



Interactions between winter temperatures and duration of exposure may structure Arctic microarthropod communities

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ABSTRACT

The Arctic has a diverse terrestrial microarthropod fauna which overwinters *in situ* in soil and vegetation. This fauna is involved in key ecosystem processes, for example decomposition and pollination, and has tolerance to the Arctic's winter conditions. However, the Arctic is undergoing rapid change. Svalbard is experiencing warming rates up to four times the global average as well as alterations in precipitation (quantity and form; snow or rain) and wind direction. These will modify the conditions experienced by the overwintering fauna. Since laboratory experiments often fail to capture the diversity of environmental stressors, we employed a manipulation experiment using the naturally accumulating snow pack to moderate soil winter soil temperatures, combined with an extended incubator treatment, to map the duration limits of naturally induced cold tolerance. We demonstrate that the Collembola fauna can tolerate temperatures of $-25\text{ }^{\circ}\text{C}$ but that, in areas devoid of snow accumulation and when soil temperatures dip below $-30\text{ }^{\circ}\text{C}$ there is significant mortality. Furthermore, we demonstrate that exposure to a further extended 12 month period at $-6\text{ }^{\circ}\text{C}$, as a simple model of a situation where snow cover is not lost during the short Arctic summer, results in additional mortality with relatively few Collembola surviving. By contrast, while oribatid mites displayed similar survival over a natural winter as the Collembola, they were highly resistant to the extended exposure at $-6\text{ }^{\circ}\text{C}$, with no additional mortality occurring. We also documented survival amongst other invertebrate groups, including Nematocera and Brachycera larvae, Hemiptera (*Acyrtosiphon svalbardicum*), Coleoptera (*Isochnus flagellum*), and Araneae (Linyphiidae). We conclude that snow depth and winter air temperatures interact to regulate soil microarthropod populations over local scales and therefore the functioning of the Arctic soil ecosystem. Moreover, the environmental changes currently being observed in polar regions will continue to modify this fauna and its local and micro-scale distribution.

1. Introduction

There is considerable microarthropod diversity in the Arctic (Hodkinson, 2013; Coulson et al., 2014; Gillespie et al., 2020, Seniczak et al., 2020) performing a multitude of key functional roles in terrestrial ecosystems. The recent state of the terrestrial ecosystem CAFF report (Aronsson et al., 2021 and citations therein) identified six functional ecosystem components (FEC) for the microarthropod fauna that describe their key roles: blood-feeding, pollinators, decomposers, herbivores, vertebrate prey, and predators. Many of these species are present in the soil for all or part of their life cycles and the soil environment therefore has an impact on them and, consequently, the species dependent on

them. Moreover, the community is highly heterogeneous with its composition often differing in detail over short local spatial scales (Coulson et al., 2003; Seniczak et al., 2014).

The majority of the world's terrestrial carbon is stored in the soil (Crowther et al., 2016), including large reservoirs in the Arctic (Schuur et al., 2008), and processes affecting this reservoir are important to fully comprehend. Changes in the composition of the soil microarthropod community will alter the dynamics of carbon cycling processes with consequences for the system as a whole.

The terrestrial environment of the Arctic is characterised by strong seasonality, with long cold winters and short but relatively warm summers. Soil temperatures in the winter can fall below $-20\text{ }^{\circ}\text{C}$ while in the

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summer they may exceed +20 °C (Convey et al., 2018). However, this summer period where the ground is unfrozen may be short, for example five months on the west coast of Svalbard. This short summer active period during which development can occur results in many species requiring several years to complete each generation (Søvik and Leinaas, 2003; Søvik, 2004). The microarthropod fauna remains *in situ* throughout the year and hence experiences the cold winter period in the active layer of the permafrost which is subject to seasonal freezing. During this cold period the body temperature of the overwintering microarthropods will approximate that of the surrounding soil environment and it therefore follows that they must be tolerant of these conditions for populations to persist (Ávila-Jiménez et al., 2010).

The Arctic environment is changing (Gulev et al., 2021). Arctic latitudes overall are warming at twice the global mean, while specific regions are experiencing rates twice as fast as the Arctic mean (Nordli et al., 2020). Climate projections indicate warmer winters, increased snow fall, increased occurrence of winter rain (rain-on-snow events) and changing wind patterns (Hanssen-Bauer et al., 2019) and the duration of snow cover is decreasing across the Arctic generally (Meredith et al., 2019; Pedersen et al., 2022). A characteristic of High Arctic Svalbard is that snow lie and accumulation are greatly influenced by wind re-distribution (Zweigel et al., 2021). Changes in prevailing winds therefore affect snow accumulation patterns with implications for winter soil temperatures, timing of ground thaw in spring and even mass-balance relations of regions of permanent ice.

While of great significance to the functioning of the terrestrial ecosystem, the resilience of the Arctic microarthropod fauna to these changes is not well understood (but see Beet et al. (2022) for a recent review for the Collembola). In particular, comprehension of the role of the cold season in structuring microarthropod communities in the Arctic is lacking. This is complicated by the fact that survival of these species in the face of low temperature exposure is often assessed via laboratory studies using established protocols that are designed to provide a rapid assessment of cold tolerance and enable direct comparison between species. These protocols generally fail to replicate the exposure durations, temperature cycling, rates of temperature change (Hodkinson et al., 1998; Convey and Worland 2000; Convey et al., 2018) or other relevant environmental factors such as soil pore humidity, desiccation effects or even surface icing such as through rain-on-snow events (Coulson et al., 2000; Ávila-Jiménez et al., 2010; Graham et al., 2020), or recognise the possibility of interactions between these stressors.

That the Arctic microarthropod fauna may be extremely tolerant of extended exposure to sub-zero temperatures had been hinted at previously (Coulson and Birkemoe 2000; Convey et al., 2015). This emphasises the importance of the use of controlled field studies to determine the relevance of standard laboratory protocols to the natural winter conditions, and of the inclusion of a duration of exposure element. Such field studies may demonstrate different tolerance of low temperature exposure to that which may be inferred from exclusively laboratory-based studies. Some field manipulation studies have also inferred apparently surprising cold tolerance of certain sections of the arthropod fauna, including some Coleoptera and Araneae, which might not have been expected from solely laboratory-based extrapolations (Renault et al., 2002; Convey et al., 2015). Moreover, detailed laboratory studies are almost inevitably limited to a small number/proportion of species, while the field community diversity is much greater and field manipulations obviously extend the diversity assessed. Furthermore, there are few studies that attempt to map the durational limits of the low temperature tolerance of the Arctic microarthropod fauna. Apart from the intrinsic interest in determining the boundaries of survival, this understanding is important in a changing environmental landscape.

This study uses a field manipulation combined with extended exposure laboratory incubator approaches to investigate overwintering survival of the Svalbard soil microarthropod fauna. Specifically, we first took advantage of differing natural snow depth accumulation in the field to vary exposure to ambient winter temperatures and test whether snow

accumulation has an influence on overwintering microarthropod survival in cores of natural substrate and, hence, a role in spatially structuring the microarthropod communities observed in the summer. Second, we exposed a subset of these cores to a second one-year period at -6 °C in a laboratory incubator as a simple but practically realistic proxy for snow melt not occurring over terrestrial habitat in the Arctic summer and the underlying substrate remaining frozen for an extended period.

2. Materials and methods

2.1. Experimental design

Sixty soil cores, nominally of 10 × 10 cm area and c. 5 cm depth and including surface vegetation, were cut with a sharp knife and carefully removed from a patch of *Dryas octopetala* tundra close to the ITEX sites in Endalen (78° 11.1'N 015° 45.5'E) near to Longyearbyen, Svalbard, on 28/08/2019 (Fig. 1).

2.2. Sample treatment

Each soil core was placed in a plastic food freezer bag. These bags were not sealed, allowing air exchange. The cores were then randomly assigned to one of three treatments or a control. The control cores (14) were extracted immediately using Tullgren funnels (Burkard Scientific Ltd., Uxbridge, U.K.) at the University Centre in Svalbard (UNIS). The extractors are fitted with 25W vivarium bulbs (YIMO Crawler) and located in a container laboratory with an internal air temperature during the extraction period of approximately 15 °C. Soil cores were extracted into 96% ethanol until the soil was fully dry (approximately seven days). For each of the treatments, 16 soil cores (in their individual plastic bags) were fixed to the ground by means of a sheet of chicken wire pinned down with tent pegs at each of three locations known to accumulate different snow depths during the winter. The three treatments were (a) No Snow (on the observation deck located on the roof of the Research Park, Longyearbyen), (b) Shallow Snow (c. 30 cm depth) and (c) Deep Snow (c. 100 cm depth). Treatments b and c were located close to the Nordlystasjon (Northern Light Station) in Adventdalen. See Convey et al. (2015) for further details of the methodology and Figs. S1, S2, and S3 online supplementary material for images of the sites.

The treatment cores were recovered while still frozen under snow cover on 06/05/20 after being *in situ* for one full Arctic winter following

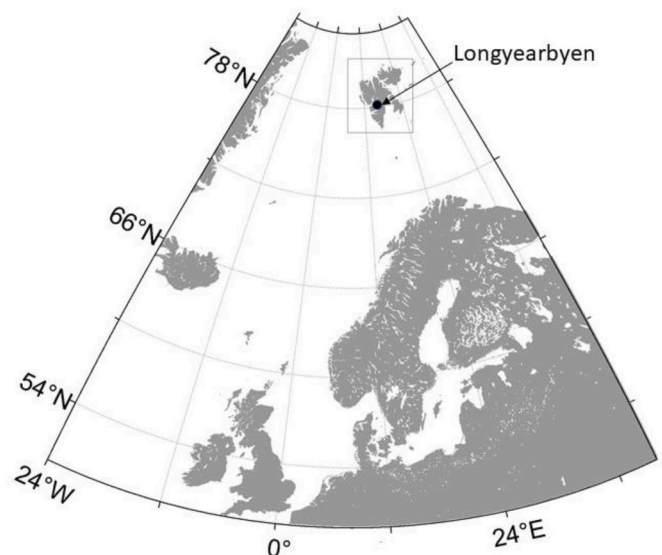


Fig. 1. Location of Svalbard (box) in the European High Arctic and the position of the field sites at Longyearbyen.

their deployment. Half of the cores in each treatment were thawed at +5 °C for one week prior to Tullgren extraction. The remaining cores were immediately placed at −6 °C in a controlled temperature incubator (Termaks KB 8182) at UNIS. These samples remained at −6 °C for a further year until 03/05/21 to mimic failure of winter snow to completely thaw over a full summer period followed by a second Arctic winter. They were then transferred to +5 °C for 10 days prior to subsequent extraction in Tullgren funnels.

Extracted microarthropods were classified into Oribatida, Collembola (Entomobryomorpha, Poduromorpha, Symphypleona), Diptera (larvae of Nematocera and Cychlorrhapha), Hemiptera, Coleoptera (Curculionidae) and Araneae (Linyphiidae). Recognising the well-known patchiness of soil faunal distribution in polar terrestrial habitats (Usher and Booth 1986; Seniczak et al., 2014; Coulson et al., 2014) and the enforced limited sample size available for analysis, we did not attempt to either describe or identify differences in community composition at the species level. Larval mites were not assessed due to uncertain taxonomy and larval extraction success being highly dependent on extraction conditions.

2.3. Soil and air temperatures

Soil temperatures were recorded using a Tinytag logger (TGP-4020, Gemini, Chichester, West Sussex, U.K.) set to record each hour and fitted with a PB-5009 thermistor lead deployed under one soil core for each treatment. Standard hourly air temperature records were obtained from the Norwegian Meteorological Institute portal (www.seklima.met.no) for the Adventdalen station (station SN99870) located within 100 m of the Nordlysstasjon, 4 km south-east of Longyearbyen.

2.4. Statistical analyses

The data obtained were analysed per group as described under section 2.2. Since the data did not follow a normal- or Poisson distribution and transformations failed to adequately normalise the dataset, non-parametric methods were used for analysis. Sample sizes of the treatments varied between 7 and 14 soil cores (Table 1). Kruskal-Wallis tests with Dunn's *post-hoc* comparisons were carried out to test for significant differences between treatments. A Bonferroni correction was applied to correct for repeated tests. The Mann-Whitney *U* test was used to test for differences between years within a treatment. All analyses were carried out using R version 4.1.2 (R core Team, 2021). The Dunn's *post-hoc* analyses were performed using the *Dunn.test* package.

2.5. Data access

The raw data are lodged with the Norwegian national Research Data Archive (NIRD) and the Global Biodiversity Information Facility (GBIF) (Coulson, 2023a,b).

The extracted specimens are deposited in the invertebrate collection at UNIS.

Table 1

Mean abundance per sample of other occurring taxa (¹ adult aphids, ² fundatrix hatching from overwintering aphid eggs). Deep = Deep snow (c. 100 cm), Shallow = Shallow snow cover (c. 30 cm), No = No snow cover.

Taxa	2019	2020	2021				
Sample size (n)	14	8	7	8	7	9	8
		Deep	Shallow	No	Deep	Shallow	No
Enchytraeidae	0.07	–	–	–	–	–	–
Araneae (Linyphiidae)	0.50	0.25	0.75	–	–	–	–
Hemiptera (<i>A. svalbardicum</i>)	0.64 ¹	13.0 ²	8.25 ²	12.43 ²	–	–	–
Coleoptera (<i>I. flagellum</i>)	0.93	0.25	0.75	–	–	–	–
Nematocera larvae	0.43	–	0.25	0.14	–	0.13	–
Brachycera larvae	–	0.14	0.13	–	–	0.13	–

3. Results

3.1. Temperatures and snow accumulation

During the winter and spring of 2019–20 winter air temperatures briefly reached a minimum of −34.6 °C (Fig. 2a) and repeatedly dropped below −20 °C. Temperature variability was high, with large and rapid temperature swings of around 20 °C. Soils with no snow cover tracked air temperature closely (Fig. 2b), but the presence of snow cover decoupled the air and soil temperatures, with the degree of decoupling depending on snow depth and timing of snow accumulation. Under c. 30 cm snow depth a minimum temperature of −24.1 °C was recorded in January 2020. After this point further accumulation of snow resulted in temperatures not declining again below −20 °C despite an air temperature extreme minimum (−34.6 °C, Fig. 3) in March. Soils under snow also did not display the rapid and large temperature fluctuations characteristic of both air temperature and soils with no snow cover. The effect of 100 cm snow cover was more striking, with a soil temperature minimum of only −9.2 °C being recorded and temperature fluctuations being dampened to an even greater extent. The winter of 2019–20 was considerably colder than encountered in an observation series with similar treatments at this location during the winter of 2012–13 (Fig. 2b; see also Convey et al., 2015), with the lower air temperatures in late winter 2019–20 and less snow accumulation (Fig. 4) driving soil temperatures lower than in 2012–13.

During the prolonged exposure to −6 °C air temperatures briefly exceeded 0 °C on two occasions (Fig. 2b) during the incubators' auto-defrost cycle but it is not believed that the soil thawed during these brief periods.

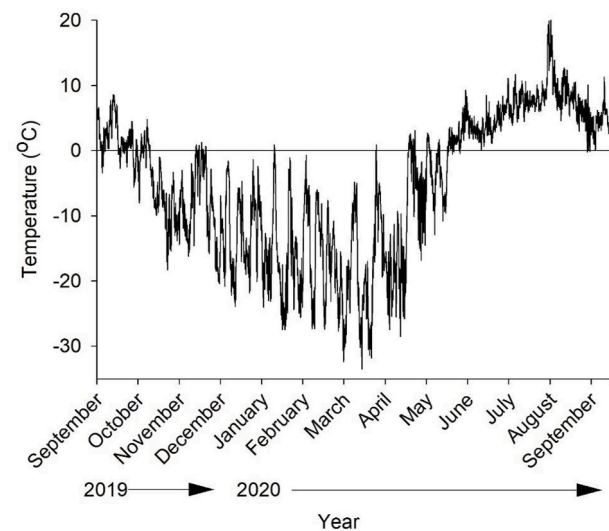


Fig. 2a. Daily air temperatures, Adventdalen. 0 °C reference line included. Data downloaded from the Norwegian Meteorological Institute (www.seklima.no).

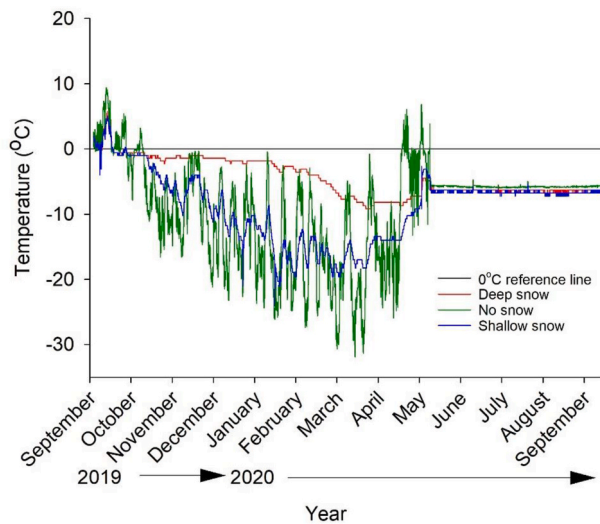


Fig. 2b. Daily temperatures in the treatment soil cores; No snow cover, Shallow snow (c. 30 cm) and Deep snow (c. 120 cm).

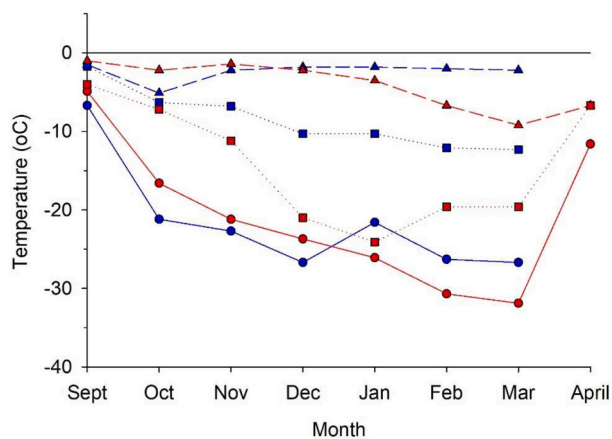


Fig. 3. Minimum monthly soil core (1 cm depth) temperatures during the winters of 2012–13 (adapted from Convey et al., 2015) and 2019–2020 (this study). Blue lines and symbols = 2012–13, red lines and symbols = 2019–21. Solid line = No snow, short dash = Shallow snow (c. 30 cm), dotted = Deep snow (c. 120 cm). Black solid line = 0 °C reference.

In winter 2012–13 snow accumulation measured at the nearby Svalbard airport (Norwegian Meteorological Institute, 2022) was minimal and rarely exceeded 5 cm while in 2019–20 a depth of 5 cm occurred in mid-November and for the majority of the winter the depth was >15 cm (Fig. 4).

3.2. Response of the fauna

3.2.1. Collembola

Collembola abundances differed over treatments ($H(3) = 15.051$, $p = 0.002$). They displayed great tolerance to the conditions encountered under shallow or deep snow (Fig. 5a, Table S1a,b), and numbers of individuals surviving the first winter exposure were nearly identical to those present in the initial samples extracted in November 2019. However, there was a dramatic and highly significant decrease in abundance in soils with no snow cover which experienced similar temperature cycles and absolute minima to air temperatures (Fig. 3, Table S1a,b). In the latter regime mean abundances decreased to 18% of the initial pre-winter densities.

Survival of all three winter treatments declined after a further 12

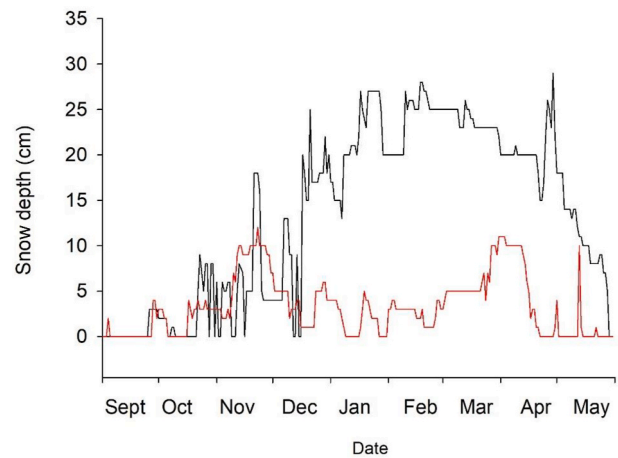


Fig. 4. Snow accumulation (cm) during the winters of 2012–13 and 2019–20 measured at Svalbard airport 5 km from the Gamla Nordlystasjon (Old Northern Light Station) in the same valley, Adventdalen. Red = 2012–13. Black = 2019–20. Norwegian Meteorological Institute (www.seklima.no).

month experimental exposure to -6 °C, being 22% in the Deep snow treatment ($W = 56$, $p < 0.001$) and 34% in the Shallow snow treatment ($W = 60$, $p = 0.002$) and only 1.3% in the No snow treatment ($W = 59$, $p = 0.004$) (Fig. 5a). Nonetheless, abundances in the Deep snow treatment whereas abundances in the Shallow snow and No snow treatments showed no significant difference (Fig. 5a).

Very few Symphypleona were obtained and were not further analysed. The response patterns of the remaining two collembolan orders to the experimental treatments reflected the overall response of the Collembola although the percentage decline of the Poduromorpha was less than that of the Entomobryomorpha (Fig. 5c and d). An additional 12 months at -6 °C resulted in significantly reduced abundances (Fig. 5c and d Tables S1a,b) but only marginal differences between treatment effects.

3.2.2. Oribatida

Oribatid mites demonstrated a similar significant ($H(3) = 17.053$, $p < 0.001$) initial response to the winter treatments 2019–20, similar to the Collembola (Fig. 5b). Further inspection revealed that while there were no significant differences in abundance between the Deep snow and Shallow snow treatments and the initial abundances in 2019 (Table S1a,b), there was a strong response observed between the initial abundances and the No snow treatment where abundances declined by 78% ($p < 0.001$).

The subsequent prolonged exposure at -6 °C resulted no significant additional mortality ($p > 0.05$, Table S1b) and abundances between all three treatments were not significantly different (Table S1a).

3.2.3. Remaining taxa

Although the extraction technique used is most efficient for targeting the Collembola and mite faunas, some additional taxa were recovered (Table 1). Low abundances preclude statistical analysis, nonetheless it is notable that representatives of these groups survived the treatments. One nematoceran larvae and one brachyceran larvae were recovered from the Shallow snow treatments after prolonged exposure to -6 °C (i.e. individuals survived the entire two year experiment). However, while some linyphiid spiders and weevils (*Isochnus flagellum*) survived the first natural winter under shallow and deep snow covers, none were recovered from the No snow treatment or the subsequent 'second winter' incubator exposure to -6 °C. Aphids (*Acyrtosiphon svalbardicum*) recovered from the cores in 2019 were adults while those in 2020 were juveniles, hence the adults did not survive the treatments.

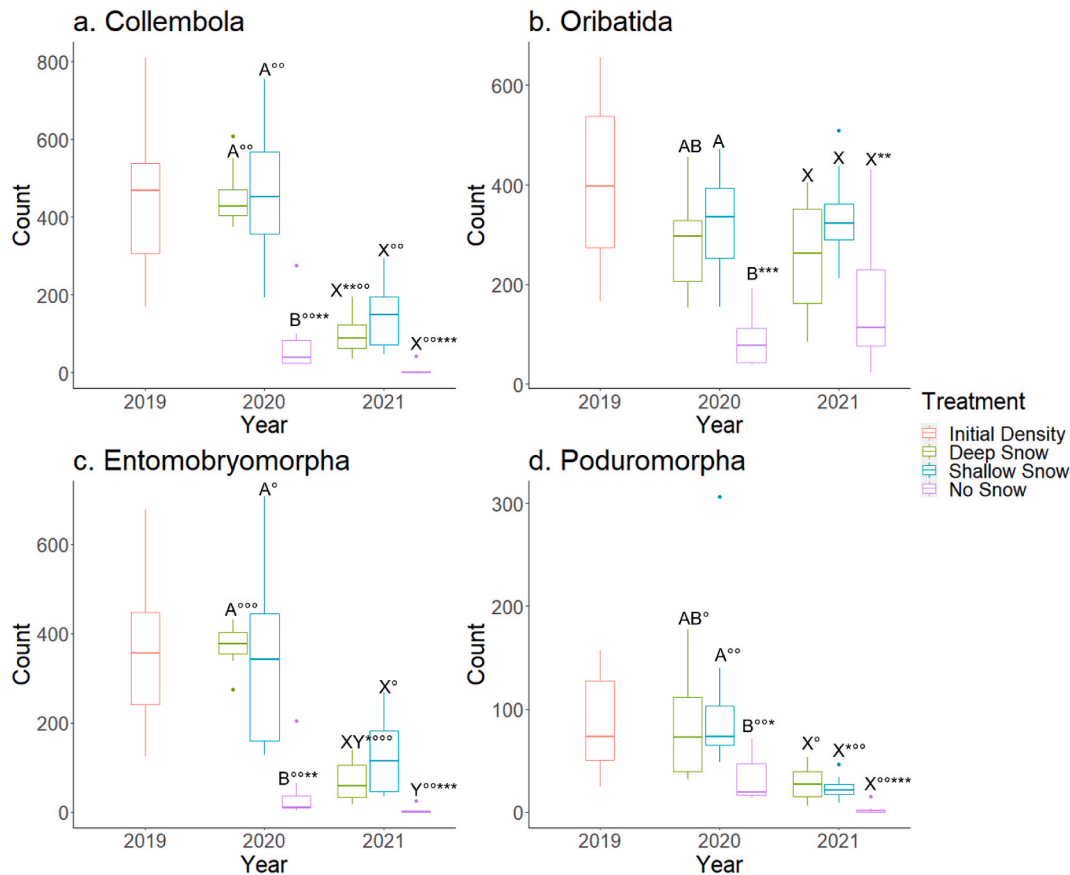


Fig. 5. Box plot of abundances a) total Collembola; b) Oribatida; c) Poduromorpha; d) Entomobryomorpha. Red = initial abundances 28/08/19, Green = Deep snow, Blue = Shallow snow, and purple = No snow. Median, first and third quartiles. Outliers indicated by a dot. Letters indicate significantly different abundances (initial sample in 2019 omitted from this manner of indicating significant differences for clarity), stars (*) indicate a significant difference with the initial count and circle (°) indicates a significant difference between years (2020–2021). Symbols indicate level of significance, i.e. */°: 0.01 < p < 0.05, **/°°: 0.001 < p < 0.01, ***/°°°: p < 0.001. Year = the year the samples were extracted (2019 = 28/08/19; 2020 = 06/05/20; 2021 = 03/05/21).

4. Discussion

Snow cover influence on the temperature of the soil is clear. Soil temperatures match air temperatures where there is no snow in both this study and others (e.g. Convey et al., 2015, 2018; Rixen et al., 2022). Where there is snow cover the soil is insulated and displays not only warmer temperatures but more thermal stability, with temperature fluctuations of decreased magnitude and rate compared to snow-free treatments. Snow accumulation at our study site in 2019–20 was delayed compared to 2012–13 and hence the soil was exposed to low air temperatures and became chilled before an insulating snow layer had accumulated. The reduced overall snow cover and delayed accumulation of snow in winter 2019–20 compared with 2012–13 will also have contributed to the lower soil temperatures experienced during 2019–20 than in 2012–13.

Survival of the soil fauna during the first winter of this study in the natural environment was evidently dependent on the snow depth. Moreover, the proportion of surviving individuals varied between the two principal groups of soil microarthropods, Collembola and Oribatida. Post-winter abundances for both groups declined significantly and considerably in the No snow treatment. Lacking the thermal insulation provided by snow cover this treatment tracked air temperatures closely, demonstrating similar large and rapid temperature variation and extremely low minima. This result contrasts with the observations reported by Convey et al. (2015), where high survival was observed in all three treatments (No snow, Shallow and Deep snow) and no statistical differences in survival detected. However, the winter temperature regimes experienced in the No snow treatments differed considerably

between 2012–13 and 2019–20. Whereas the minimum monthly No snow treatment temperatures experienced in winter 2012–13 was -26.7°C , in 2019–20 they regularly fell below -30°C with a low of -31.9°C in March. This additional low temperature stress may explain the dramatic mortality observed in 2019–20 in the No snow treatment. The SCPs of oribatid mites are generally somewhat lower than those of Collembola and this may partially explain the different survival rates of Collembola and the oribatid mites. However, as noted above, care must be exercised in using laboratory measurements of freezing temperatures and employing them directly to interpret results from field experiments. Moreover, some Collembola employ a freeze desiccation strategy (Sørensen and Holmstrup, 2011) which may further invalidate direct comparison of short-term laboratory experiments determining SCPs with survival of complex natural field conditions. Very few Symphyleona were extracted from the samples examined, almost certainly due to this group being highly surface active and difficulties in efficiently sampling them by means of soil cores (Bretfeld, 2000). That the two orders of Collembola assessed here (Entomobryomorpha and Poduromorpha), which are characterised by variations in habits, may display differing tolerance to extreme cold exposure may suggest additional consequences for the ecosystem. Nonetheless, these data should be interpreted with caution owing to low sample size and levels of alpha diversity.

Consistent with the observations of Convey et al. (2015), our data provide further direct evidence that Arctic Coleoptera, in this case the weevil *I. flagellum*, and linyphiid spiders can tolerate winter conditions under shallow or deep snow. By contrast, there was no evidence that they could survive the No snow treatment during winter 2019–20. While

this may be due to the low sample size, the observed trend is again indicative that the especially low temperature regime of the 2019/20 winter could have been lethal to these two groups. It is notable that several nematoceran larva were extracted from the No snow and other treatments even though the Tullgren funnel extraction method employed is not optimal for groups such Diptera larvae. This, combined with the likely low densities in the soils sampled, would have resulted in few individuals being collected. However, the extraction of live individuals demonstrates that this group possesses extreme cold tolerance under natural field conditions. Survival of the aphid, *A. svalbardicum*, in all three treatments applied here would be expected. This species overwinters as an extremely cold tolerant egg (Strathdee et al., 1995) whose SCP is typically in the region of -40°C . The individuals recorded in autumn 2019 were adults while those extracted in spring 2020 would have been juveniles hatching from the previous summer's eggs while in the extractor. This demonstrates the rapid development of this species, the local distribution of which is considered to be constrained by winter snow accumulation and restricted to localities that become clear of snow early in the summer (Ávila-Jiménez et al., 2010).

Survival after the natural winter experimental manipulations and subsequent prolonged exposure for 12 months at -6°C varied between groups. Collembola demonstrated a significant decline in abundance between 2020 and 2021, indicating that the extended sub-zero period led to mortality. Indeed, survival after the extended -6°C exposure was further reduced in the No snow treatment that already showed much reduced abundance after the natural winter period. Oribatid mites, in contrast, showed no additional mortality, demonstrating considerable and extended cold resistance in this group. It is also appropriate to note that oribatid mites generally have much greater desiccation resistance than springtails (Coulson et al., 1993; Holmstrup et al., 2002) and thus are likely to have lost less water by the desiccation inevitable from being surrounded by ice crystals during the extended winter periods. However, the observation that there was no further survival of the aphid *A. svalbardicum* was unexpected. As noted, overwintering eggs of this species are extremely cold tolerant and it might have been expected that these eggs would be able to tolerate the extended exposure to sub-zero temperatures, but this appears not to be the case. One further nematoceran and one brachyceran larva was recovered after the prolonged period of exposure to -6°C . The same caveats concerning extraction limitations apply here as to the 2020 samples, but this observation again confirms that a proportion of Diptera larvae could tolerate the experimentally extended period of exposure to 'winter' conditions.

This study did not set out to characterise the functional role of the soil microarthropod fauna in detail, but it is already clear that it has an important role in a variety of processes affecting, for example, soil structure (Maaß et al., 2015), C/N mineralisation (Lenoir et al., 2007) and decomposition (Seastedt 1984; Kampichler and Bruckner, 2009). Given the different feeding strategies and guilds of oribatid mites (Siepel and Maaskamp 1994; Schneider et al., 2004) and Collembola (Potapov et al., 2020) it would be expected that these processes will be altered as a consequence of any changes in microarthropod community composition. The differential survival of Collembola and oribatid mites to the cold exposures imposed in this study demonstrates that the interaction of snow cover with low winter air temperatures can be one factor determining the patchy local micro-distribution of these animals often observed (Seniczak et al., 2014). Based on our data, cold winters combined with little snow accumulation (either as a result of low precipitation or wind redistribution of fallen snow) may lead to a reduction in the abundance of Collembola but have less effect on populations of oribatid mites. This will lead to changes in the functioning of the soil ecosystem as the proportion of Collembola to oribatid mites fluctuates, as well as an overall decrease in abundance of detritivores due to mortality of Collembola. The generation time of oribatid mites is in the order of five years or more (Søvik, 2004) while that of Collembola is shorter and approximately one year in the Arctic tundra (Birkemoe and Sømme, 1998). This rapid generation time of the Collembola may enable

populations to recover quickly even in the absence of local dispersal. In the absence of detailed autecological studies of most members of polar terrestrial faunas (Hogg et al., 2006), the degree of functional redundancy and extent to which biodiversity *per se* can be used as a determinant or proxy of system functioning are unclear. However, dynamic changes in the total abundances and proportions of oribatid mites to Collembola will clearly have implications for the functioning of these soil ecosystems at local scale. This may be particularly relevant for high latitude regions where soil engineers such as lumbricid earthworms are absent (Coulson et al., 2014). While this study focusses on the winter conditions it must be appreciated that community compositions entering the winter are also a product of summer environmental conditions, which themselves are changing. Lack of detailed monitoring makes it difficult to determine community changes with certainty, but some trends are becoming evident such as increased abundance of Collembola but decreased alpha diversity at the Nuuk monitoring site in Greenland (Gillespie et al., 2020). Nonetheless, it is difficult to predict consequences due to a fundamental lack of knowledge of the detailed functional role of microarthropods in some ecosystem processes (Kampichler and Bruckner, 2009; Maaß et al., 2015).

4.1. Conclusions

For many species overwintering ability is often extrapolated from laboratory studies. This is perhaps particularly the case for polar species and there are few studies that have experimentally assessed winter survival in the natural environment (but see Convey, 1994a, b). It is clear that the soil microarthropod fauna of Arctic regions requires cold tolerance adaptations to successfully persist. However, the limits of this tolerance are unclear, in particular concerning the role cold tolerance has in determining community composition and local distribution, and hence ecosystem function, on both broad and local scales. In an era of particularly rapid environmental change in the polar regions this gap in understanding is extremely pertinent.

This study demonstrates the contrasting effects that cold winters may have on different groups of High Arctic soil microarthropods. In the majority of winters, where air temperatures do not drop below -30°C the microarthropod fauna is largely unaffected. Even if there is limited mortality the community is largely unaltered in structure. However, where minimum temperatures reach -30°C in combination with no, or minimal, snow cover mortality increases. Hence snow accumulation acts to structure the soil microarthropod community at micro- or local scales and therefore moderate soil processes involving this community. Furthermore, should redistribution of snow be combined with a cold summer period where the local soils are never released from snow cover our data suggest that the mortality of Collembola and aphid eggs may approach 100%. By contrast, the oribatid mite community may be relatively unaffected by any extended sub-zero exposure. In such a situation, the soil microarthropod community may switch from a numerical dominance of Collembola to that of Oribatida. It is therefore important to understand the recent snow accumulation and soil temperature history of the environment in order to interpret soil microarthropod populations and patchiness observed during the summer. In summary, the soil microarthropod fauna appears extremely tolerant of exposure to low temperature, but that this tolerance varies between groups. Mosaics of differing snow depths with consequential effects on soil temperatures and durations of the winter period will impact these different microarthropod groups in varying manners with the result that the microarthropod community composition will change. Since species traits rather than biodiversity largely determine ecological functions, changes in the balance between species groups will have effects on the soil structure and processes.

Ethical review board

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CRediT authorship contribution statement

Stephen James Coulson: Conceptualization, Methodology, Formal analysis, writing. **Peter Convey:** Conceptualization, writing. **Sil Schuur:** writing, Formal analysis. **Simone Iris Lang:** Conceptualization, Methodology, writing.

Declaration of competing interest

The authors know of no competing interests.

Data availability

Data is currently being archived as Darwin Core Archive at both GBIF and NIRD. Coulson 2023a,b

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2023.103499>.

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