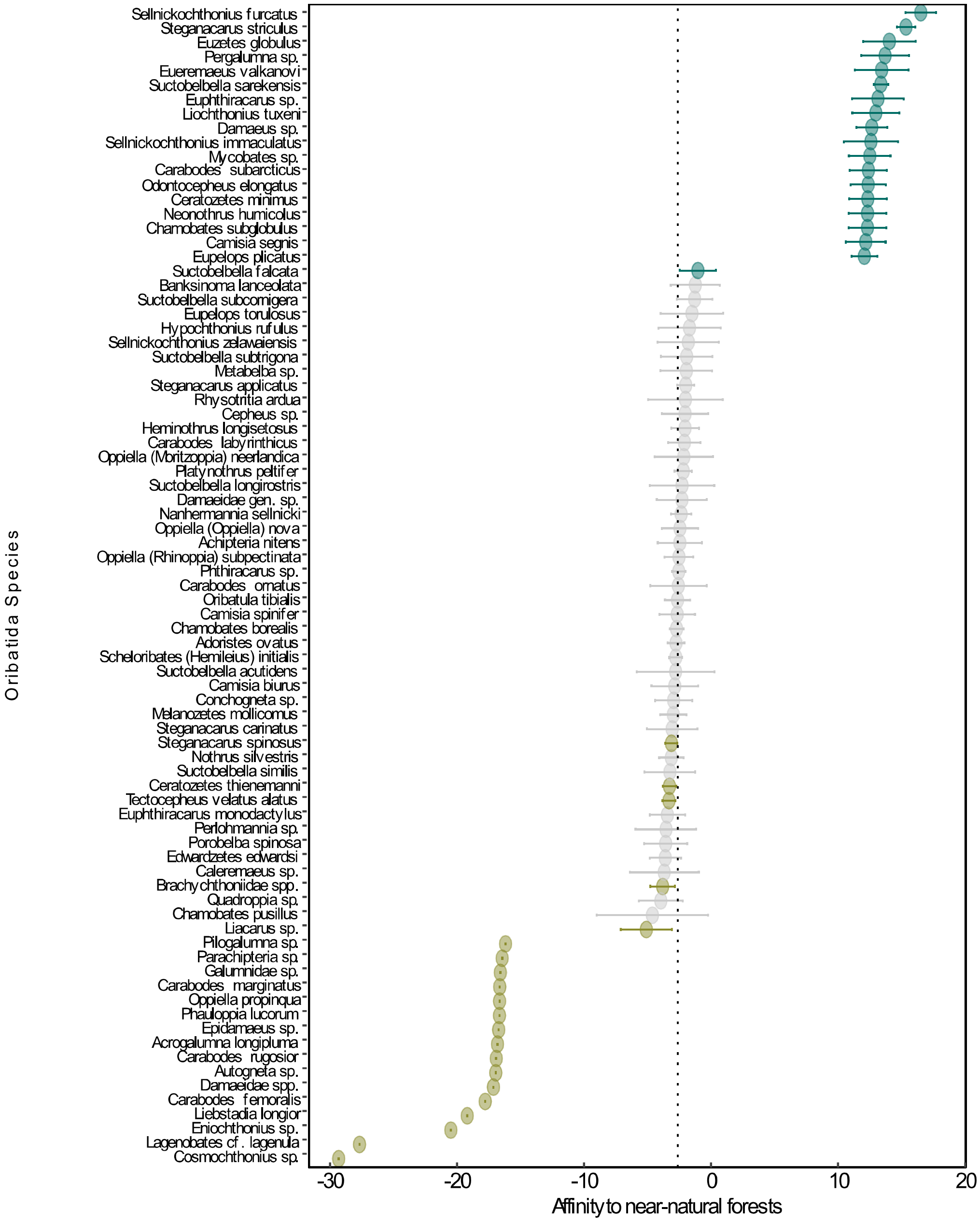

Figure 10: CCA of Oribatida species in relation to forest management types (CC and NN).

Table 10: Permutation test for CCA on Oribatida species constrained by forest management type and conditioned on environmental variables (999 permutations).

	Df	**Chi-square**	**F**	**p-value**
Model	1	0.082	2.945	**0.002***
Residual	139	3.867		

4. Discussion

In this study, I examined the long-term effects of forest clear-cutting on the diversity and community structure of the soil microarthropods Oribatida and Collembola. Contrary to my first hypothesis, I did not find higher species richness and abundance in near-natural forests compared with previously clear-cut ones. Likewise, the results do not support the second hypothesis, that the composition of functional groups would differ, and the relative abundance of species among functional groups was similar between near-natural and previously clear-cut forests. Interestingly, there is support for the third hypothesis, and there was a significant difference in community composition between the two forest management types when accounting for environmental factors.

Although overall species richness was similar in the two forest management types, I found a clear shift in the species composition of Collembola and Oribatida. This highlights the importance of considering species identity rather than simply α-diversity. In a disturbed ecosystem, the overall diversity metrics can remain stable when species turnover occurs, potentially due to functional redundancy and replacement of specialist species with generalists, masking underlying shifts in community structure. Consistent with this present study, research across different-aged beech stands showed that changes in Collembola community composition were more prominent than changes in species richness, with shifts of dominant species rather than an overall increase in richness (Chauvat et al., 2011). Similarly, in clear-cut spruce forest stands, there was a shift in community composition, although the number of species was constant, leading to drastic shifts in functional groups' proportion for Collembola over 45 years (Chauvat, 2004). A comparable pattern was found for Oribatida, where forest management strategy after large-scale disturbances in mountain spruce forests influences the community composition even after 15 years (KokoŘová & Starý, 2017). The difference in community composition can suggest that forest management alters habitat conditions enough to influence the Collembola and Oribatida community structure, reflecting species-specific habitat preferences.

Similarly, patterns of delayed community shifts can be seen in succession rates after disturbance events, such as glacier recession. In such a study examining primary successions of soils, several oribatid mites were present 30 years after recession, while others used up to 100-200 years to appear (Hågvar et al., 2009). They discovered that some species with high abundance in young soils were often pioneer species, such as *Tectocepheus velatus.* However, such species have decreasing abundance over time, while other species, such as *Platynothrus punctatus,* show up later in the succession stage. Likewise, in a spruce forest study, species richness and abundance significantly increased between 5- and 25-year-old stands, primarily driven by a few opportunistic species such as

T. velatus and *Oppiella nova* (Zaitsev et al., 2002). Similarly, in this present study, *T. velatus* was found in high abundance and showed a significant affinity for previously clear-cut plots. Meanwhile, *P. punctatus* had a higher occurrence in near-natural plots than previously clear-cut plots, but did not have a significant affinity to near-natural forests. Nevertheless, this suggests that the high abundance and richness observed in previously clear-cut plots may partly result from the dominance of early-successional, disturbance-tolerant species.

Glacier recession studies of Collembola show similar trends, with species colonizing at different speeds, but with the pioneers also occurring in older soils (Hågvar, 2010). However, unlike the Oribatida, only two species, *Tetranchella sp*. and *Isotomiella minor*, were absent in soils after 70 years of glacier recession. Collembola are rapid colonizers, and seemingly have faster recovery rates than Oribatida after disturbances, which also makes up a larger proportion of species that fail to recover (Hågvar et al., 2020; Lindberg & Bengtsson, 2005). However, fundamental changes in forest structure and conditions following a disturbance such as clear-cutting might also mean that species composition never fully returns to its original state, and sometimes even after seven decades, naturally regenerated forests after clear-cuts do not achieve the same Collembola assemblages as old-growth deciduous forests (Sławski & Sławska, 2019). Nevertheless, in this present study, there was less community difference for Collembola between forest management types than for Oribatida, pointing to how community differences can be linked to succession speed.

In addition, while overall species richness was similar between the forest management types NN and CC, the richness response to environmental factors varied between the two forest management types for Collembola. This suggests community responses to environmental conditions might be context-dependent. The interaction between forest management type and soil pH significantly affects Collembola species richness, with near-natural forests having increasing species richness with soil pH. At the same time, there is seemingly no such relationship in the previously clear-cut forests. Artificial changes in soil pH show how particular species favor acidic conditions, while others favor more alkaline conditions, causing certain species of Collembola to increase or decrease with increasing pH (Hågvar, 1987). Another forest stand study shows how soil pH and food resource availability matter more to Collembola species than tree species composition (Salamon & Alphei, 2009). Specifically, it showed that hemiedaphic species strongly depend on abiotic factors such as pH, whereas acidotolerant, euedaphic species, like the genus *Mesaphorura,* responded to increased fungal biomass. This pattern is also reflected in this study, with euedaphic species having a slightly higher proportion in previously clear-cut forests than near-natural forests, and several *Mesaphorura* species exhibited a strong affinity for previously clear-cut forests. This may reflect the species' tolerance to lower pH conditions. Altogether, this supports the idea that soil conditions and resources are essential, and what might drive the different responses in previously clear-cut and near-natural forests.

The stability of overall species metrics, while still showing context-dependent responses to environmental variables, can be linked to how abiotic conditions shape soil microarthropod communities. Soil conditions such as pH, C/N ratio, and temperature are decisive influences on both taxonomic and functional composition of Collembola (Zhang et al., 2025). These trends can also be found for Oribatida, where soil pH, moisture, and temperature are strong community structure drivers (Pan et al., 2023). Similar patterns were found in relation to elevation, where soil acidity played a greater role in determining Collembola communities than differences in altitude (Loranger-Merciris et al., 2001). This suggests that environmental factors may be a more decisive factor in species distributions than those related to previous forest management, and may offer a better explanation of the patterns observed in our study.

In addition to local soil conditions, broader-scale factors such as regional climate conditions and soil resource quality are dominant drivers of Collembola community dynamics, and temporal variation in abundance, community composition, and biomass seems stronger than differences in forest management type (Pollierer & Scheu, 2017). Similarly, year-to-year variation in Oribatida populations is strongly related to weather conditions, especially temperature and precipitation (Behan-Pelletier & Lindo, 2022). A study on post-fire recovery of Oribatida found that their recovery depended on long-term changes in the soil environment, rather than just time since the disturbance event (Farská et al., 2024). Therefore, after 70 years, long-term climatic and soil trends might have overridden short-term disturbances from clear-cutting. In previously clear-cut forests, recovery might not just be about time passed, but a complex interaction with environmental changes caused by disturbances.

Structural forest factors may also influence soil fauna. Although not statistically significant, the Tree Influence Factor (TIF) appeared to affect Oribatida and Collembola abundance in near-natural forests positively. At the same time, abundance appears stable or slightly negative in previously clear-cut forests with increasing TIF. The near-natural plots displayed a greater tree size heterogeneity and fewer yet larger trees than previously clear-cut plots, resulting in a wider variation in light conditions (Asplund et al., 2024). Although speculative in this context, such variation in canopy structure has been suggested to influence microhabitat diversity, soil food web complexity, and temperature buffering (Chen et al., 2025; Schnabel et al., 2025). These conditions may support higher species abundance in near-natural forests, while in previously clear-cut plots, the benefits of TIF for species could be diminished because of less diversity in tree size. However, given the lack of significance, these interpretations should be treated cautiously and warrant further study.

Several limitations to this study should be acknowledged. While some environmental factors are included, other potentially important variables, like soil nutrient level, microbial activity, and litter quality, were not included and may contribute to shaping the communities. Additionally, this study does not consider year-to-year or seasonal differences in the communities, which can affect soil microarthropod dynamics and obscure long-term trends. Another limitation is that species identification was likely affected by some samples drying during transport, potentially leading to some taxa being underrepresented in the results. Lastly, the study was limited to a specific forest type, which may limit the generalizability of the findings. Because of this, the results should be interpreted with caution. Still, the findings are consistent with what is already known about forest structure and species recovery after disturbance, and the results match well with findings from other research, which gives confidence to the main conclusions.

5. Conclusion

In conclusion, these results indicate that species richness, abundance, and functional group distribution of the soil microarthropods Oribatida and Collembola are similar in the near-natural and previously clear-cut forests. However, it subtly affects community structure when environmental gradients such as moisture, soil pH, and temperature are considered. It therefore remains unclear whether 70 years is enough for full community recovery, given that some species may require much longer to recolonize, particularly those with specific habitat requirements and slow dispersal rates. While some more disturbance-tolerant pioneer species dominate the previously clear-cut, late-successional specialists were more common in near-natural forests, suggesting incomplete community recovery. These long-lasting shifts suggest species-specific responses, driven by soil pH, moisture, and temperature factors, persist decades after a disturbance occurs. This study also highlights how looking at only metrics such as richness and abundance might underestimate the consequences of forest management, and it contributes additional knowledge about the long-term effects of disturbances such as clear-cutting on soil communities. The underlying changes in species identity and composition highlight the need to look beyond α-diversity when evaluating ecological recovery, and future soil biodiversity assessments should incorporate fine-scale environmental data and species-level analysis to fully understand the long-term consequences of forest management.

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Appendix:

Appendix 1: Environmental variables in each Plot ID. Includes soil temperature, pH, tree influence factor (TIF), and gravimetric water content (GWC). Temperature data (drange) is the averages of 6 sensors (TMS-4,Tomst) at each plot measuring soil (8cm) temperatures from 24.may until 19.july 2023. TIF and GWC are averaged over six subplots.

Plot ID	pH	TIF	GWC	Temperature
SKO NN	3.92	0.432	2.053	1.351
SKO CC	3.80	0.604	1.709	1.127
GUL NN	3.76	0.362	2.423	0.997
GUL CC	3.61	0.891	1.839	1.113
HEM NN	3.86	0.436	2.617	1.236
HEM CC	3.91	0.253	1.679	0.989
BRA NN	3.97	0.316	1.445	1.120
BRA CC	3.97	0.524	1.179	1.131
SAR NN	3.87	0.091	2.029	1.316
SAR CC	3.91	0.224	1.947	1.438
OYT NN	3.69	0.231	2.489	1.432
OYT CC	3.57	0.705	2.199	1.116
TRE NN	3.79	0.259	0.845	1.216
TRE CC	3.85	0.343	0.901	1.038
HAL NN	3.56	0.428	1.862	2.424
HAL CC	3.71	0.314	2.249	2.021
BLA NN	3.85	0.389	1.779	1.870
BLA CC	3.46	0.436	1.829	1.537
STR NN	3.90	0.427	2.053	1.351
STR CC	3.66	0.679	2.666	1.127
MRK NN	3.81	0.275	1.763	1.858
MRK CC	4.31	0.389	1.636	1.736
LAN NN	3.93	0.631	1.247	1.036
LAN CC	4.30	0.727	0.926	1.523

Appendix 2: Abundance of functional groups for Collembola.

Forest management type	Functional Group	Total Abundance	Total per forest management type
CC	Epigeic	595	13513
CC	Hemiedaphic	5877	
CC	Euedaphic	7041	
NN	Epigeic	903	12830
NN	Hemiedaphic	6162	
NN	Euedaphic	5765	

Appendix 3: Abundance of functional groups for Oribatida.

Forest management type	Functional Group	Total Abundance	Total per forest management type
CC	Phytophages	3323	20499
CC	Primary Decomposer	7828	
CC	Predator/Scavenger	131	
CC	Secondary Decomposer	9217	
NN	Phytophages	1889	15885
NN	Primary Decomposer	6137	
NN	Predator/Scavenger	203	
NN	Secondary Decomposer	7656	

Appendix 4: Collembola species (epg = Epigeic, hed = Hemieudapic, eud = Euedaphic).

Taxa	Functional group	NN	CC	Total
Anurophorus septentrionalis	**epg**	393	204	597
Allacma fuscsa	**epg**	2	2	4
Appendisotoma abiskoensis	**epg**	91	113	204
Ceratophysella granulate	**epg**	0	1	1
Desoria olivacea	**epg**	79	74	153
Entomobryidae (juvenile)	**epg**	33	49	82
Folsomia palearctica	**hed**	3	25	28
Folsomia sensibilis	**hed**	1890	1449	3339
Folsomia quadrioculata	**hed**	164	252	416
Friesea mirabilis	**hed**	8	46	54
Friesea truncata	**eud**	785	917	1702
Hymenaphorura polonica	**eud**	0	18	18
Isotomiella minor	**eud**	1474	1856	3330
Isotoma anglicana	**epg**	0	8	8
Isotoma viridis	**epg**	93	16	109
Isotoma sp. (juvenile)	**epg**	66	77	143
Karlstejnia norvegica	**eud**	2	0	2
Lepidocyrtus cyaneus	**epg**	83	74	157
Lepidocyrtus lignorum	**epg**	84	80	164
Lepidocyrtus violaceus	**epg**	4	0	4
Liptrix lubbocki	**epg**	30	3	33
Megalothorax minimus	**eud**	88	55	143
Mesaphorura critica	**eud**	314	386	700
Mesaphorura macrochaeta	**eud**	974	1182	2156
Mesaphorura italica	**eud**	213	294	507
Mesophorura sylvatica	**eud**	518	568	1086
Mesaphorura yosii	**eud**	0	183	183
Micranurida forsslundi	**hed**	132	104	236
Micranurida pygmaea	**hed**	3	42	45
Micranurida granulate	**hed**	90	81	171
Micraphorura absoloni	**eud**	648	808	1456
Neanura muscorum	**hed**	6	7	13
Orchesella bifasciata	**epg**	17	0	17
Orchesella flavescens	**epg**	2	1	3
Oligaphorura ursi	**hed**	26	36	62
Paratullbergia callipygos	**eud**	91	23	114
Parisotoma notabilis	**hed**	1620	1400	2020
Protaphorura pseudovanderdrifti	**eud**	740	799	1539
Pseudanurophorus binoculatus	**hed**	445	424	869
Pseudachorutes subcrassus	**epg**	6	10	16
Pseudachorutes corticicolus	**epg**	20	1	21
Sminthurinus aureus	**epg**	0	8	8
Tetracanthella fjellbergi	**hed**	23	13	36

Willemia anophthalma	**hed**	978	1158	2136
Willemia denisi	**hed**	337	320	657
Willemia scandinavica	**hed**	297	511	808
Willemia sp.	**eud**	19	0	19

Appendix 5: Oribatida species. phy = Phytophages, prs = Predator/Scavanger, prd = Primary decomposers, sed = Secondary decomposers

Taxa	**Functional Group**	**NN**	**CC**	**Total**
Autogneta sp.		0	1	1
Acrogalumna longipluma	**sed**	1	0	1
Adoristes ovatus	**prd**	28	31	59
Achipteria nitens	**phy**	3	4	7
Achipteria sp.	**phy**	141	551	692
Banksinoma lanceolata	**sed**	49	2	52
Brachychthoniidae spp.		1408	2558	3966
Caleremaeus sp.	**sed**	1	7	8
Camisia biurus	**phy**	6	4	10
Camisia segnis	**phy**	1	0	1
Camisia sp.	**phy**	2	0	2
Camisia spinifer	**phy**	5	6	11
Carabodes femoralis	**sed**	0	4	4
Carabodes labyrinthicus	**phy**	14	6	20
Carabodes marginatus	**phy**	0	1	1
Carabodes ornatus	**phy**	5	3	7
Carabodes rugosior	**phy**	0	1	1
Carabodes spp.		117	87	204
Carabodes subarcticus	**phy**	1	0	1
Cepheus sp.	**sed**	3	8	11
Ceratozetes minimus	**sed**	0	1	1
Ceratozetes sp.	**sed**	0	3	3
Ceratozetes thienemanni	**sed**	364	665	1029
Ceratozetidae spp.		83	541	624
Chammobates borealis	**sed**	498	594	1092
Chamobates pusilius	**sed**	2	3	5
Chamobates sp.	**sed**	129	164	293
Chamobates subglobus	**sed**	0	1	1
Conchogneta sp.	**sed**	47	22	69
Cosmochthonius sp.	**prd**	0	8	8
Damaeidae spp.		3	4	7
Damaeus sp.	**sed**	1	0	1
Edwardzetes edwardsi	**prd**	16	21	37
Eniochthonius sp.	**sed**	0	29	29
Epidamaeus sp.	**sed**	0	1	1
Eueremaeus sp.		123	29	152
Eueremaeus valkanovi	**sed**	10	0	10
Eupelops plicatus	**sed**	2	0	2
Eupelops sp.	**sed**	26	28	54
Eupelops torulosus	**sed**	6	1	7
Euphthiracarus monodactylus	**sed**	4	37	41
Euphthiracarus sp.		2	0	2
Euzetes globulus	**prd**	1	0	1
Euzetes sp.	**prd**	1	0	1
Galumnidae sp.		0	2	2
Heminothrus longisetosus	**phy**	122	60	182
Heminothrus sp.	**phy**	44	44	88
Hypochthonius rufulus	**prs**	4	3	7
Hypochthonius sp.	**prs**	7	0	7
Lagenobates cf. lagenula		0	6	6
Liacarus sp.	**prd**	0	22	22
Liebstadia longior		0	1	1
Liebstadia sp.		0	2	2
Liochthonius sp.	**phy**	0	1	1
Liochthonius tuxeni	**phy**	23	0	23
Melanozetes mollicomus	**phy**	30	45	75
Metalbelba sp.		4	2	6

Mycobates sp.	**sed**	1	0	1
Nanhermannia sp.	**prd**	806	666	1472
Nanthermannia sellnicki	**prd**	186	137	323
Neonothrus humicolus	**sed**	1	0	1
Nothrus silvestris	**prd**	1196	1061	2257
Odontocepheus elongatus	**phy**	1	0	1
Oppiella (Moritzoppia) neerlandica	**sed**	12	12	24
Oppiella (Oppiella) nova	**sed**	1094	346	1440
Oppiella (Oppiella) propinqua	**sed**	0	1	1
Oppiella (Rhinoppia) subpectinata	**sed**	215	64	279
Oppiella sp.	**sed**	1	2	3
Oppiidae spp.		3118	5083	
Oribatella sp.		1	2	3
Oribatida gen. spp.		1102	1108	2210
Oribatula gen. spp. (juvenile)		187	221	408
Oribatula sp.	**prd**	5	17	22
Oribatula tibialis	**sed**	129	47	176
Parachipteria sp.	**sed**	0	1	1
Pergalumna sp.	**prs**	1	0	1
Perlohmannia sp.		2	3	5
Phauloppia lucorum	**prd**	0	1	1
Phauloppia sp.	**prd**	0	1	1
Phthiracarus spp.		211	171	382
Pilogalumna sp.	**prs**	0	1	1
Platynothrus sp.		0	1	1
Platynothrus peltifer	**prs**	191	125	316
Porobelba sp.	**sed**	21	16	37
Porobelba spinosa	**sed**	2	5	7
Quadroppia sp.	**sed**	5	15	20
Rhysotritia ardua	**prd**	2	2	4
Sellnickochthonius furcatus	**sed**	108	0	108
Sellnickochthonius immaculatus	**sed**	3	0	3
Sellnickochthonius zelawaiensis	**sed**	71	7	78
Scheloribates (Hemileius) initialis	**sed**	91	105	196
Scheloribatidae spp.		18	115	133
Steganacarus applicatus	**prd**	59	17	76
Steganacarus carinatus	**prd**	156	289	445
Steganacarus spinosus	**prd**	245	419	664
Steganacarus striculus	**prd**	5	0	5
Suctobelbella acutidens	**prd**	1	1	2
Suctobelbella falcata	**sed**	29	3	32
Suctobelbella longirostris	**sed**	3	4	7
Suctobelbella sarekensis	**sed**	36	0	36
Suctobelbella similis	**sed**	2	4	6
Suctobelbella sp.	**sed**	3	2	5
Suctobelbella subcornigera	**sed**	166	12	178
Suctobelbella subtrigona	**sed**	8	2	10
Suctobelbidae spp.		1215	1387	2602
Tectocepheus velatus alatus	**prd**	378	557	935

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