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# Groundbreaking effects: Goose grubbing changes how warming and rain-on-snow events affect soil invertebrate abundances in the High Arctic

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"Fredrik, this is groundbreaking science".

Ida C. Apalnes, during soil core extraction 2023.

# Acknowledgements

Svalbard has always fascinated me with its endless beautiful wilderness and its strange and exciting plants and animals. Moving here for studies as a bachelor student back in 2021 taught me that besides amazing nature, Svalbard hosts a community of amazing people. My first stay at Svalbard left such a want for more that the first thing I did after finding out that I would be doing my biology master at NMBU back in 2022, was to contact Steve and Simone, to plan a master thesis. This allowed me to go back to Svalbard and work on this thesis from the spring of 2023 to the spring of 2024. To again be allowed to work with science in Svalbard and with the people up here, has been an enormous privilege. To be allowed to pursue my lifelong passion for invertebrates on top of this is truly a gift.

# Abstract

The High Arctic is currently going through large changes because of anthropogenic climate change. This includes direct changes like higher and more varied temperatures, as well as indirect changes such as changes in species composition and animal abundances. For animals living in Arctic soils, increased temperatures, more frequent winter rain events, and increased populations of geese will be important. This will in turn have consequences for the ecosystem services these animals provide, as well as the release of climate gasses from the soil to the atmosphere. Little is known, however, about how these changes will affect the soil invertebrates. There are no previous studies looking at how geese grubbing, where the geese dig up the ground in search of forage, affects Arctic soil invertebrates. Further, how winter rain events affect soil animals is still largely unresolved. In addition, it is likely that warming and winter rain events will affect soil invertebrates differently, depending on both habitat and whether the ground has been grubbed by geese. In this study, we established an experiment simulating the effects of warming, grubbing and winter rain events in two habitats close to Longyearbyen at Svalbard. I found geese grubbing to have a negative effect on invertebrate abundances in moss and *Dryas*-dominated tundra. Winter rain treatments were found to negatively affect Trombidiform mites and the Collembola *Hypogastrura tullbergi* in *Dryas*-dominated tundra, whereas no effects were recorded in the moss-dominated tundra. Similarly, warming was found to affect the abundances of Trombidiformes and the mesostigmatid mite family *Ascidae* in *Dryas*-dominated tundra. More invertebrate taxa were affected by treatments in the *Dryas*-dominated tundra than moss-dominated tundra. In plots simulating two treatments at once, the effect of each individual treatment was found to be both increased and decreased compared to the same treatments in single treatment plots. Overall, invertebrate taxa were found to react to all treatments, as well as reacting to combinations of different treatments in ways not predicted by each treatment alone. Furthermore, these reactions were found to vary between habitats. These results indicate future shifts in the Arctic soil invertebrate community and highlight the importance of considering both habitat as well as interactions between environmental factors when assessing how these populations will develop in the future.

# Sammendrag

Høyarktis gjennomgår store endringer som del av menneskeskapte klimaendringer. Disse endringene inkluderer både direkte effekter som varmere og mer varierte temperaturer, men også indirekte endringer i artssammensetning og mengden dyr. For dyrene som lever i arktisk jord vil økte temperaturer, vinterregnvær og økte bestander av gås være viktig. Dette vil ha videre konsekvenser for både de økosystemtjenestene som er avhengige av jordinvertebratene, men også for globale klimaendringer. Imidlertid vet vi lite om hvordan disse endringene vil påvirke jordinvertebratene. Det er ingen tidligere studier som har sett på hvordan gravingen til gjess («grubbing») påvirker arktiske jordinvertebrater, og man vet lite om hvordan vinterregn påvirker jordinvertebrater. I tillegg til dette er det sannsynlig at både vinterregn og effekten av grubbing på jordinvertebrater, vil avhenge både av habitat og av hvorvidt bakken allerede har blitt grubbet av gjess. I denne studien utførte vi et eksperiment som simulerte effekten av økte temperaturer, grubbing og vinterregn i to habitater nær Longyearbyen på Svalbard. Jeg fant at grubbing hadde en negativ effekt på jordinvertebrater i både *Dryas*-dominert tundra og i mosedominert tundra. Vinterregn påvirket negativt midd fra orden Trombidiformes og Collembolaen Hypogastrura tullbergi i *Dryas*-dominert tundra, men hadde ingen effekt på jordinvertebratene som levde i mose-dominert tundra. Økte temperaturer hadde et lignende resultat, der midd i ordenen Trombidiformes og midd i familien *Ascidae* ble påvirket i *Dryas*-dominert tundra, men ikke i mosedominert tundra. Totalt sett var det *Dryas*-dominert tundra som hadde flest taxa som ble påvirket av behandlinger. I plott der jeg simulerte to behandlinger samtidig fant jeg at effekten av hver individuell behandling både økte og minket, sammenlignet med effekten av de samme behandlingene i plot der bare en behandling ble simulert av gangen. Det ble funnet jordinvertebrattaxa som reagerte på alle de forskjellige behandlingene. I tillegg ble det funnet reaksjoner som ikke kunne bli forutsett av å se på enkeltstressfaktorer alene, jeg fant også at disse reaksjonene varierte mellom habitater. Dette indikerer fremtidige skifter i det arktiske jordinvertebratsamfunnet, og viser viktigheten av å se på sammenhengen mellom habitat og interaksjoner mellom ulike økosystem faktorer for å kunne forutse hvordan disse faktorene vil påvirke jordinvertebratene i fremtiden.

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# 1 Introduction

Soils are of vital importance to terrestrial life. It consists of organic and inorganic particles and the living organisms in between. Soils provide a wide array of ecosystem services, regulating floods, erosion and climate gasses, it supplies foods and organic material for human use, and supports services such as nutrient cycling (Adhikari & Hartemink, 2016; Wall, 2012). Many of these services are dependent upon soil biodiversity, such as fungi, bacteria and invertebrates (Delgado-Baquerizo et al., 2020).

Over 80% of terrestrial plant primary production enter the detrital food web annually (Cebrian & Lartigue, 2004). This energy input supports large numbers of invertebrates living in the soil, and ecosystems with more than a million mites per square meter are not uncommon (Walter & Proctord, 2013). Mites and other soil animals provide a vital role facilitating decomposition and releasing nutrients back to the plants (Delgado-Baquerizo et al., 2020).

Soil invertebrates will likely be affected by global warming (Alatalo et al., 2017; Convey et al., 2002; Coulson et al., 1996; Dollery et al., 2006; Hodkinson et al., 1996; Hågvar & Klanderud, 2009; Krab et al., 2013; Markkula et al., 2019). The global temperature averages are currently increasing as a consequence of anthropogenic climate gas emissions (Stocker et al., 2013). The High Arctic Archipelago of Svalbard is particularly affected, with temperatures increasing at twice the rate of the global average (Cohen et al., 2014). The release of soil carbon to the atmosphere is based on the soil carbon cycle which in turn is influenced by the soil invertebrate community (Briones et al., 2007; Koltz et al., 2018; Lubbers et al., 2020). Koltz et al. (2018) found detrital resources to account for as much as 99.6% of invertebrate processed carbon in her study site in northern Alaska. Our understanding of local soil processes like nutrient cycling, as well as our understanding of future climate change, will therefore be dependent on our knowledge about the Arctic soil invertebrates.

Invertebrate diversity decreases with latitude (Gillespie et al., 2020). Thus, Svalbard's natural soil ecosystems lack many of the important decomposers found further south such as Terrestrial Gastropods, Isopoda, Myriapoda and most importantly lumbricid worms (Coulson et al., 2013; Coulson et al., 2014). Although the role of species diversity on ecosystem functioning is unresolved (Gillespie et al., 2020), Collembola and mites are likely to be important for soil ecosystem functioning, and can be found in high densities at Svalbard. For instance, has the Collembola *Folsomia quadrioculata* been reported in concentrations above 80 000 animals per

m$^2$ (Sømme & Birkemoe, 1999), and mites above 60 000 per m$^2$ (Byzova et al., 1995). Thus, mites and Collembola are therefore the most obvious invertebrates to study in these Arctic soils.

Mite and Collembola abundance are dependent upon several environmental factors (Alatalo et al., 2017; Convey et al., 2002; Coulson et al., 1996; Coulson et al., 2000; Dollery et al., 2006; Hodkinson et al., 1996; Hågvar & Klanderud, 2009; Krab et al., 2013; Thakur et al., 2023). Warming has previously been found to change soil invertebrate abundances (Alatalo et al., 2017; Coulson et al., 1996; Dollery et al., 2006; Markkula et al., 2019). Indeed, Collembola abundance respond negatively to warming (Convey et al., 2002; Coulson et al., 1996; Dollery et al., 2006; Hågvar & Klanderud, 2009; Krab et al., 2013; Thakur et al., 2023), whereas oribatid mite abundance show more resilience to the negative effects of warming (Alatalo et al., 2017; Coulson et al., 1996; Dollery et al., 2006; Hågvar & Klanderud, 2009; Markkula et al., 2019; Thakur et al., 2023). This may be a result of moisture constraints, with Collembola being more vulnerable to drought than oribatid mites (Hodkinson et al., 1996). Collembola also show higher tolerance to warming in moist habitats (Hodkinson et al., 1996). Importantly, earlier studies investigating the effects of warming on Collembola and oribatid mites looked at whole year (Alatalo et al., 2017; Dollery et al., 2006; Hågvar & Klanderud, 2009; Markkula et al., 2019) or full season effects (Convey et al., 2002; Coulson et al., 1996), neglecting the specific effect of shoulder season warming, which will be the focus in my study. However, effects of warming may occur in the winter as well as during summer; Winter periods with temperatures above zero degrees Celsius are becoming increasingly common in the High Arctic (Graham et al., 2017), which is likely to increase risk of winter rain, or so-called rain-on-snow events (ROS). These events may lead to thick ice layers on the ground (Hansen et al., 2014). The effect of rain-on-snow events and subsequent icing on soil invertebrates is mostly unknown, but Coulson et al. (2000) found Collembola abundance to be negatively affected. During the last decades, the number of pink footed geese (*Anser brachyrhynchus*) has increased across the Arctic due to changing farming practices in the birds winter habitats, climate change, and management policies (Fox et al., 2005; Madsen et al., 2017). Pink footed geese forage for plant roots using their beaks, digging small holes in the tundra, a process termed grubbing (Fox & Bergersen, 2005). While grubbing may change avian/surface dwelling (Milakovic & Jefferies, 2003), and benthic (Sherfy & Kirkpatrick, 2003) invertebrate populations, their effect on Arctic soil invertebrates is currently unknown. Grubbing removes vegetation layers and disturbs the underlying soil, which is likely to influence the soil invertebrate community negatively. On the other hand, the addition of nutrients from geese faeces may have a positive effect on

invertebrate abundance (Flemming et al., 2022; Hågvar & Klanderud, 2009). The stress of grubbing and warming are likely to be habitat dependent, as earlier studies have found vegetation in *Dryas*-dominated tundra to be more vulnerable to grubbing than vegetation in moss-dominated tundra (Speed et al., 2010; Van der Wal et al., 2020). In addition, mosses are known to have cooling effect on soils (Gornall et al., 2007; Park et al., 2018; Van der Wal et al., 2001). The different environmental effects are also likely to interact with each other. Interactions between environmental factors have previously been investigated in terms of moisture, and nutrient availability with warming (Convey et al., 2002; Hodkinson et al., 1996; Hågvar & Klanderud, 2009; Koltz et al., 2018). However, geese grubbing seems likely to increase the adverse effects of both warming and icing on soil invertebrates, yet such an interaction has to my knowledge never before been investigated.

In this study, I will investigate the effects of shoulder season warming, rain-on-snow events (ROS) and grubbing on soil Arctic invertebrate populations. In addition, I will study the interactive effects of several environmental changes at work. The study will look at the invertebrate communities in two contrasting tundra habitats in Adventdalen on Svalbard,  a mesic tundra dominated by *Dryas octopetala* and a moist moss-dominated tundra. I hypothesize that (i) both rain-on-snow and shoulder season warming will affect Collembola negatively, whilst the oribatid mites will react negatively to grubbing; (ii) soil invertebrates will be less affected in the moss-dominated tundra than the *Dryas*-dominated tundra, (iii) ROS and warming treatments will interact with the grubbing treatment, changing invertebrate communities in ways not predicted by each treatment alone.

# 2 Materials and Methods

This study was done as part of the project TERRA – "Thawing permafrost in the High Arctic. Understanding climate, herbivore and belowground feedbacks" (TERRA, n.d). My study aimed to investigate how icing, shoulder season warming and grubbing affect invertebrates with future implications for soil carbon and nitrogen stocks.

## 2.1 Location

The field sites were located in Adventdalen valley, east of Longyearbyen, Svalbard. Five sites were located in moist moss-dominated tundra and five in mesic *Dryas-octopetala* (hereafter *Dryas*)-dominated tundra. Coordinates for all plots can be found in Appendix (Table 3). The mean annual temperature of 2022 and 2023 was -3.3℃ and -2.7℃ respectively. The highest/lowest temperature of 2022 was +16.5℃/-35 ℃ and +17 ℃/-28.8 ℃ for 2023, and the annual precipitation was 119 mm in 2020 and 242 mm in 2023 (Norsk klimaservicesenter, n.d).
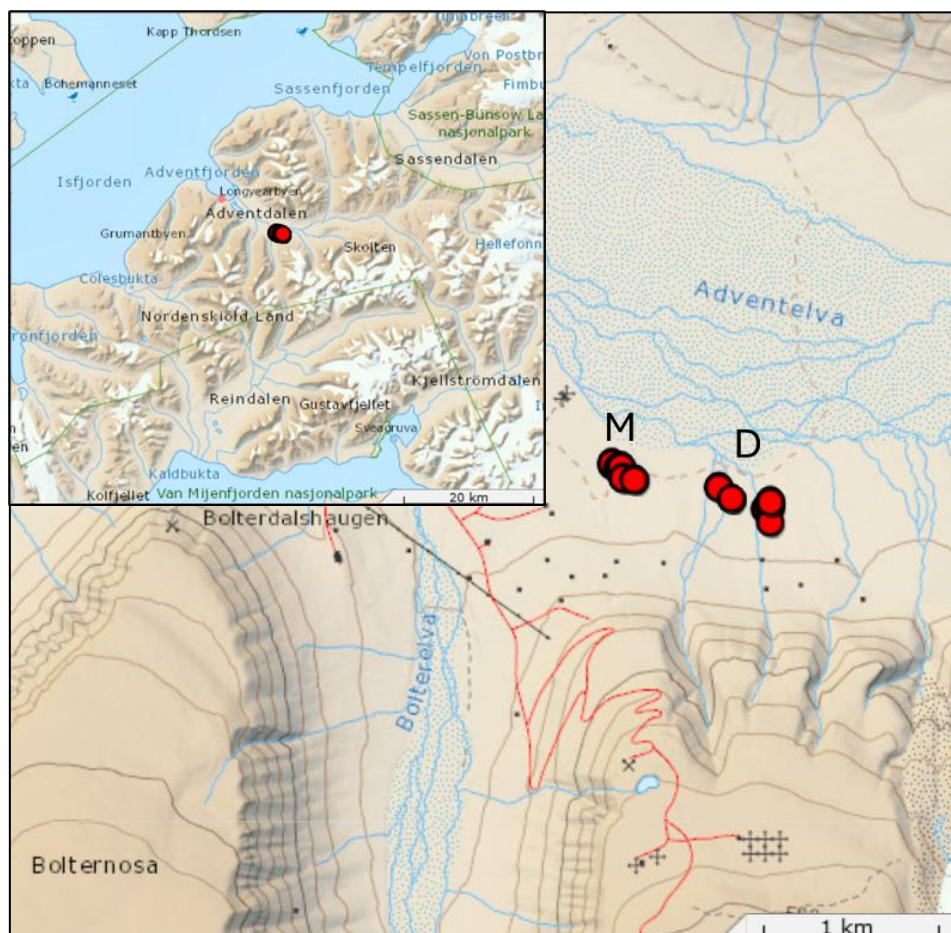


**Figure 1.** Overview of field sites on Svalbard (*TopoSvalbard*, 2018). Red circles marked with "M" show the moss-dominated tundra sites. Red circles marked with "D" show the *Dryas*-dominated tundra sites, for a total of 30 plots for each habitat, coordinates appendix (Table 3).

## 2.2 Experimental design

At each of the ten field sites, six square shaped plots of 1x1m were selected during the autumn of 2021. Moss-dominated tundra sites were selected based on the presence of the herb *Bistorta vivipara* and the shrub *Salix polaris* as well as the moss species *Aulacomnium palustre, Aulacomnium turgidum* and *Tomenthypnum nitens*. Areas with *Eriophorum* were excluded, as it indicated wetter habitats. *Dryas*-dominated sites (mesic tundra) were dominated by grasses from the genera *Poa* and *Festuca*, and the dwarf shrubs *Dryas octopetala, Salix polaris* and *Bistorta vivipara*, as well as the mosses *Hylocomium splendens*, *Sanionia uncinata* and *Polytrichum spp.* The inter-plot distance was a minimum of one meter. After the establishment of the six plots, distribution of treatment and control plots were randomly distributed. The treatments (Figure 2) were as follows:
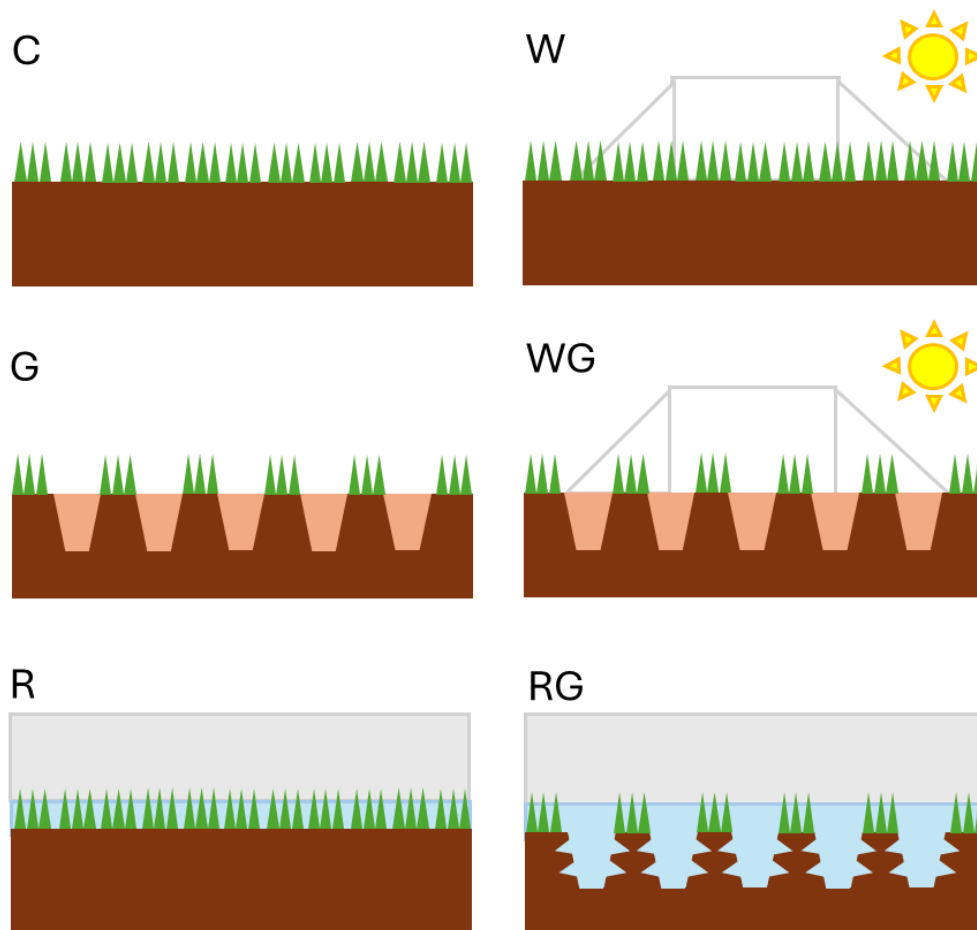


**Figure 2.** The different treatments. C; Control, no treatment. W; experimental spring and autumn warming using OTCs. G; Grubbing. GW; Grubbing and warming. R; Rain-on-snow events, shown with snow and ice layers, light blue layer = ice, white = snow. RG; Icing and grubbing, shown with snow and ice layers. Sun symbol indicates warming treatment. All treatments had five replicates in both moss-dominated and *Dryas*-dominated tundra, resulting in a total of 60 plots (N=5 for each treatment).

**Warming** was achieved by using hexagon shaped open top chambers (OTCs) (Danish Polar Center, 1996). As the experiment aimed to investigate spring and autumn warming, the OTCs were placed from 23,8-27,9 during the autumn of 2022 and from 02,06-04,07 during the spring of 2023.

**Geese grubbing** was simulated by removing moss by hand during the spring of 2022. The holes were dug by pushing two fingers approximately five cm deep into the soil, pinching, and removing the vegetation between the fingers. To ensure equal treatment in all plots, a 1x1 m frame divided into 10x10 cm squares was used when grubbing. Two holes were made per 10x10cm square, one in the lower left and one in the upper right corner. The simulated grubbing, about half of the total vegetation cover was removed. In order to exclude any natural grubbing from the experiments, exclosure (iron frame with chicken wire around and above) was used during the spring and early summer, as this is the time when the majority of geese grubbing takes place (Van Der WAL et al., 2007). As the warming plots were equipped with OTCs in the same period, they were covered with a 1 x 1m chicken wire at the same time. As part of the grubbing treatment, all goose faeces were removed from the plots in spring 2023 to ensure an even starting point for all the plots before new faeces were added. Goose faeces were sampled along the road to Adventdalen. Care was taken to include only fresh faeces. The samples were stored in a freezer before being added to the grubbing treatment. Wet geese faeces were then placed evenly onto the plots, the amount of faeces added was decided based upon their dry weight as described in Petit Bon et al. (2021).

**Rain-on-snow** (ROS) was simulated 30,1 - 4,2,23 Snow was firstly removed from all plots. This was done in order to give the same disturbance in the snowpack across all plots. The snow was then placed back on all the plots except the ROS plots. Wooden frames 1 x 1 m wide and 20 cm tall were placed on the now snowless ROS plots. Water was then used to make a snow water mix, or in other words slush. The slush was then applied to both the inside and the outside of the frames filling the gap between the ground and the frame, and then allowed to freeze. The frames were then filled with a thin layer of water. This was done once or twice per day for four days allowing the water to completely freeze each time before adding more, leaving the frames completely filled with ice by the end of the treatment. The frames were then removed in spring after the ice had melted away.

### 2.2.1 Abiotic measurements

Soil moisture was measured using EC5 Soil Moisture Smart Sensors (Onset Data Loggers, USA). Soil temperature was measured using Tinytag Plus 2 with TGP-4017 sensors (Gemini Data Loggers Ltd, United Kingdom) at 5 cm and 10 cm below ground. Tinytag Talk 2 — TK-4014 (Gemini Data Loggers Ltd, United Kingdom) sensors were utilised to measure air temperature throughout the summer, in two of the moss-dominated tundra sites and two of the *Dryas*-dominated tundra sites. The belowground sensors were buried in the southwestern corner of each plot. The data were stored in H21-USB HOBO Micro Station dataloggers (Onset Data Loggers, USA). Some Hobo data was lost as a very wet spring led to several of the HOBO seals failing, letting in water, and destroying the HOBO loggers and the logged data.

Weather data was gathered using HOBO weather stations, one in each habitat. Each station was equipped with Photosynthetic Light (PAR), Solar Radiation (Silicon Pyranometer) and Temperature/Relative Humidity (2m cable) Smart Sensors (Onset Data Loggers, USA), measuring PAR µmol/m²/s, solar radiation W/m2, RH% and temperature data. The weather stations operated from 16th June to 11th September 2023. Weather stations were only operating in this period in order to reduce damage from winter weather, and from reindeer during the rutting season.

### 2.2.1 Invertebrate sampling

Invertebrates were sampled on 4th June 2023 by two 8 cm deep and 5.6 cm in diameter soil cores from each plot, resulting in a total of 120 cores. The cores were placed independently in plastic bags and transported to the lab. The soil cores were placed in a McFayden extractor (ecoTech GmbH, Germany) for a total of 10 days. The extractor was programmed to keep a temperature, measured in the middle of each chamber, 20°C for the first 48 hours, 30°C for the second 48 hours and 40°C for the rest of the extraction run time. The animals were extracted directly into falcon tubes and kept in a 96% ethanol solution. The animals were counted using a Leica M205 C microscope (Leica Microsystems GmbH, Germany). The animals were identified to the lowest possible taxonomical level, keyed according to Fjellberg (1994) and Seniczak (2023). Due to time constraints, only one sample per plot, or 60 samples in total, were included in this study.

## 2.3 Statistics

Data analyses were done with R (R Core Team, 2022) and R Studio (Posit team, 2024), Shapiro–Wilk tests were used to check for normality. Log and square root transformation methods were used to normalise the invertebrate count data, without success. In further analyses I therefore only used models that did not assume normality. The experiment was set up as blocks and not as individual sites. I therefore did not consider nested design in the analyses.

Effects of treatments on invertebrate counts were assessed using negative binomial regression modelling (Negative binomial GLM) through the MASS package (Venables & Ripley, 2002). This model was selected based upon its ability to handle overdispersed data. In addition, quasi-Poisson modelling was performed, yet the negative binomial regression modelling was selected as it showed lower residual deviance levels, indicating a better fit. In the negative binomial regression model, the main effects of rain-on-snow (R), grubbing (G), warming (W) and the interaction terms grubbing x warming (GxW) and grubbing X rain-on-snow (GxR) were included. Each treatment was included as present (1) or absent (0) in the analyses. Each taxon was analysed separately. Since habitat might lead to different treatment effects, analyses were done separately for moss-dominated tundra and *Dryas*-dominated tundra. Because of the nature of the negative binomial GLM test, testing for all main effects and interaction terms as part of one calculation, and all taxa being tested individually, thus not using any data for more than one test, Bonferroni corrections were not applied.

Analyses of the treatment effects on the soil invertebrate community on an order level were done through ordination. Redundancy analysis (RDA) was selected based upon DCA1 values (Lepš & Šmilauer, 2003), and conducted through the vegan package (Oksanen et al., 2022). The significance of the different environmental factors in the RDA model was tested using the ordistep function from the vegan package (Oksanen et al., 2022). Principal component analysis (PCA) was used to visualise the community's distribution amongst the different treatment plots using the vegan package (Oksanen et al., 2022). All count data were centred before use.

# 3 Results

## 3.2 Soil animal densities

There were large differences in animal densities between taxa. The most common orders were the mites from Sarcoptiformes and the Collembola from Entomobryomorpha (Figure 3). The orders of Trombidiformes (mite), Poduromorpha (Collembola) and Mesostigmata (mite) were rarer (Figure 3). At family level, *Peloppiidae* were the most common with the mite families

*Ascidae, Zerconidae* and *Diapterobates* being rarer (Figure 3). At species level, the Collembola *Folsomia quadrioculata* was the most abundant, with the mite *Diapterobates notatus* and the Collembola *Hypogastrura tullbergi* being less abundant (Figure 3). See appendix (Figure 6-13) for boxplot for all taxa and treatments.
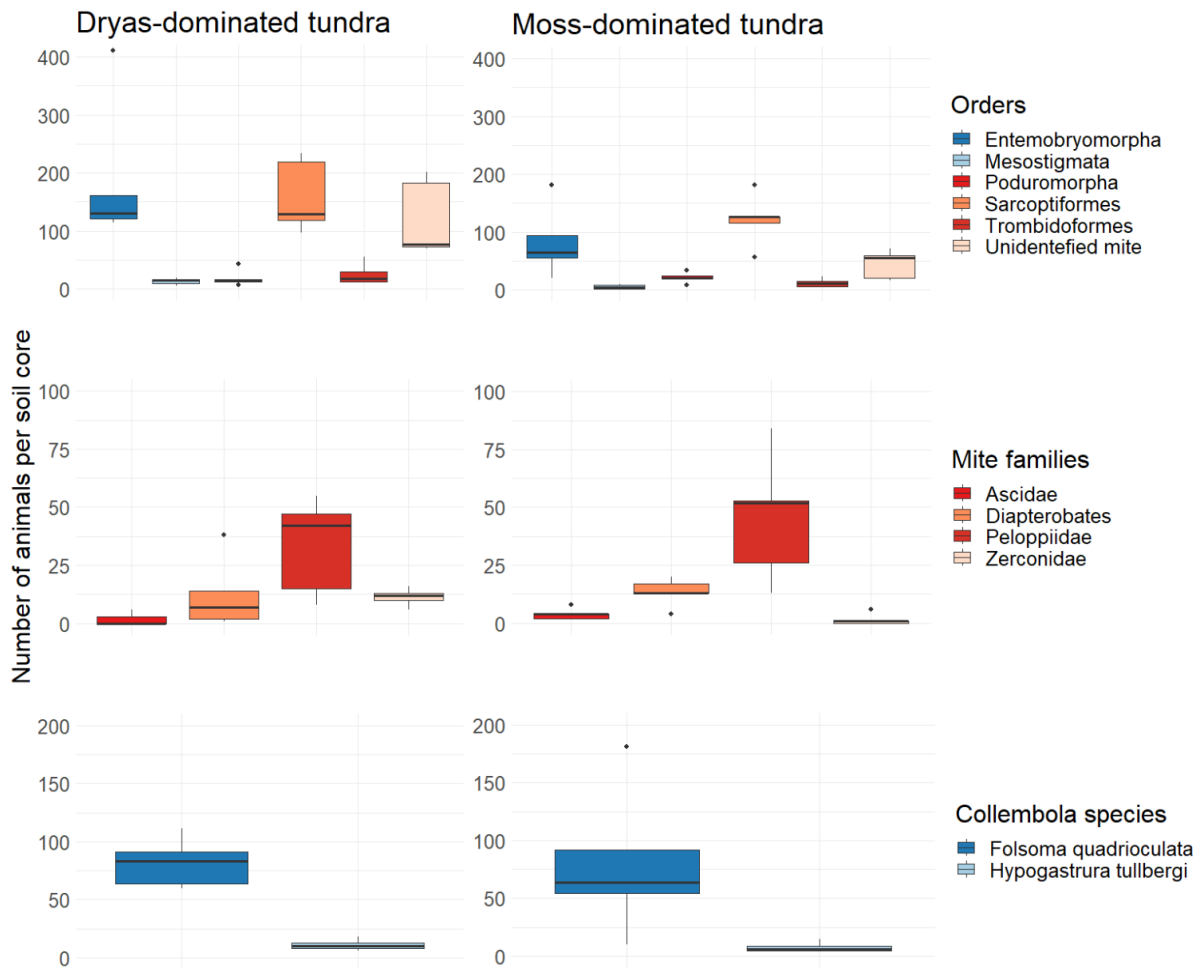


**Figure 3.** Boxplots showing control plot counts for soil invertebrate orders, mite families and two Collembola species, in moss and *Dryas*-dominated tundra. Collembola (blue), mites (red/brown). The mite family Diapterobates was only represented by one species *Diapterobates notatus*. The thick black line inside the boxes shows the median. Whiskers show range of data points with dots showing outliers. (N=5 for each habitat).

## 3.3 Treatment effects on soil invertebrate abundance

**Table 1** Negative binomial regressions, showing the relation between different treatments and soil invertebrate counts in *Dryas*-dominated tundra. Each row represents a single negative binomial GLM test where the taxa is the response variable, the warming, rain-on-snow (ROS) and grubbing are the predictor variables and the grubbing x warming and grubbing x ROS are the interaction terms. In other words, the model can be explained by $Y=\beta0+\beta1W+\beta2R+\beta3G+\beta4(G\times R)+\beta5(G\times W)+\epsilon$ where warming= W, ROS = R and Grubbing, Y = abundance of an invertebrate taxa for example Collembola, and Beta is the effect of the different treatments on the invertebrate abundances. Significant p-values are marked in bold, near significant values are underlined (N=5).

| Taxa (response variable) | Warming | | ROS | | Grubbing | | Grubbing X warming | | Grubbing X ROS | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) |
| Total mites | 0.447 | 0.107 | 0.243 | 0.381 | -0.591 | **0.034*** | -0.111 | 0.777 | -0.043 | 0.912 |
| Mesostigmata | -0.112 | 0.811 | -0.047 | 0.921 | -0.693 | 0.152 | 0.676 | 0.317 | -0.049 | 0.943 |
| *Zerconidae* | -0.909 | 0.109 | -0.305 | 0.577 | -1.047 | 0.067. | 1.047 | 0.202 | 0.200 | 0.806 |
| *Ascidae* | 1.386 | **0.018*** | 0.847 | 0.161 | 0.368 | 0.559 | -0.396 | 0.626 | -0.927 | 0.279 |
| Trombidiformes | -0.618 | **0.047*** | -0.678 | **0.030*** | -0.827 | **0.009**** | 0.980 | **0.028*** | 1.237 | **0.006**** |
| Oribatida | 0.415 | 0.109 | 0.068 | 0.794 | -0.820 | **0.002**** | 0.023 | 0.950 | 0.408 | 0.270 |
| *Diapterobates notatus* | 0.395 | 0.555 | -0.795 | 0.247 | -0.572 | 0.401 | -0.100 | 0.917 | 0.977 | 0.314 |
| Adult *D. notatus* | 1.281 | 0.126 | 0.337 | 0.705 | >0.001 | 1.000 | - 1.504 | 0.234 | -0.154 | 0.903 |
| Juvenile *D. notatus* | 0.261 | 0.703 | -0.999 | 0.159 | -0.642 | 0.359 | 0.099 | 0.920 | 1.181 | 0.238 |
| *Peloppiidae* | 0.064 | 0.891 | -0.012 | 0.979 | -0.664 | 0.160 | 0.745 | 0.261 | 0.645 | 0.331 |
| Unidentified mites | 0.598 | 0.147 | 0.562 | 0.173 | -0.405 | 0.328 | -0.120 | 0.838 | -0.245 | 0.675 |
| Total Collembola | -0.520 | <u>0.093.</u> | -0.238 | 0.440 | -0.498 | 0.107 | 0.597 | 0.173 | -0.067 | 0.879 |
| Entomobryomorpha | -0.554 | 0.136 | -0.239 | 0.520 | -0.710 | <u>0.056.</u> | 0.860 | 0.102 | -0.102 | 0.847 |
| *Folsomia quadrioculata* | -0.438 | 0.156 | 0.158 | 0.605 | -0.492 | 0.111 | 0.623 | 0.154 | -0.277 | 0.526 |
| Poduromorpha | -0.239 | 0.598 | -0.228 | 0.619 | -0.339 | 0.457 | -0.034 | 0.959 | 0.132 | 0.838 |
| *Hypogastrura tullbergi* | -0.319 | 0.355 | -0.916 | **0.014*** | -2.909 | **>0.001*** | 1.417 | 0.076. | 2.526 | **>0.001**** |

**Table 2** Results from negative binomial regressions, showing the association between different treatments and soil invertebrate numbers in moss-dominated tundra. Each row represents a single negative binomial GLM test where the taxa is the response variable, the warming, rain-on-snow (ROS) and grubbing are the predictor variables and the grubbing x warming and grubbing x ROS are the interaction terms. In other words, the model can be explained by $Y=\beta0+\beta1$ $W+\beta2R+\beta3G+\beta4(G\times R)+\beta5(G\times W)+\epsilon$ where warming= W, ROS = R and Grubbing, Y = abundance of an invertebrate taxa for example Collembola, and Beta is the effect of the different treatments on the invertebrate abundances. Significant p-values are marked in bold, near significant values are underlined (N=5).

| Taxa (response variable) | Warming | | Rain-on-snow event | | Grubbing | | Grubbing X Warming | | Grubbing X ROS | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) | Estimate | Pr(>\|z\|) |
| Total mites | -0.030 | 0.895 | 0.199 | 0.379 | -0.380 | <u>0.096.</u> | -0.004 | 0.990 | -0.230 | 0.475 |
| Mesostigmata | -0.288 | 0.519 | 0.069 | 0.873 | -0.442 | 0.332 | 0.442 | 0.495 | 0.373 | 0.552 |
| *Zerconidae* | 0.2231 | 0.756 | 0.629 | 0.366 | -0.693 | 0.396 | >-0.001 | 1.000 | -0.069 | 0.949 |
| *Ascidae* | -0.598 | 0.235 | -0.288 | 0.548 | -0.357 | 0.461 | 0.731 | 0.301 | 0.693 | 0.308 |
| Trombidiformes | -0.483 | 0.179 | 0.065 | 0.851 | -0.357 | 0.316 | -0.035 | 0.947 | -0.113 | 0.822 |
| Oribatida | -0.119 | 0.639 | 0.053 | 0.834 | -0.408 | 0.109 | 0.182 | 0.614 | -0.036 | 0.921 |
| *Diapterobates notatus* | -0.334 | 0.311 | 0.113 | 0.722 | 0.165 | 0.602 | -0.858 | <u>0.077.</u> | -0.531 | 0.241 |
| Adult *D. notatus* | -0.241 | 0.697 | 0.580 | 0.314 | 0.728 | 0.203 | -0.929 | 0.283 | -1.382 | <u>0.090.</u> |
| Juvenile *D. notatus* | -0.360 | 0.293 | -0.058 | 0.860 | -0.058 | 0.860 | -0.845 | 0.107 | -0.190 | 0.689 |
| *Peloppiidae* | -0.162 | 0.613 | -0.495 | 0.125 | -0.757 | **0.020*** | 0.625 | 0.173 | 0.417 | 0.369 |
| Unidentified mites | 0.270 | 0.432 | 0.544 | 0.112 | -0.313 | 0.367 | -0.496 | 0.313 | -0.777 | 0.113 |
| Total Collembola | -0.054 | 0.854 | 0.092 | 0.755 | -0.231 | 0.437 | -0.160 | 0.704 | 0.020 | 0.961 |
| Entomobryomorpha | -0.032 | 0.920 | 0.058 | 0.854 | -0.293 | 0.355 | -0.084 | 0.851 | 0.102 | 0.820 |
| *Folsomia quadrioculata* | -0.198 | 0.561 | -0.005 | 0.988 | -0.790 | **0.022*** | 0.236 | 0.629 | 0.569 | 0.240 |
| Poduromorpha | -0.048 | 0.891 | 0.204 | 0.560 | -0.110 | 0.757 | -0.535 | 0.293 | -0.163 | 0.744 |
| *Hypogastrura tullbergi* | 0.095 | 0.841 | -0.598 | 0.230 | -0.856 | <u>0.094.</u> | -1.137 | 0.151 | 0.473 | 0.524 |

The negative binomial regression models revealed grubbing to be the treatment that affected the most soil taxa (Table 1 and 2). Oribatid mites were negatively affected by grubbing in the *Dryas*-dominated tundra, whereas the oribatid mites in moss-dominated tundra decreased, but not significantly (P<0.11).

In the *Dryas*-dominated tundra, total and trombidiform mites as well as the Collembola *H. tullbergi* were negatively affected by grubbing, and a close to significant negative effect was also found for Entomobryomorpha abundance (P<0.056). In the moss-dominated tundra, *F. quadrioculata* were also negatively affected by grubbing. In addition, trombidiform mites and *Peloppiidae*. *H. tullbergi* (P<0.094) and all mites (P<0.096) also decreased in the moss-dominated tundra, but the effect was not significant.

ROS had no effect on any invertebrate taxa in the moss-dominated tundra ecosystem (Table 2). In the *Dryas*-dominated tundra, however, Trombidiformes mites and *H. tullbergi* decreased in numbers with the treatment.

The effect of warming and grubbing combined was found to be positive for Trombidiformes mites in the *Dryas*-dominated tundra as well as for *H. tullbergi* (P<0.076), although the latter was not significant. No significant effects were found in the moss-dominated tundra, but a tendency for *D. notatus* adults to decrease with this combination of treatments (P<0.077) was found.

The effect of grubbing and ROS together was very similar to the effects of the warming and grubbing combined. Trombidiformes mites and *H. tullbergi* increased as a response to this two-environmental factor treatment in the *Dryas*-dominated tundra. However, *D. notatus* juveniles decreased as a response to this treatment in the moss-dominated tundra although the effect was not significant (P<0.089).

## 3.3 Treatment effects on soil invertebrate communities

Redundancy analysis for invertebrate orders showed grubbing to have a significant effect on invertebrate abundances on an order level (P<0.006 *Dryas*-dominated tundra, P<0.005 moss-dominated tundra, full table in Appendix (Table 10-11)) (Figure 5). The redundancy analyses included only grubbing as explanatory variable based upon ordistep selection function (Grubbing = P<0.02 *Dryas*-dominated tundra, P<0.06 moss-dominated tundra, full table Appendix (Table 8-9)).

For PCA analyses for all invertebrate orders for *Dryas*-dominated tundra (Figure 4 A) PCA1 was explained 59% and PCA 2 explained 39% of the variance. Full table in appendix (Table 13). For moss-dominated tundra (Figure 4 B), PCA1 and PCA2 explained 65% and 31% of variance respectively, full table in appendix (Table 12).
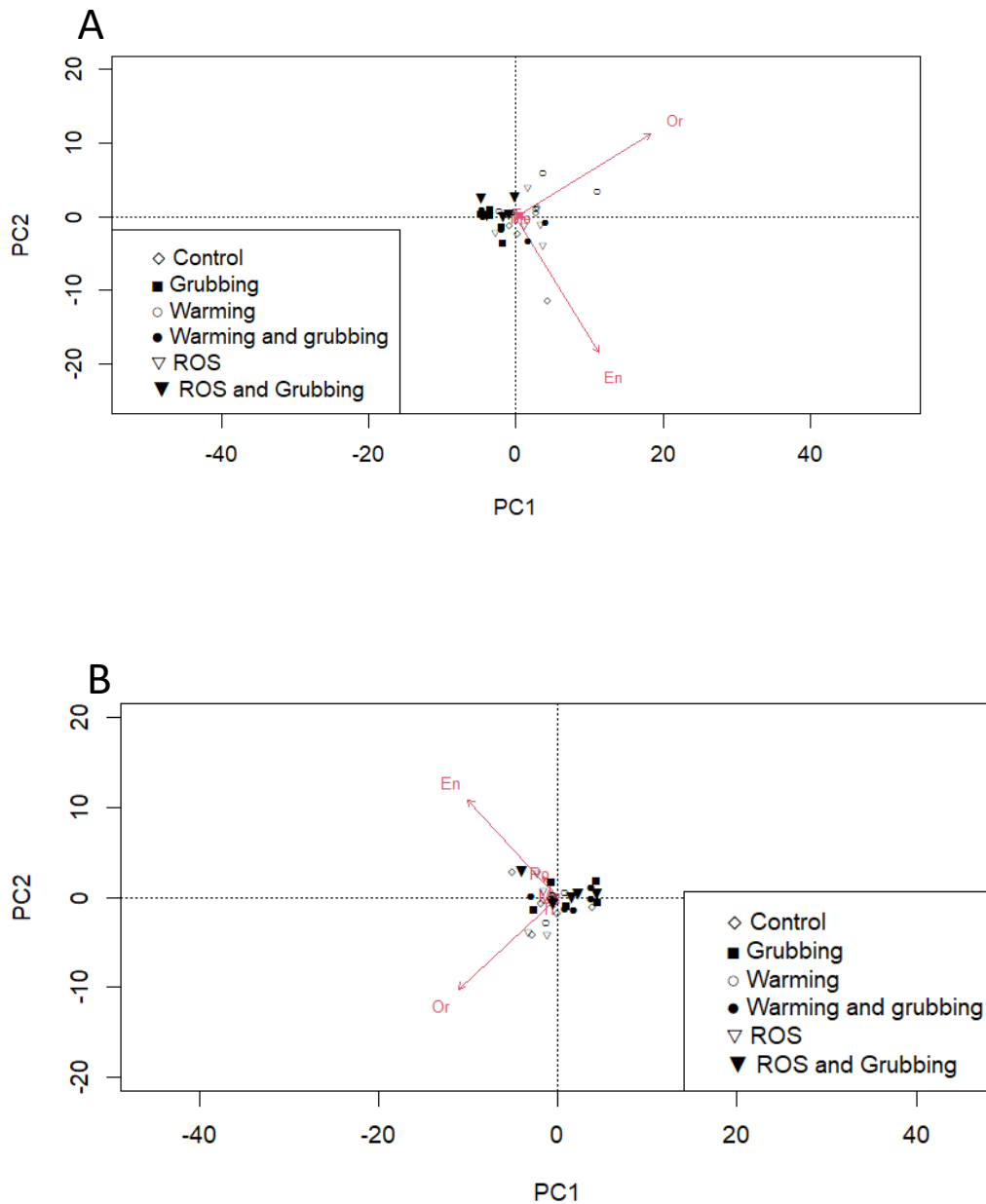


**Figure 4.** PCA for soil invertebrate orders. *Dryas*-dominated tundra site (A), moss-dominated tundra site (B). Or= Oribatida, En = Entomobryomorpha, Po = Poduromorpha, Tr= Trombidiformes, Me = Mesostigmata. Orbatida were here used as label despite being a suborder, as all Sarcoptiformes counted in this study were Oribatida. (N = 30).

**Figure 5**. RDA plot for soil invertebrate orders. *Dryas*-dominated tundra (A), moss-dominated tundra (B). En = Entomobryomorpha, Po = Poduromorpha, Tr= Trombidiformes, Me = Mesostigmata. Or = Orbatida. Orbatida were here used despite being a suborder, as all Sarcoptiformes counted in this study were Oribatida. Euclidian distances are sc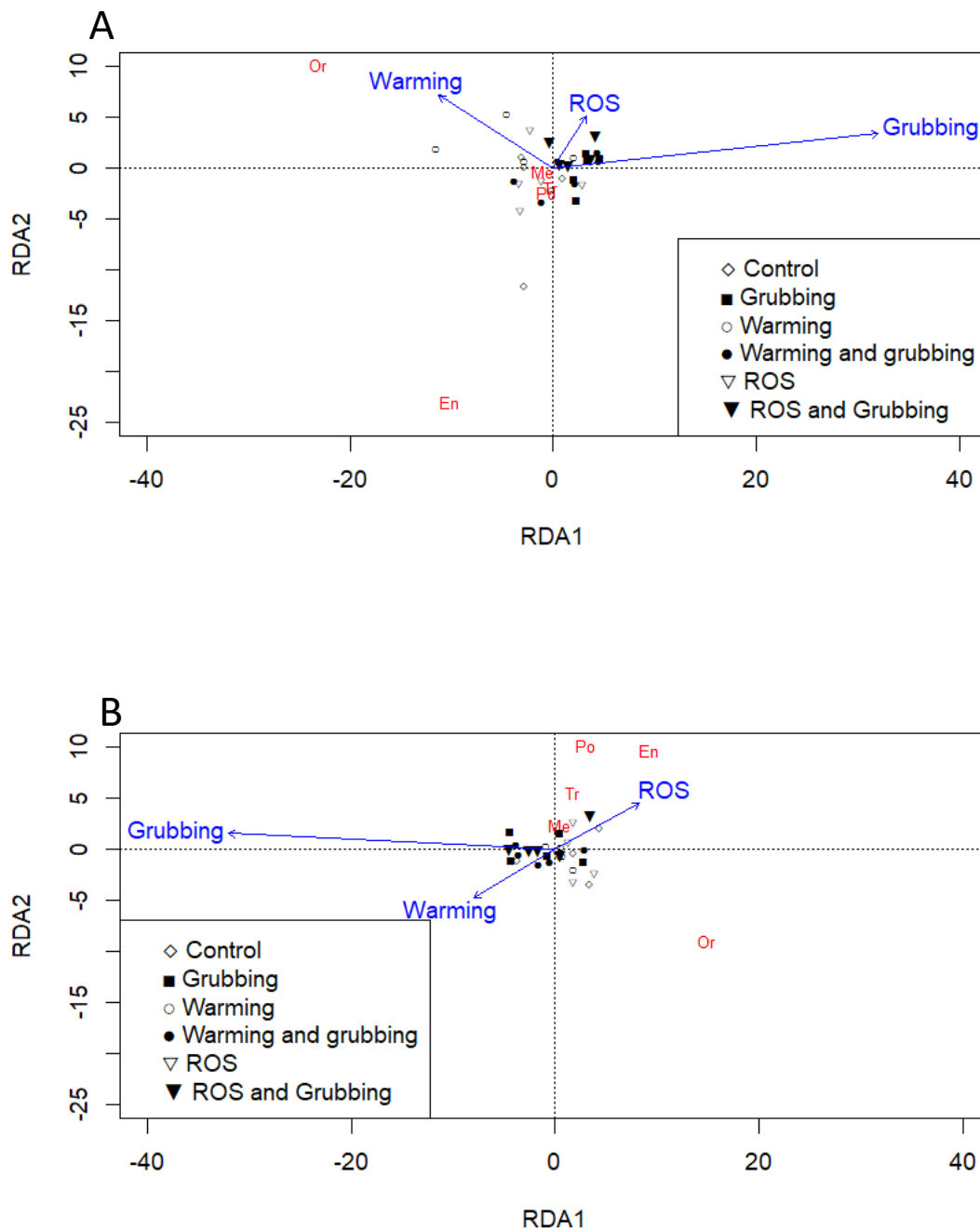aled with type 1 scaling. Arrows show the corelation between the environmental factors and the different taxa. The ordistep forewords selection formula and RDA analyses showed grubbing was the only significant environmental variable. (N = 30).

# 4 Discussion

## 4.1 Grubbing had a negative effect on soil invertebrate abundance

Of all treatments, grubbing was found to have the largest effect on the invertebrate community; as expected, it decreased oribatid mites, though not significantly in the moss-dominated tundra ($P<0.109$). Grubbing also reduced total mite numbers as well as the Collembola *H. tullbergi* and trombidiform mites in *Dryas*-dominated tundra. In addition, grubbing decreased the Collembola *F. quadrioculata* and the *Peloppiidae* mites in the moss-dominated tundra.

Grubbing may affect the soil invertebrates through the removal of moss, soil and animals, habitat disturbance, changing of microclimate due to vegetation loss, and increasing soil nitrogen through adding of geese droppings.

Soil invertebrates may have been removed as part of the initial grubbing treatment. This is similar to what has been suggested to be the reason for declines in benthic invertebrates following natural geese foraging (Sherfy & Kirkpatrick, 2003). While it would explain the general loss of animals across taxa, it does, however, not explain why some taxa were seemingly unaffected. Recolonization may explain why the abundance of highly movable taxa like the Mesostigmata were unaffected (Walter & Proctord, 2013), whilst the slow moving Oribatida (Maraun & Scheu, 2000) were negatively affected. Further, the placement of animals within the soil layers may have led to varying responses, with animals deeper in the soil being less likely targeted by grubbing.

Destruction or change of habitats by grubbing may have a negative impact on invertebrate numbers, as seen for spiders in northern Canada (Milakovic & Jefferies, 2003). Further destruction that changes the soil structure, as seen with tillage, may be detrimental to invertebrates (Hülsmann & Wolters, 1998). Oribatida may be particularly vulnerable to such changes, as has been seen in highly disturbed imported soils in the Pyramiden settlement on Svalbard, where Oribatida are almost non-existent (Coulson et al., 2015). Though the stressor in that example was manmade (Coulson et al., 2015), geese grubbing may potentially lead to disturbances in soil structure, which may explain why Oribatida were negatively associated with goose grubbing in my study.

Increased drought stress and temperature fluctuations due to removal of vegetation may also negatively affect soil invertebrate abundance. Moss layers are known to regulate temperatures and maintain moisture (Gornall et al., 2007; Park et al., 2018; Van der Wal et al., 2001). The

direct effect of moisture and temperature on either system cannot be confirmed as moisture and temperature data was lost due to equipment failure. Yet I can assume that conditions in *Dryas*-dominated tundra are drier compared to moss-dominated tundra as the sites were chosen based on key plant species and soil moisture characteristics (SVALBARDFLORA, n.d). Thus, effects on soil invertebrates may be more prominent in *Dryas*-dominated tundra while high moisture levels in moss-dominated tundra may balance treatment effects.

Fertilization has been found to increase invertebrate abundance (Hågvar & Klanderud, 2009) or have a neutral (Milakovic & Jefferies, 2003) or nuanced (Zmudczyńska-Skarbek et al., 2015) effect upon soil animal abundance. It is therefore unlikely to have caused the declines seen in my study. As Arctic vegetation has a slow turnover rate, an increase in soil animals due to an increase in food availability is unlikely to have happened in the one-year period from first fertilisation to sampling.

It should be considered that in this study I simulated the grubbing of geese by removing plant matter in a standardized way, grubbing the plots evenly. Geese would likely have grubbed selectively, targeting the roots of certain preferred plant (Fox et al., 2005; Van der Wal et al., 2020). As such, natural geese grubbing may to a larger degree affect soil invertebrate taxa associated with plant roots, than what was the case for the simulated grubbing in this study.

## 4.2 Warming showed varied effects on invertebrate abundance

Effects of warming were only found in *Dryas*-dominated tundra with a decrease in trombidiform mites, and an increase in the mite family *Ascidae*. As expected, a decline in total abundance of Collembola was also observed, although the latter was not significant (P<0.093). The possible effect of warming on Collembola was expected as matching results were found in other warming studies (Convey et al., 2002; Coulson et al., 1996; Dollery et al., 2006; Hågvar & Klanderud, 2009; Krab et al., 2013). *Folsomia quadrioculata* did not decrease in my study, in contrast to studies in the Subarctic showing a strong decrease in response to warming (Krab et al., 2013). However, Krab et al. (2013) increased temperature by 4°C, which is likely a higher temperature increase than what was achieved in my study. Scheiner (in prep) found that similar OTCs setup at a nearby site, only achieved a temperature increase of 0.5-1 °C. Supporting my findings, a warming study in Endalen, (Dollery et al., 2006) close to my field site in Adventdalen, did not find a decrease in *F. quadrioculata*. They did however find significant declines in *H. tullbergi,* that were not apparent in my study (Table 1 and 2). However*,* as I found on average five individuals of *H. tullbergi* per plot, I might not be able to detect any effects due

to too small numbers. In accordance to my study, (Dollery et al., 2006) found no effect of warming on Mesostigmatid mites. However, the lack of effect in my study may be the result of opposite reactions to warming in the two main Mesostigmatid families in *Dryas*-dominated tundra (*Zerconidae*, *Ascidae*). The mean number of animals found in each family was small, however, and may have led to unreliable results (*Zerconidae* 6 Arctoceus 4). Overall it should be noted that the changes in invertebrate abundance in this study were found from warming treatments only covering the shoulder seasons, not full seasons or years like previous studies (Alatalo et al., 2017; Convey et al., 2002; Coulson et al., 1996; Dollery et al., 2006; Hågvar & Klanderud, 2009; Markkula et al., 2019), showing the importance of warming even in these short periods.

## 4.3 ROS had a negative effect on Trombidiformes and *H. tullbergi*

Icing negatively affected Trombidiformes and *H. tullbergi* abundance in *Dryas*-dominated tundra but not in moss-dominated tundra. The decline in *H. tullbergi* is similar to what was observed by Coulson et al. (2000), yet unlike Coulson et al. (2000), my study found no effect of ROS on *F. quadrioculata*. This may be a result of differences in the studies where Coulson restricted recolonisation by creating sand barriers (Coulson et al., 2000), which the overall experimental setup of the larger TERRA project did not allow for. Further, *F. quadrioculata* may be more resilient to icing events compared to H. *tullbergi*, being recorded to likely having a lower winter mortality than *H. tullbergi* (Birkemoe & Sømme, 1998). *Diapterobates notatus* had no effect of icing in either mine or Coulson et al. (2000) study. In addition, natural icing events may obscure the difference between the ROS plots and the control plots in my study. Overall were Collembola as well as most other taxa not affected by the ROS treatment. This weakened my hypothesis of Collembola being more vulnerable to icing than Oribatida.

## 4.4 Combinations of treatments showed conflicting effects

The combined effect of two treatments, i.e. grubbing and warming, and grubbing and icing, did not increase the negative effects of either factor in *Dryas*-dominated tundra. Rather, the negative effects of warming and grubbing were reduced within the combination plots, compared to the effect of either stress factor within the individual treatment plots. Similarly, ROS combined with grubbing treatment did not give a larger negative effect on Trombidiformes and *H. tullbergi* than seen with the two treatments alone. The reduction in the individual factors effect in the *Dryas*-dominated tundra, combination plots may be explained by both treatments in the individual plots being negatively associated with the animals' abundances (Table 1). The logic

being that the animals that died or were displaced due to one treatment, no longer could die, or be displaced due to the second treatment; thus, leading to an overall less negative effects of either treatment within a combination plot, compared to the negative effects of the same treatment in a single treatment plot. If this is the case, it may indicate that besides the subgroupings that die due to one treatment, there are also certain subgroupings within each taxon that are more resilient, and able to withstand multiple stressors at once, which indicates a certain resilience in the system to multiple stressors.

In the moss-dominated tundra, I found that the combined effect of grubbing and icing indicated a negative effect ($P<0.077$) on total *D. notatus* numbers, an effect not found in either of the treatments alone. Similarly, the effect of warming and grubbing also indicated a negative effect on *D. notatus* adults ($P<0.090$). Again, this effect was not encountered by each treatment alone. These negative reactions may therefore be a result of the combined effect of two treatments. For instance, warming may be insufficient to cause water loss, but combined with grubbing, water loss might be much more severe. Alternatively, icing itself may not be sufficient to affect the abundance of animals, unless the ground was grubbed enabling the ice to penetrate the soil more thoroughly. While other studies found that the *D. notatus* are resilient to the negative effects of both warming (Dollery et al., 2006; Hodkinson et al., 1996) and icing (Coulson et al., 2000), my study highlights that the combined effect of stressors may prove too much for the animals. Overall, these findings support my hypothesis, as treatments did interact with each other, changing invertebrate communities in ways not predicted by each treatment alone These findings indicate the importance of studying combinations of stressors as they also occur in nature.

## 4.5 Most of the treatment effects were found in the *Dryas*-dominated tundra

Supporting my hypothesis, soil invertebrate abundances were more often affected by ROS and warming treatments in the *Dryas*-dominated tundra compared to the moss-dominated tundra. However contrary to my hypothesis, grubbing was found to affect similar amounts of soil invertebrate taxa in both habitats.

Grubbing affected similar numbers of taxa in the two habitat types, three in the *Dryas*-dominated tundra and two in the moss-dominated tundra, as well as near significant effects on one taxon in the *Dryas*-dominated tundra, and two in the moss-dominated tundra. This could indicate that habitat does not strongly affect the number of taxa affected by grubbing.

Warming-induced invertebrate decreases are often theorised to be a result of water loss due to warming (Alatalo et al., 2017; Coulson et al., 1996; Dollery et al., 2006; Hodkinson et al., 1996; Krab et al., 2013). This may explain why my results indicated Collembola abundances to be negatively affected ($P<0.093$) by warming in the mesic *Dryas*-dominated tundra, yet not within the moist moss-dominated tundra, while the oribatid mites were not negatively affected at either site, as predicted in my hypothesis. This is in line with Hodkinson (et al 1996) who found that moisture had little effect on warming-related mortality in Svalbard mites, while it increased the Collembolas' ability to survive elevated temperatures. The latter being supported by Coulson et al. (1996) who found Collembola to be negatively associated with warmer and presumably dryer conditions. Water loss may also explain why I only observed declines in Trombidiformes abundance in the *Dryas*-dominated tundra (Table 1). Prostigmata are the only Trombidiformes on Svalbard (Seniczak et al., 2020) and have been theorised to be susceptible to warming due to some species having a permeable membrane (Dollery et al., 2006). Dollery et al. (2006) did not see this effect in their study, rather Prostigmatic were mites increased in abundance in their OTC plots. This increase was theorised by Dollery et al. (2006) to be the result of an abundance of aphid prey capable of mitigating for the extra water loss due to the warming treatment. I cannot, however, assess the potential influence of aphid abundances on Prostigmata in my study, as their abundance was not measured.

The variation in invertebrate responses that I found may also be explained by different effects of the OTCs on ground temperatures. Moss-dominated tundra had a thicker moss cover (S. Lang, personal communication, May 2024), potentially limiting the effect of the OTCs on the overall temperature of the habitat (Gornall et al., 2007; Van der Wal et al., 2001). This difference in mosses may explain why *Ascidae* as well as Oribatida and total mite numbers, though the last two were not significant ($P<0.109$ and $P<0.107$, respectively), were positively associated with the warming treatment in *Dryas*-dominated tundra but not in the moss-dominated tundra.

Though this increase in oribatid mites in the *Dryas*-dominated tundra was not significant ($P<0.109$) , it should still be considered (Dollery et al., 2006; Thakur et al., 2023). Oribatid mites have limited migration (Maraun & Scheu, 2000), and Arctic oribatid mites typically have a multi-year life cycle (Walter & Proctord, 2013), so the increases found in my study are likely caused by increased juvenile abundance. As such, the full extent of warming related increases in abundance cannot be assessed before these animals reach adulthood. Secondly, the reduction in Collembola numbers, and the potential increase in Oribatida numbers may signify a

community shift with more oribatid mites and less Collembola as hypothesised in (Thakur et al., 2023) and (Hodkinson et al., 1996) with unknown consequences for the larger system.

Further, the effect of icing and combination plots also varied between habitats. Icing was only found to have changed animal abundances in the *Dryas*-dominated tundra, and combination plot effects varied between habitats, having negative effects in the moss-dominated tundra and positive effects on the abundance of taxa in the *Dryas*-dominated tundra. These findings add to my general conclusion that treatment effects are dependent upon habitat type.

## 4.6 Future consequences

Warming, icing, and grubbing by geese are all expected to increase in the future (Graham et al., 2017; Hansen et al., 2011; Hansen et al., 2014; Jensen et al., 2014; Jensen et al., 2008; Stocker et al., 2013), potentially affecting the soil biota and the systems and animals that relay on them.

Svalbard pink footed geese populations have increased from 25000 in 1990 to over 70 000 in 2020 (Heldbjerg et al., 2020; Madsen et al., 2017). Even though Svalbard pink footed geese populations seem to have stabilised as a result of international management practises (Madsen et al., 2017), climate change is expected to further increase geese population growth (Jensen et al., 2014; Jensen et al., 2008). My study indicates that an increase in grubbing species of Arctic geese will likely cause declines in Collembola and mite abundances. Such decline is likely to reduce the quality and/or quantity of the ecosystem services these animals may provide, potentially affecting factors like nutrient turnover and carbon cycling (Koltz et al., 2018), with potential wider consequences for vegetation and carbon emissions.

The full extent of the effect of geese grubbing will depend upon the habitat's recovery time and may vary between *Dryas*-dominated and moss-dominated tundra. Moss-dominated tundra vegetation is known to recover from grubbing faster than *Dryas*-dominated tundra (Speed et al., 2010; Van der Wal et al., 2020) which may also result in faster recovery in invertebrate populations. Moss-dominated tundra is, however, more favoured as a feeding habitat than *Dryas*-dominated tundra and may therefore experience more rapid grubbing events (Van der Wal et al., 2020) potentially counteracting the shorter recovery time. While my study investigated the short-term effects of grubbing on invertebrates, long-term effects may differ. For example, geese droppings change nutrient availability over time, potentially increasing numbers of certain invertebrate taxa in proximity to geese breeding grounds (Flemming et al., 2022).

The effects of increased icing and warming will likely grow more severe in the future, as climate change progress (Hansen et al., 2011; Hansen et al., 2014; Stocker et al., 2013). In my study icing was found to have limited effect on soil invertebrates, only affecting two taxa, potentially indicating an overall robustness in the invertebrate community against this stressor. Warming was found to reduce populations of Collembola yet potentially increase Oribatida in *Dryas*-dominated tundra, potentially leading to a community shift (Hodkinson et al., 1996; Thakur et al., 2023), with potential effects on the soil tundra ecosystem. Both these treatments were only found to affect invertebrates in *Dryas*-dominated tundra, possibly indicating soil invertebrates in this system to be more vulnerable to this type of ecosystem change than in the moss-dominated tundra.

While all the above factors affected abundances of soil invertebrates, in nature they are likely to be affected by multiple environmental factors at once. The negative effects of warming and grubbing, as well as grubbing and ROS were reduced within the combination plots in the *Dryas*-dominated tundra compared to the effect of either stress factor within the individual treatment plots. This may indicate that there are subgroups within these taxa that are especially resilient to changing environmental factors and able to withstand multiple stressors at once. Conversely, the negative reactions to combined treatments in the moss-dominated tundra may show that some taxa resistant to one stressor, may be overwhelmed by the effect of multiple stressors at once. Either scenario may have importance for the future of soil ecosystem services and should be considered in future analyses.

The rate of these stressors will be an important determinator for the invertebrate communities in the coming decades. Some of these taxa need several years to reach adulthood (Birkemoe & Sømme, 1998) and may therefore be affected by multiple stress events throughout their life cycle. Further, the rate of stressors may have wider consequences for environmental factors like vegetation structure and soil carbon content (Van Der WAL et al., 2007; Van der Wal et al., 2020). This may over time create new habitats, influencing the soil invertebrates in ways beyond the direct effects of single environmental factors.

# Conclusion

This study found geese grubbing to suppress invertebrate abundances, amongst these the abundance of oribatid mites in *Dryas*-dominated tundra. Further, warming negatively affected overall Collembola abundance in *Dryas*-dominated tundra, whereas oribatid mites were not negatively affected in either habitat. ROS showed no negative effect on total Collembola abundance, though a decline in *H. tullbergi* was observed. Moss-dominated tundra was found to be more resilient towards all treatments, treatments having effects on fewer taxa. Combinations of treatments were found to change communities in ways not predicted by each treatment alone. In conclusion, this study highlights the importance of geese grubbing, shoulder season warming and ROS as controlling agents for soil invertebrate populations, with potential wider implications for the Arctic ecosystem. Additionally, this study illustrates the importance of looking at multiple environmental factors simultaneously when assessing potential shifts in the soil arthropod community, as well as the importance of habitat for determining these effects. Importantly, long-term follow-up studies are needed both to assess the recovery time of the system after a grubbing or ROS event, and to assess the effects of successive events and their long-term consequences on both soil invertebrates and ecosystem services as temperature increases.

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# Appendix

**Table 3.** Shows the placements of all plots, for 60 plots total. With shortening. M stands for moss-dominated tundra. D for *Dryas*-dominated tundra. Numbers are for Site numbers within tundra habitat. W= warming, G= grubbing, R= ROS/icing.

| PLOT | EAST/LONG | NORTH/LAT | Plot | EAST/LONG | NORTH/LAT |
|---|---|---|---|---|---|
| M6WG | 16.02425 | 78.17323 | D2WG | 16.05076 | 78.17189 |
| M6C | 16.02419 | 78.17322 | D2G | 16.05094 | 78.17191 |
| M6WG | 16.02416 | 78.17314 | D2C | 16.05087 | 78.17188 |
| M6R | 16.02412 | 78.1731 | D2W | 16.05104 | 78.17187 |
| M6G | 16.02419 | 78.1731 | D2R | 16.05089 | 78.17185 |
| M6RG | 16.02428 | 78.17313 | D2RG | 16.05094 | 78.17182 |
| M7C | 16.02557 | 78.17299 | D3R | 16.05384 | 78.17121 |
| M7RG | 16.02567 | 78.17291 | D3WG | 16.054 | 78.17123 |
| M7WG | 16.02576 | 78.17288 | D3W | 16.05392 | 78.1713 |
| M7R | 16.02581 | 78.1729 | D3G | 16.05418 | 78.17123 |
| M7W | 16.02579 | 78.17293 | D3C | 16.0539 | 78.17126 |
| M7G | 16.02588 | 78.17287 | D3RG | 16.05404 | 78.17128 |
| M1G | 16.02613 | 78.17307 | D7RG | 16.06252 | 78.17071 |
| M1C | 16.02625 | 78.17304 | D7WG | 16.06241 | 78.17066 |
| M1W | 16.02637 | 78.17302 | D7G | 16.06266 | 78.17065 |
| M1R | 16.02655 | 78.17302 | D7C | 16.06265 | 78.17071 |
| M1RG | 16.02649 | 78.17297 | D7W | 16.062;78 | 78.17066 |
| M1WG | 16.02637 | 78.17298 | D7R | 16.06264 | 78.17072 |
| M8W | 16.0268 | 78.17244 | D6RG | 16.06363 | 78.17081 |
| M8RG | 16.02703 | 78.17245 | D6G | 16.06379 | 78.17083 |
| M8G | 16.02695 | 78.17242 | D6W | 16.06382 | 78.17078 |
| M8WG | 16.02708 | 78.17241 | D6C | 16.06376 | 78.17075 |
| M8R | 16.02687 | 78.17239 | D6WG | 16.06361 | 78.17076 |
| M8C | 16.02683 | 78.17236 | D6R | 16.06365 | 78.17078 |
| M2W | 16.02962 | 78.17236 | D5RG | 16.06377 | 78.17114 |
| M2C | 16.02963 | 78.17239 | D5WG | 16.06361 | 78.1711 |
| M2R | 16.02984 | 78.17235 | D5C | 16.0638 | 78.17112 |
| M2WG | 16.02982 | 78.17231 | D5W | 16.06376 | 78.1711 |
| M2G | 16.02994 | 78.17229 | D5R | 16.06359 | 78.17108 |
| M2RG | 16.02979 | 78.17225 | D5G | 16.06374 | 78.17107 |

**Table 4.** Negative binomial regression model results. Here for *Dryas*-dominated tundra main effects, Std. Error and z value included. Each row represents a single negative binomial GLM test where the taxa is the response variable, the warming, rain-on-snow (ROS) and grubbing are the predictor variables and the grubbing x warming and grubbing x ROS are the interaction terms. In other words, the model can be explained by $Y=\beta0+\beta1W+\beta2R+\beta3G+\beta4(G\times R)+\beta5(G\times W)+\epsilon$ where warming= W, ROS = R and Grubbing, Y = abundance of an invertebrate taxa for example collembola, and Beta is the effect of the different treatments on the invertebrate abundances. Significant p-values are marked in bold, near significant values are underlined (N=5).

| Taxa (response variable) | Warming | | | | ROS | | | | Grubbing | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | z value | Pr(>\|z\|) | Estimate | Std. Error | z value | Pr(>\|z\|) | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Total mites | 0.447 | 0.277 | 1.613 | 0.107 | 0.243 | 0.277 | 0.876 | 0.381 | -0.591 | 0.278 | -2.123 | **0.034*** |
| Mesostigmata | -0.112 | 0.469 | -0.239 | 0.811 | -0.047 | 0.468 | -0.099 | 0.921 | -0.693 | 0.483 | -1.434 | 0.152 |
| *Zerconidae* | -0.909 | 0.566 | -1.604 | 0.109 | -0.305 | 0.548 | -0.557 | 0.577 | -1.047 | 0.571 | -1.833 | 0.067. |
| *Ascidae* | 1.386 | 0.588 | 2.357 | **0.018*** | 0.847 | 0.605 | 1.401 | 0.161 | 0.3677 | 0.629 | 0.585 | 0.559 |
| Trombidiformes | -0.618 | 0.312 | -1.983 | **0.047*** | -0.678 | 0.313 | -2.165 | **0.030*** | -0.827 | 0.317 | -2.609 | **0.009**** |
| Oribatida | 0.415 | 0.259 | 1.604 | 0.109 | 0.068 | 0.259 | 0.262 | 0.794 | -0.820 | 0.263 | -3.122 | **0.002**** |
| *Diapterobates notatus* | 0.395 | 0.668 | 0.591 | 0.555 | -0.795 | 0.686 | -1.158 | 0.247 | -0.572 | 0.681 | -0.839 | 0.401 |
| Adult *D. notatus* | 1.281 | 0.837 | 1.531 | 0.126 | 0.337 | 0.887 | 0.379 | 0.705 | >0.001 | 0.919 | 0.000 | 1.000 |
| Juvenile *D. notatus* | 0.261 | 0.685 | 0.381 | 0.703 | -0.999 | 0.709 | -1.408 | 0.159 | -0.642 | 0.699 | -0.918 | 0.359 |
| *Peloppiidae* | 0.064 | 0.466 | 0.137 | 0.891 | -0.012 | 0.466 | -0.026 | 0.979 | -0.664 | 0.472 | -1.405 | 0.160 |
| Unidentified mites | 0.598 | 0.412 | 1.452 | 0.147 | 0.562 | 0.412 | 1.364 | 0.173 | -0.405 | 0.414 | -0.978 | 0.328 |
| Total Collembola | -0.520 | 0.309 | -1.682 | <u>0.093.</u> | -0.238 | 0.309 | -0.772 | 0.440 | -0.498 | 0.309 | -1.610 | 0.107 |
| Entomobryomorpha | -0.554 | 0.372 | -1.491 | 0.136 | -0.239 | 0.371 | -0.643 | 0.520 | -0.710 | 0.372 | -1.909 | <u>0.056.</u> |
| *Folsomia quadrioculata* | -0.438 | 0.308 | -1.420 | 0.156 | 0.158 | 0.305 | 0.517 | 0.605 | -0.492 | 0.309 | -1.595 | 0.111 |
| *Poduromorpha* | -0.239 | 0.454 | -0.527 | 0.598 | -0.228 | 0.454 | -0.498 | 0.619 | -0.339 | 0.455 | -0.744 | 0.457 |
| *Hypogastrura tullbergi* | -0.319 | 0.344 | -0.925 | 0.355 | -0.916 | 0.373 | -2.459 | **0.014*** | -2.909 | 0.653 | -4.453 | **>0.001**** |

**Table 5.** Negative binomial regression model results. Here for *Dryas*-dominated tundra interaction terms, Std. Error and z value included (N=5). Each row represents a single negative binomial GLM test where the taxa is the response variable, the warming, rain-on-snow (ROS) and grubbing are the predictor variables and the grubbing x warming and grubbing x ROS are the interaction terms. In other words, the model can be explained by $Y=\beta 0+\beta 1W+\beta 2R+\beta 3G+\beta 4(G\times R)+\beta 5(G\times W)+\epsilon$ where warming= W, ROS = R and Grubbing, Y = abundance of an invertebrate taxa for example Collembola, and Beta is the effect of the different treatments on the invertebrate abundances. Significant p-values are marked in bold,  near significant values are underlined (N=5).

| Taxa (response variable) | Grubbing X warming | | | | Grubbing X ROS | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | z value | Pr(>\|z\|) | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Total mites | -0.111 | 0.393 | -0.283 | 0.777 | -0.043 | 0.393 | -0.110 | 0.912 |
| Mesostigmata | 0.676 | 0.675 | 1.001 | 0.317 | -0.049 | 0.686 | -0.071 | 0.943 |
| *Zerconidae* | 1.047 | 0.820 | 1.277 | 0.202 | 0.200 | 0.815 | 0.245 | 0.806 |
| *Ascidae* | -0.396 | 0.811 | -0.488 | 0.626 | -0.927 | 0.856 | -1.083 | 0.279 |
| Trombidiformes | 0.980 | 0.450 | 2.196 | **0.028*** | 1.237 | 0.448 | 2.761 | **0.006**** |
| Oribatida | 0.023 | 0.370 | 0.063 | 0.950 | 0.408 | 0.370 | 1.104 | 0.270 |
| *Diapterobates  notatus* | -0.100 | 0.957 | -0.104 | 0.917 | 0.977 | 0.970 | 1.007 | 0.314 |
| Adult *D. notatus.* | -1.504 | 1.263 | -1.191 | 0.234 | -0.154 | 1.264 | -0.122 | 0.903 |
| Juvenile *D. notatus* | 0.099 | 0.982 | 0.101 | 0.920 | 1.181 | 1.001 | 1.179 | 0.238 |
| *Peloppiidae* | 0.745 | 0.663 | 1.123 | 0.261 | 0.645 | 0.664 | 0.972 | 0.331 |
| Unidentified mites | -0.120 | 0.583 | -0.205 | 0.838 | -0.245 | 0.584 | -0.420 | 0.675 |
| Total Collembola | 0.597 | 0.438 | 1.363 | 0.173 | -0.067 | 0.438 | -0.152 | 0.879 |
| *Entomobryomorpha* | 0.860 | 0.526 | 1.634 | 0.102 | -0.102 | 0.527 | -0.193 | 0.847 |
| *Folsomia quadrioculata* | 0.623 | 0.437 | 1.426 | 0.154 | -0.277 | 0.437 | -0.634 | 0.526 |
| *Poduromorpha* | -0.034 | 0.650 | -0.052 | 0.959 | 0.132 | 0.647 | 0.204 | 0.838 |
| *Hypogastrura tullbergi* | 1.417 | 0.799 | 1.774 | 0.076. | 2.526 | 0.784 | 3.223 | **0.001**** |

**Table 6.** Negative binomial regression model results. Here for moss-dominated tundra site predictor variable, Std. Error and z value included (N=5). Each row represents a single negative binomial GLM test where the taxa is the response variable, the warming, rain-on-snow (ROS) and grubbing are the predictor variables and the grubbing x warming and grubbing x ROS are the interaction terms. In other words, the model can be explained by $Y=\beta_0+\beta_1W+\beta_2R+\beta_3G+\beta_4(G\times R)+\beta_5(G\times W)+\epsilon$ where warming= W, ROS = R and Grubbing, Y = abundance of an invertebrate taxa, for example Collembola, and Beta is the effect of the different treatments on the invertebrate abundances. Significant p-values are marked in bold, near significant values are underlined (N=5).

| Taxa (response variable) | Warming | | | | ROS | | | | Grubbing | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | z value | Pr(>\|z\|) | Estimate | Std. Error | z value | Pr(>\|z\|) | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Total Mites | -0.030 | 0.227 | -0.132 | 0.895 | 0.199 | 0.227 | 0.880 | 0.379 | -0.380 | 0.228 | -1.663 | <u>0.096.</u> |
| Mesostigmata | -0.288 | 0.446 | -0.644 | 0.519 | 0.069 | 0.430 | 0.160 | 0.873 | -0.442 | 0.455 | -0.971 | 0.332 |
| *Zerconidae* | 0.2231 | 0.719 | 0.310 | 0.756 | 0.629 | 0.695 | 0.904 | 0.366 | -0.693 | 0.816 | -0.849 | 0.396 |
| *Ascidae* | -0.598 | 0.504 | -1.186 | 0.235 | -0.288 | 0.479 | -0.600 | 0.548 | -0.357 | 0.484 | -0.737 | 0.461 |
| Trombidiformes | -0.483 | 0.360 | -1.342 | 0.179 | 0.065 | 0.344 | 0.188 | 0.851 | -0.357 | 0.356 | -1.003 | 0.316 |
| Oribatida | -0.119 | 0.253 | -0.470 | 0.639 | 0.053 | 0.253 | 0.210 | 0.834 | -0.408 | 0.255 | -1.602 | 0.109 |
| *Diapterobates notatus* | -0.334 | 0.329 | -1.014 | 0.311 | 0.113 | 0.317 | 0.355 | 0.722 | 0.165 | 0.316 | 0.521 | 0.602 |
| *Adult D. notatus* | -0.241 | 0.619 | -0.390 | 0.697 | 0.580 | 0.576 | 1.006 | 0.314 | 0.728 | 0.571 | 1.275 | 0.203 |
| *Juvenile D. notatus* | -0.360 | 0.342 | -1.052 | 0.293 | -0.058 | 0.331 | -0.176 | 0.860 | -0.058 | 0.331 | -0.176 | 0.860 |
| *Peloppiidae* | -0.162 | 0.319 | -0.506 | 0.613 | -0.495 | 0.323 | -1.534 | 0.125 | -0.757 | 0.326 | -2.322 | **0.020*** |
| Unidentified mites | 0.270 | 0.343 | 0.785 | 0.432 | 0.544 | 0.342 | 1.588 | 0.112 | -0.313 | 0.347 | -0.902 | 0.367 |
| Total Collembola | -0.054 | 0.296 | -0.184 | 0.854 | 0.092 | 0.296 | 0.312 | 0.755 | -0.231 | 0.297 | -0.778 | 0.437 |
| Entomobryomorpha | -0.032 | 0.316 | -0.100 | 0.920 | 0.058 | 0.316 | 0.185 | 0.854 | -0.293 | 0.317 | -0.925 | 0.355 |
| *Folsomia quadrioculata* | -0.198 | 0.341 | -0.581 | 0.561 | -0.005 | 0.340 | -0.015 | 0.988 | -0.790 | 0.344 | -2.295 | **0.022*** |
| Poduromorpha | -0.048 | 0.353 | -0.137 | 0.891 | 0.204 | 0.350 | 0.584 | 0.560 | -0.110 | 0.354 | -0.310 | 0.757 |
| *Hypogastrura tullbergi* | 0.095 | 0.474 | 0.201 | 0.841 | -0.598 | 0.498 | -1.201 | 0.230 | -0.856 | 0.511 | -1.674 | <u>0.094.</u> |

**Table 7.** Negative binomial regression model results. Here for *Dryas*-dominated tundra site interaction terms, Std. Error and z value included (N=5). Each row represents a single negative binomial GLM test where the taxa is the response variable, the warming, rain-on-snow (ROS) and grubbing are the predictor variables and the grubbing x warming and grubbing x ROS are the interaction terms. In other words, the model can be explained by $Y=\beta0+\beta1W+\beta2R+\beta3G+\beta4(G\times R)+\beta5(G\times W)+\epsilon$ where warming= W, ROS = R and Grubbing, Y = abundance of an invertebrate taxa for example collembola, and Beta is the effect of the different treatments on the invertebrate abundances. Significant p-values are marked in bold, near significant values are underlined (N=5).

| Taxa (response variable) | Grubbing X Warming | | | | Grubbing X ROS | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | z value | Pr(>\|z\|) | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Total mites | -0.004 | 0.323 | -0.013 | 0.990 | -0.230 | 0.323 | -0.714 | 0.475 |
| Mesostigmata | 0.442 | 0.647 | 0.683 | 0.495 | 0.373 | 0.626 | 0.595 | 0.552 |
| *Zerconidae* | -5.980e-16 | 1.122 | 0.000 | 1.000 | -0.069 | 1.081 | -0.064 | 0.949 |
| *Ascidae* | 0.731 | 0.708 | 1.033 | 0.301 | 0.693 | 0.680 | 1.020 | 0.308 |
| Trombidiformes | -0.035 | 0.529 | -0.067 | 0.947 | -0.113 | 0.503 | -0.225 | 0.822 |
| *Oribatida* | 0.182 | 0.360 | 0.504 | 0.614 | -0.036 | 0.360 | -0.099 | 0.921 |
| *Diapterobates notatus* | -0.858 | 0.485 | -1.770 | <u>0.077.</u> | -0.531 | 0.453 | -1.173 | 0.241 |
| Adult *D. notatus* | -0.929 | 0.866 | -1.073 | 0.283 | -1.382 | 0.815 | -1.696 | <u>0.090.</u> |
| Juvenile *D. notatus* | -0.845 | 0.523 | -1.614 | 0.107 | -0.190 | 0.475 | -0.400 | 0.689 |
| *Peloppiidae* | 0.625 | 0.458 | 1.364 | 0.173 | 0.417 | 0.465 | 0.898 | 0.369 |
| Unidentified mites | -0.496 | 0.492 | -1.008 | 0.313 | -0.777 | 0.491 | -1.584 | 0.113 |
| Total Collembola | -0.160 | 0.420 | -0.380 | 0.704 | 0.020 | 0.419 | 0.049 | 0.961 |
| Entomobryomorpha | -0.084 | 0.449 | -0.187 | 0.851 | 0.102 | 0.448 | 0.228 | 0.820 |
| *Folsomia quadrioculata* | 0.236 | 0.487 | 0.484 | 0.629 | 0.569 | 0.484 | 1.175 | 0.240 |
| *Poduromorpha* | -0.535 | 0.509 | -1.052 | 0.293 | -0.163 | 0.498 | -0.327 | 0.744 |
| *Hypogastrura tullbergi* | -1.137 | 0.792 | -1.435 | 0.151 | 0.473 | 0.742 | 0.637 | 0.524 |

**Table 8**. Ordistep forwards selection function, selecting for explanatory variables in moss-dominated tundra, based upon permutation tests. (N=30)

| Formula = species ~ 1 | | | | |
|---|---|---|---|---|
| | DF | AIC | F | Pr(>5) |
| + Grubbing | 1 | 48.598 | 2.6046 | 0.060. |
| + Warming | 1 | 50.127 | 1.0839 | 0.320 |
| + ROS | 1 | 50.508 | 0.7162 | 0.535 |

**Table 9.** Ordistep forwards selection function, selecting for explanatory variables in *Dryas*-dominated tundra, based upon permutation tests. (N=30)

| Formula = species ~ 1 | | | | |
|---|---|---|---|---|
| | DF | AIC | F | Pr(>5) |
| + Grubbing | 1 | 47.714 | 3.5195 | 0.020* |
| + Warming | 1 | 50.607 | 0.6224 | 0.695 |
| + ROS | 1 | 51.096 | 0.1591 | 0.990 |

**Table 10.** Redundancy Analysis for invertebrate orders in reduced model, in Moss-dominated tundra, based upon ordistep selection function recommendations. (N=30)

| **Model** | RDA (formula = spe ~ Grubbing ) | | | |
|---|---|---|---|---|
| | Df | Variance | F | Pr(>F) |
| Modell | 1 | 0.4255 | 2.6045 | 0.005** |
| Residual | 28 | 4.5745 | | |

**Table 11.** Redundancy Analysis for invertebrate orders in reduced model, in *Dryas*-dominated tundra, based upon ordistep selection function recommendations. (N=30)

| **Model** | RDA (formula = spe ~ Grubbing ) | | | |
|---|---|---|---|---|
| | Df | Variance | F | Pr(>F) |
| Modell | 1 | 0.5583 | 3.5195 | 0.006** |
| Residual | 28 | 4.4417 | | |

**Table 12.** Importance of components in principal component analysis (PCA), moss-dominated tundra. (N=30)

```
Eigenvalues, and their contribution to the variance

Importance of components:
                              PC1        PC2       PC3       PC4      PC5
Eigenvalue             2264.2614 1073.8504 104.42791 22.212577 7.124674
Proportion Explained      0.6522    0.3093   0.03008  0.006398 0.002052
Cumulative Proportion     0.6522    0.9615   0.99155  0.997948 1.000000
```

**Table 13.** Importance of components in principal component analysis (PCA), *Dryas*-dominated tundra. (N=30)

```
Eigenvalues, and their contribution to the variance

Importance of components:
                              PC1        PC2      PC3       PC4      PC5
Eigenvalue             8450.1473 5604.5076 144.6777 80.399080 39.757972
Proportion Explained      0.5901    0.3914   0.0101  0.005615  0.002776
Cumulative Proportion     0.5901    0.9815   0.9916  0.997224  1.000000
```
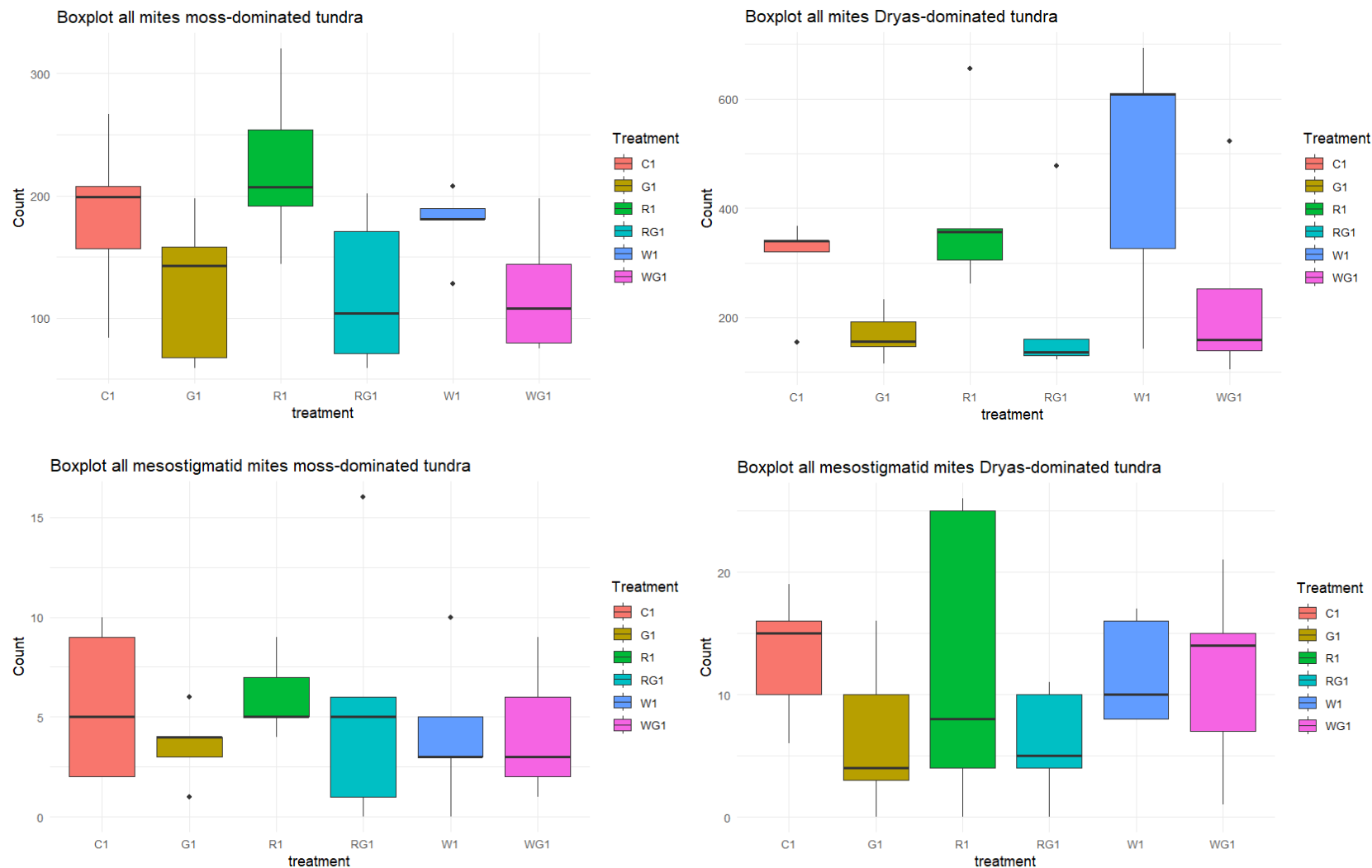
**Figure 6**. Boxplot for all mites and mesostigmatid mites in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing. The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers. (N=5).
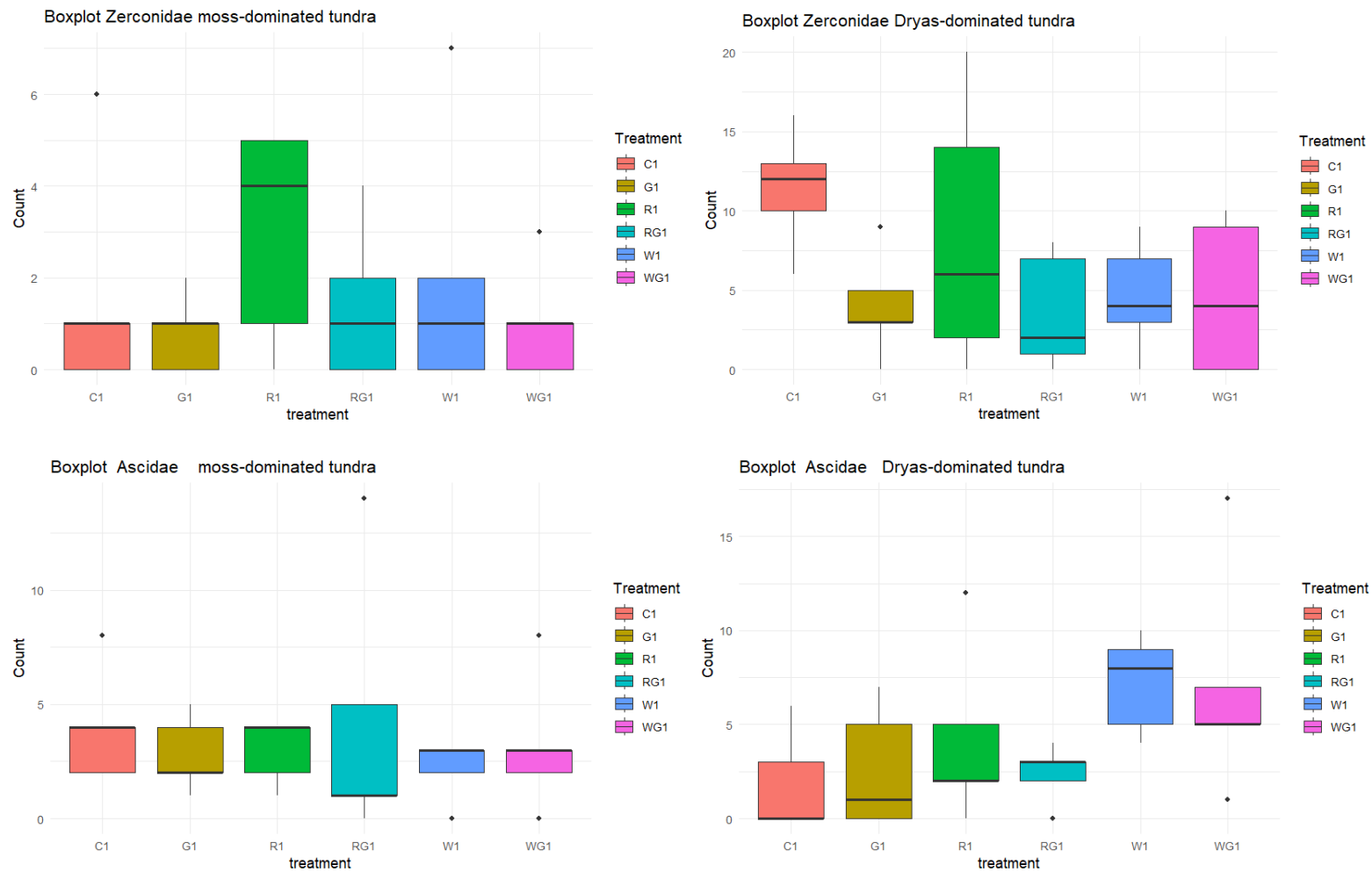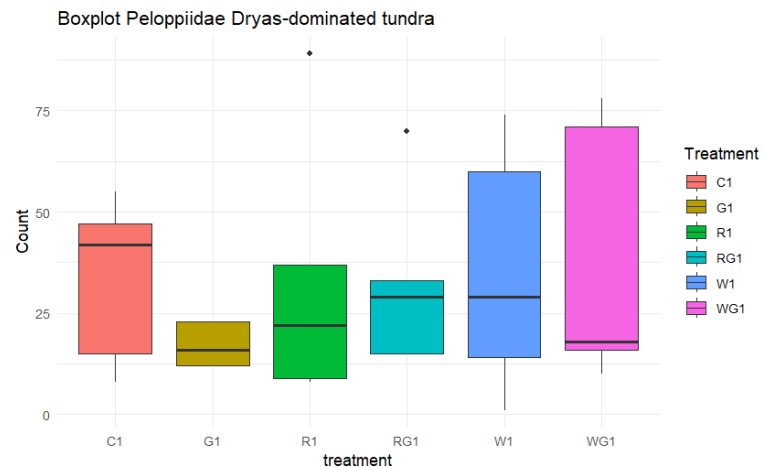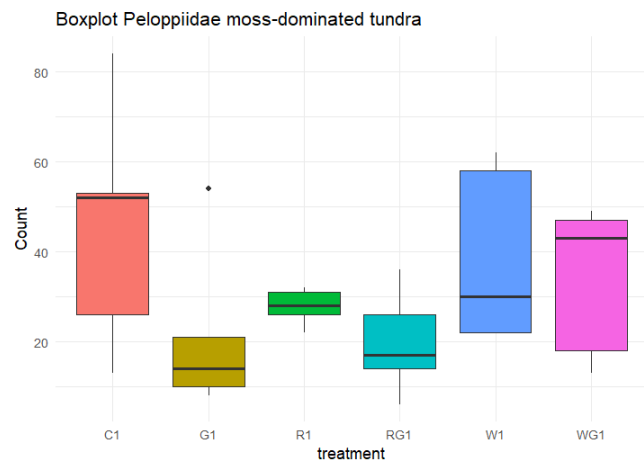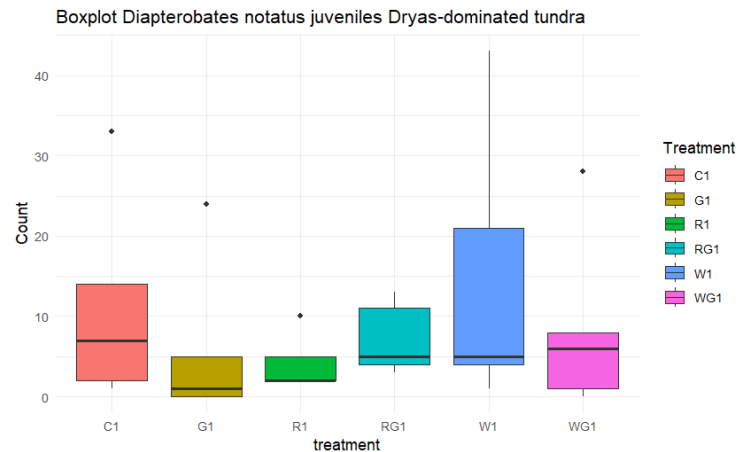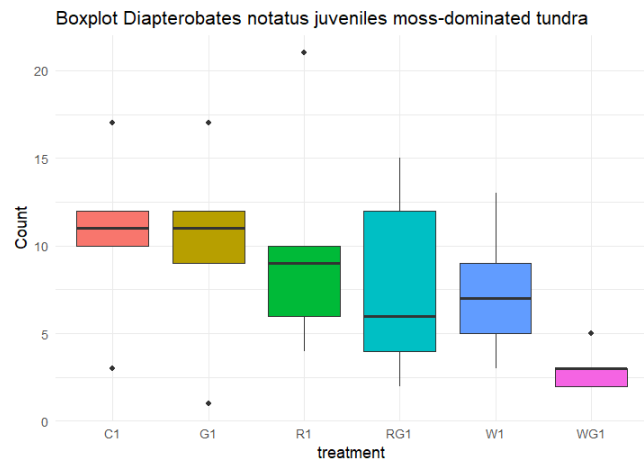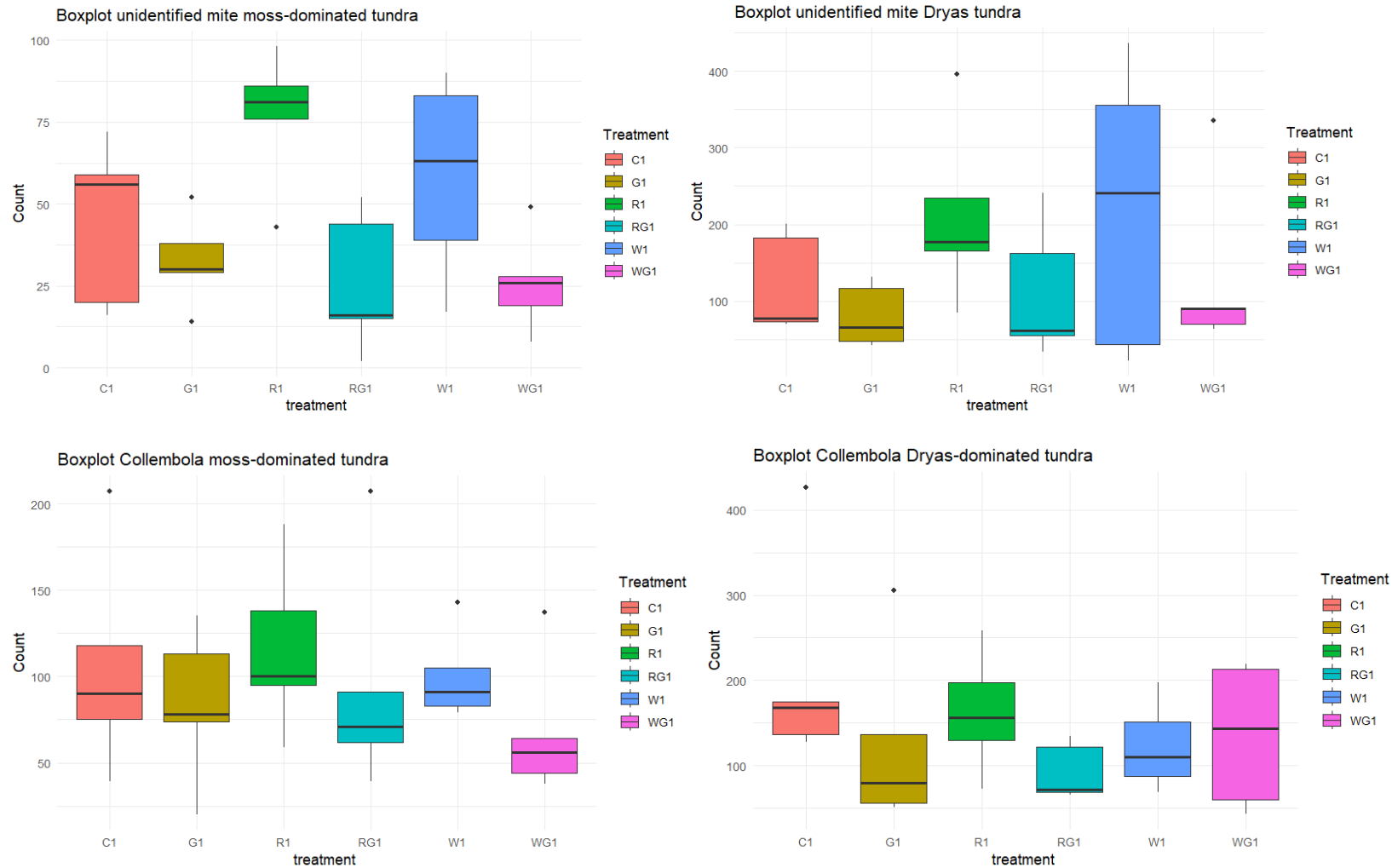
**Figure 7**. Boxplot for *Zerconidae* and *Ascidae* in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing. The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers. (N=5).
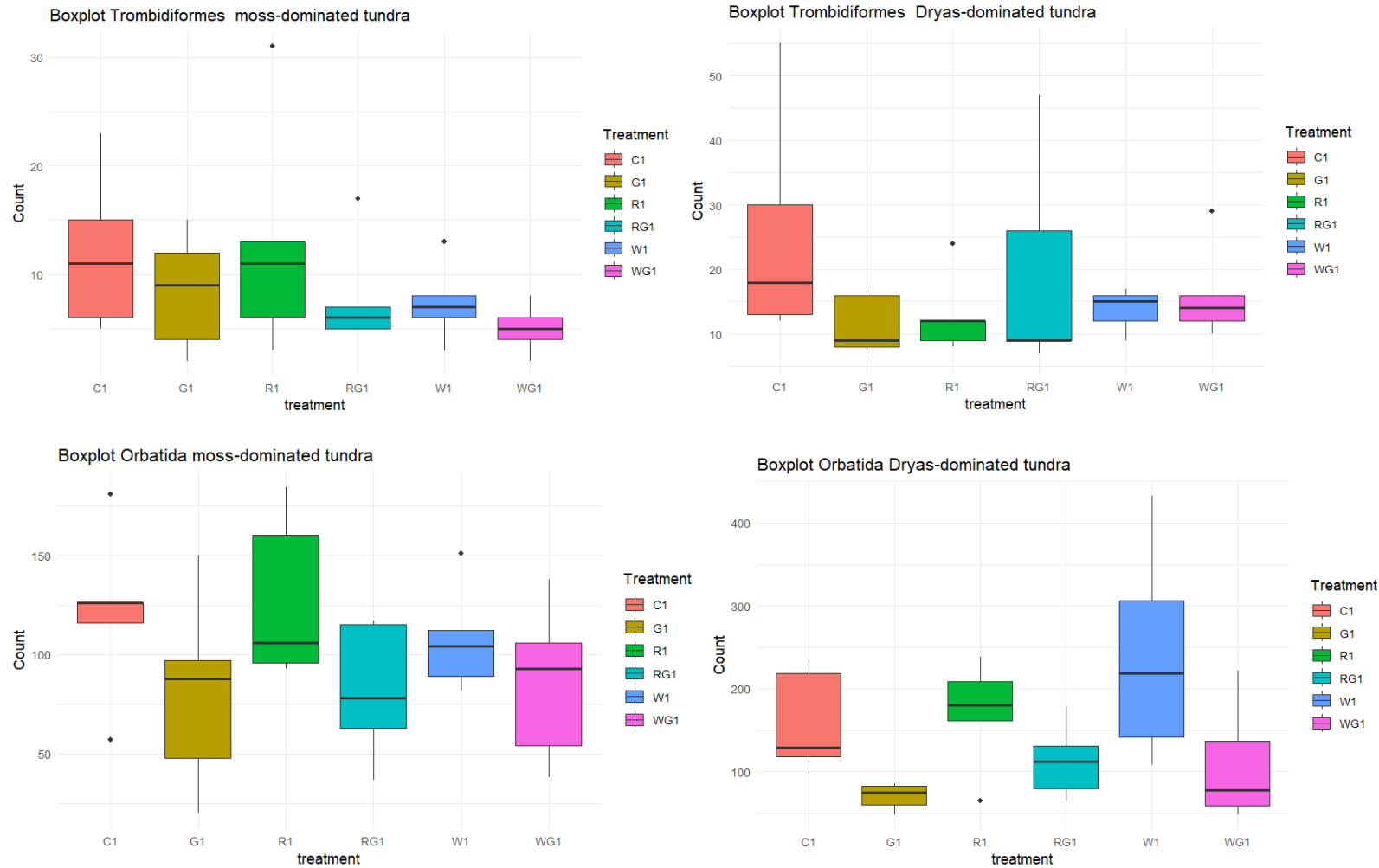
**Figure 8**. Boxplot for Trombidiformes and Oribatida in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing.  The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers.  (N=5).
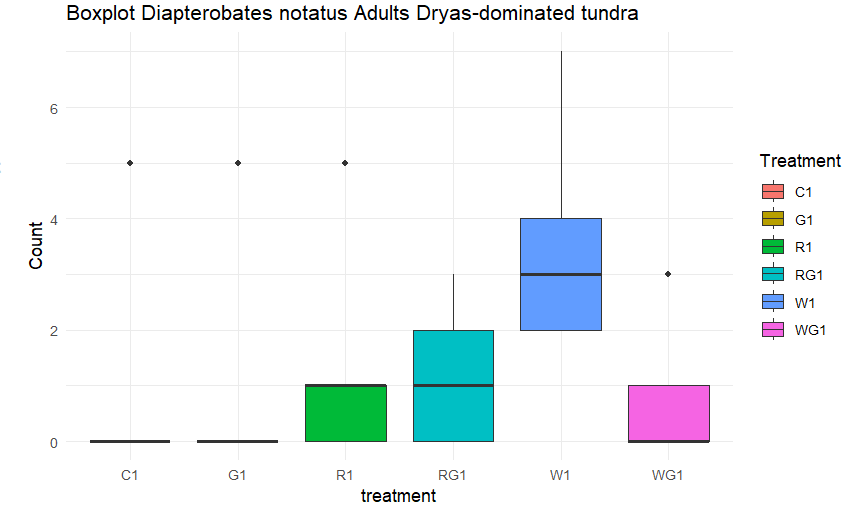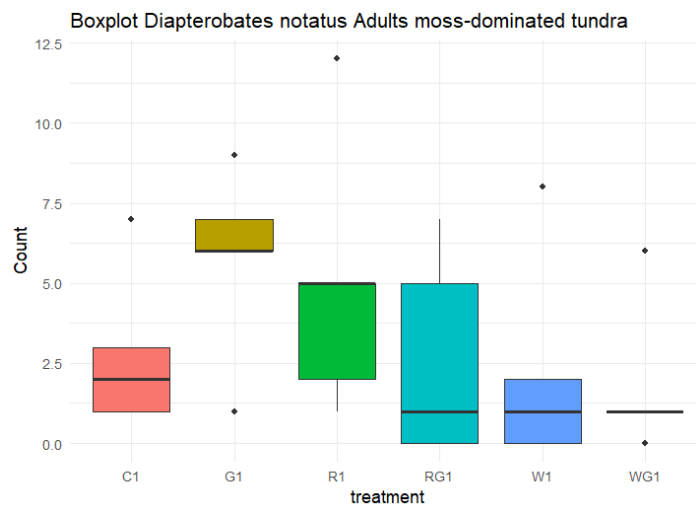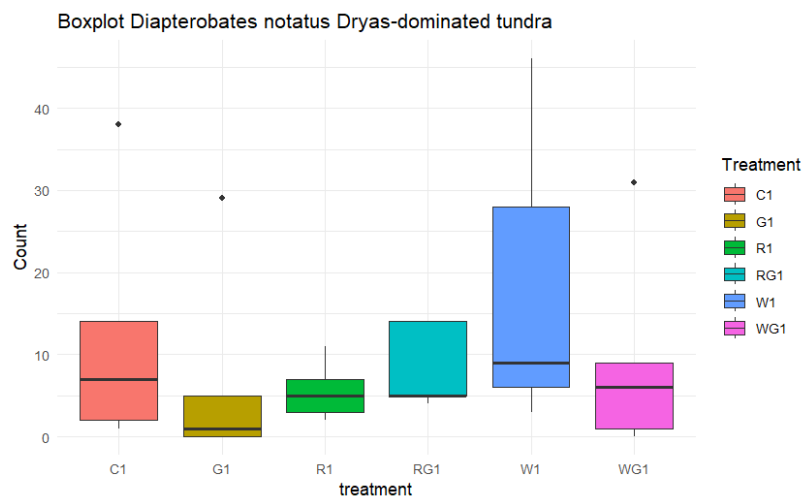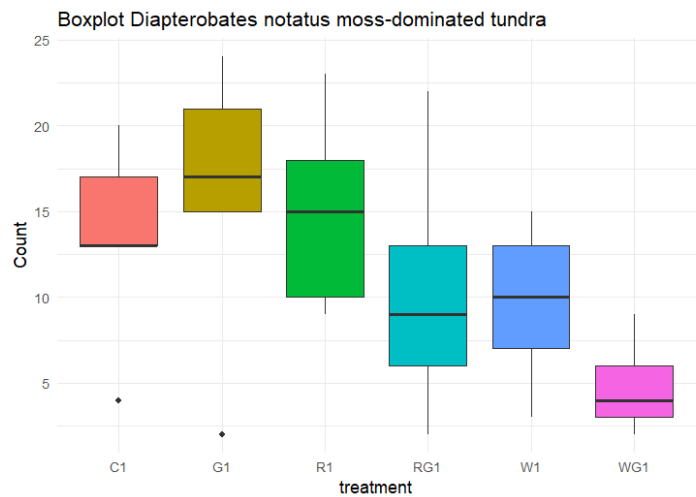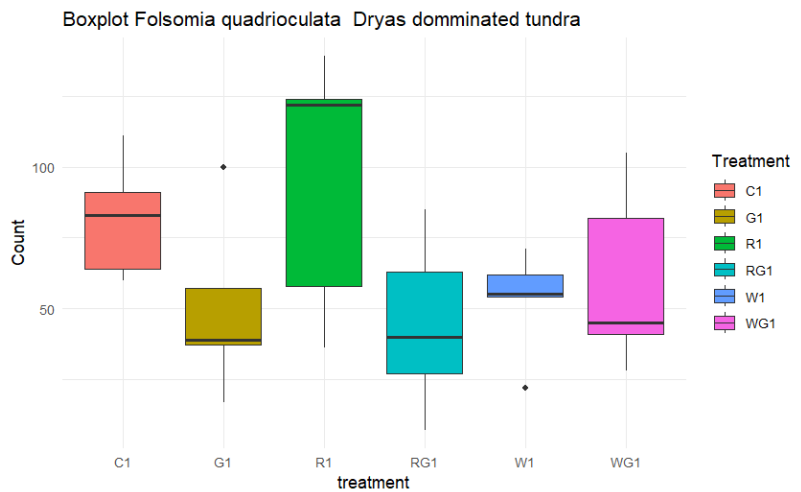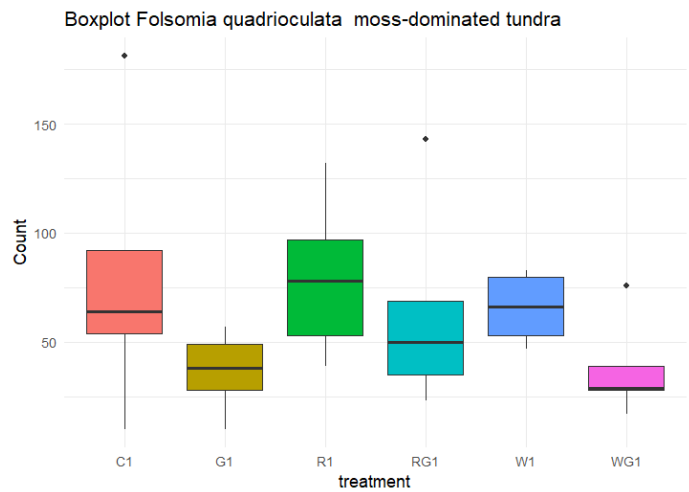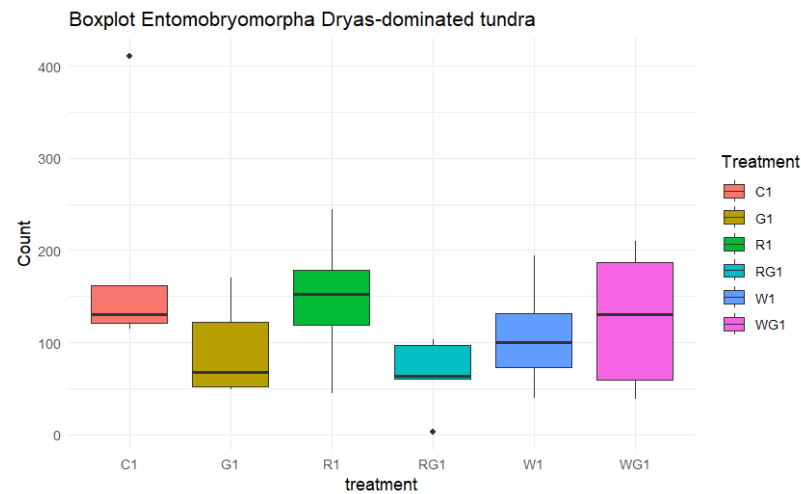
**Figure 9**. Boxplot for *Diapterobates notatus* and *Diapterobates* notatus adults in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing. The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers. (N=5).
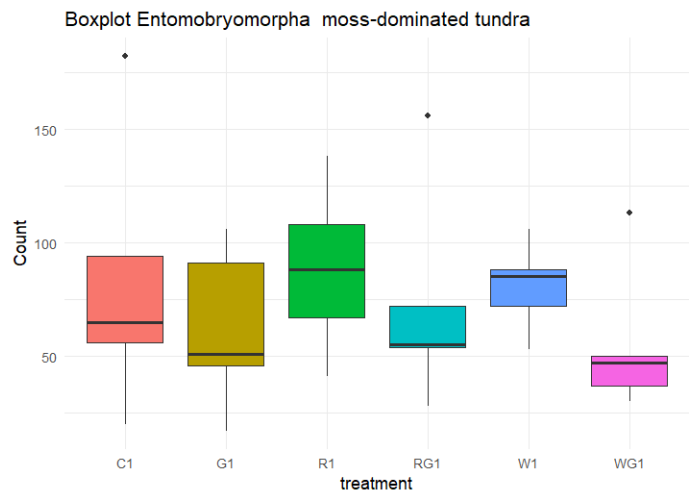
**Figure 10**. Boxplot for *Diapterobates notatus* juveniles and *Peloppiidae* in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing. The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers. (N=5).
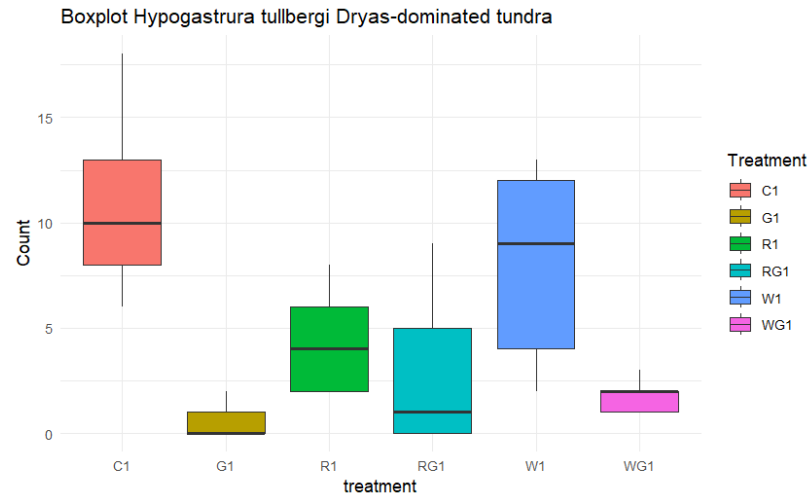
**Figure 11**. Boxplot for unidentified mites and Collembola in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing. The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers. (N=5).
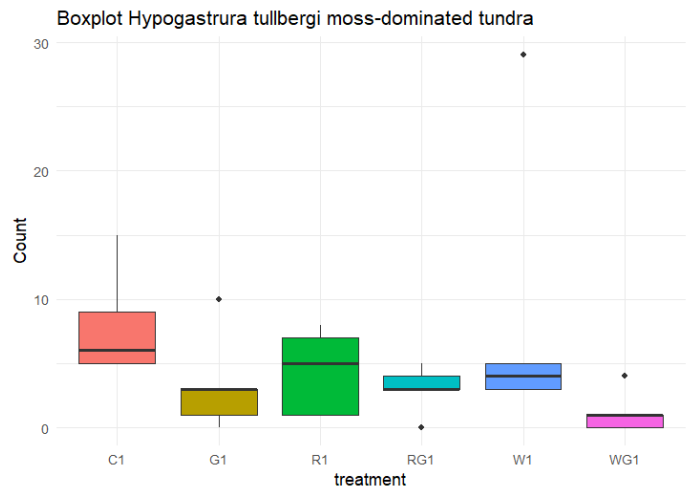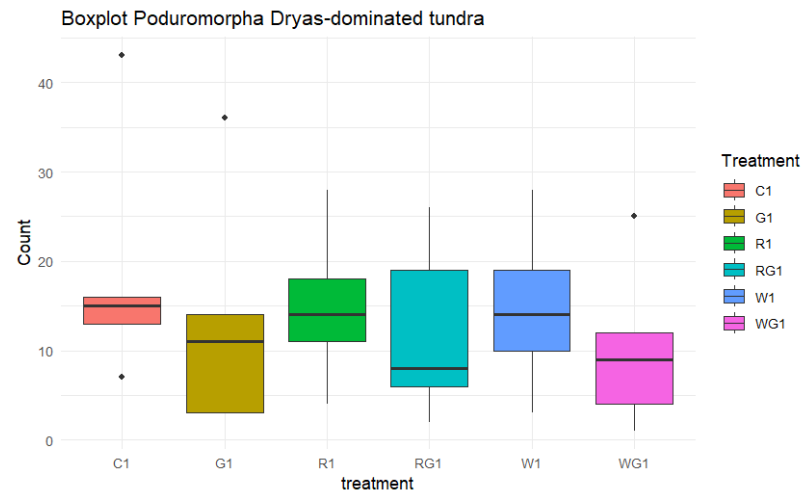
**Figure 12** Boxplot for Entomobryomorpha and *Folsomia quadrioculata* in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing.  The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers.  (N=5).
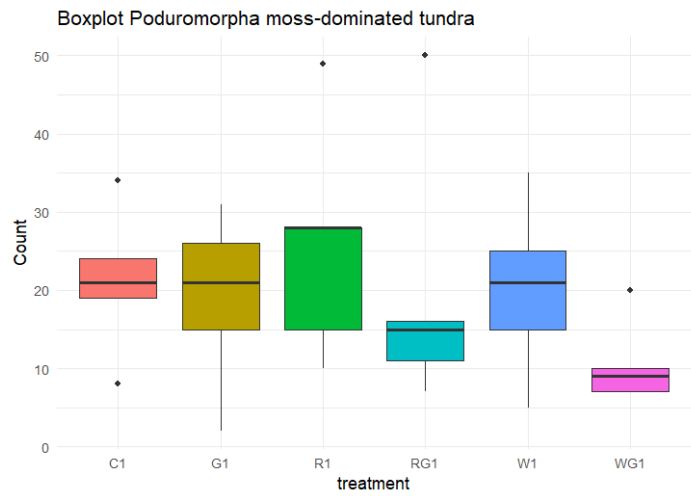
**Figure 13**. Boxplot for Poduromorpha and Hypogastrura tullbergi in *Dryas* and moss-dominated tundra, showing abundance in different treatments, C= control, G= grubbing, R= ROS, RG= ROS X Grubbing, W= warming, WG= Warming X Grubbing. The thick black line inside of boxes shows the median. Whiskers show range of data points with dots showing outliers. (N=5).