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## Survival of rapidly fluctuating natural low winter temperatures by High Arctic soil invertebrates

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## ABSTRACT

The extreme polar environment creates challenges for the resident invertebrate communities and the stress tolerance of some of these animals has been examined over many years. However, although it is well appreciated that standard air temperature records often fail to describe accurately conditions experienced at microhabitat level, few studies have explicitly set out to link field conditions experienced by natural multispecies communities with the more detailed laboratory ecophysiological studies of a small number of ‘representative’ species. This is particularly the case during winter, when snow cover may insulate terrestrial habitats from

extreme air temperature fluctuations. Further, climate projections suggest large changes in precipitation will occur in the polar regions, with the greatest changes expected during the winter period and, hence, implications for the insulation of overwintering microhabitats. To assess survival of natural High Arctic soil invertebrate communities contained in soil and vegetation cores to natural winter temperature variations, the overwintering temperatures they experienced were manipulated by deploying cores in locations with varying snow accumulation: No Snow, Shallow Snow (30cm) and Deep Snow (120cm). Air temperatures during the winter period fluctuated frequently between +3 and -24°C, and the No Snow soil temperatures reflected this variation closely, with the extreme minimum being slightly lower. Under 30cm of snow, soil temperatures varied less and did not decrease below -12°C. Those under deep snow were even more stable and did not decline below -2°C. Despite these striking differences in winter thermal regimes, there were no clear differences in survival of the invertebrate fauna between treatments, including oribatid, prostigmatid and mesostigmatid mites, Araneae, Collembola, Nematocera larvae or Coleoptera. This indicates widespread tolerance, previously undocumented for the Araneae, Nematocera or Coleoptera, of both direct exposure to at least -24°C and the rapid and large temperature fluctuations. These results suggest that the studied polar soil invertebrate community may be robust to at least one important predicted consequence of projected climate change.

**Key words:** Microarthropod, polar, freeze-thaw, snow, climate change,

## 1. Introduction

Environmental conditions in the terrestrial ecosystems of the polar regions are amongst the most extreme on the planet (Peck et al., 2006; Ávila-Jiménez et al., 2010; Convey, 2012; Convey et al., 2014). As a result, the stress tolerance adaptations of organisms within these ecosystems have formed a focus of research attention over many years. However, the link between these laboratory studies generally focussing on a small number of species, and temperature regimes experienced by the wider diversity of organisms in natural communities in their natural habitats, has received surprisingly limited attention. Further, the ‘polar amplification’ of current global

climate trends means that parts of both polar regions are also undergoing the most rapid rates of environmental change seen globally (ACIA, 2005; Turner et al., 2009, 2013; Førland et al., 2011; Nordli et al., 2014). Climate projections give an expectation of warmer winters in the Arctic with increased mean temperatures, reduced frequency of extreme cold events, changes in precipitation and greater frequency of freeze/thaw cycles (AMAP, 2011). Terrestrial ecosystems in these regions are generally regarded as being structurally simple, and their biota are often seen as sensitive biological indicators or sensors of environmental change (e.g. Callaghan and Jonasson, 1995; Walther et al., 2002).

During the polar night, when the sun stays permanently below the horizon for up to several months, terrestrial habitats of High Arctic regions such as the Svalbard archipelago face extremely low air temperatures (Coulson et al., 1995; Convey, 1996; Danks, 1999; Nordli et al., 2014). Even in summer, low temperatures and lack of available energy restrict biological activity (Coulson et al., 2014). However, it is well known that the temperature experienced at the physical scale of the organism or the microhabitat is not well described by the meteorological mean air temperature, while the pattern, rate and magnitude of variation are also important (Gaines and Denny, 1993; Sinclair, 2001; Peck, et al., 2006). Absorption of solar energy in summer by vegetation, soils and rock surfaces can result in short-term microhabitat temperature maxima as high as 30-40°C even at high polar latitudes (Smith, 1988; Hodkinson, 2005). Terrestrial invertebrates occupying these habitats may therefore face rapid and large short-term variation in temperature and, while some avoidance or buffering is possible through migration in the soil or vegetation profile, the extent to which this is achieved in practice is largely unknown.

The soil invertebrate fauna of Svalbard, as is typical of the extreme polar regions, is patchily distributed (Usher and Booth 1984; Coulson et al., 2003; Seniczac et al., in press). It comprises a wide range of groups (Jensen and Christensen, 2003; Coulson and Resfeth, 2004; Coulson et al., 2014), but those that are well represented include tardigrades, rotifers, nematodes, enchytraeid worms, mites, springtails, insects (in particular chironomid midges and staphylinid and curculionid beetles) and spiders (especially the Linyphiidae and Lycosidae). Resistance to environmental stresses, in particular cold and desiccation, is generally thought to be well developed, although the majority of detailed studies have focused on a limited number of groups

and species. Two cold tolerance strategies are utilised by many polar invertebrates (Everatt et al., 2014). Freeze avoidance involves the organism maintaining its body contents in the liquid state below the freezing point of water, while freeze tolerance involves the use of ice nucleating agents to encourage controlled ice formation in extracellular compartments, leading to concentration and lowering of the freezing point of intracellular fluids (see Block, 1990; Danks, 2007; Thomas et al., 2008; Denlinger and Lee, 2010; Ávila-Jiménez et al., 2010; Coulson et al., 2014; Everatt et al., 2014). However, detailed specific studies of the cold tolerance and survival characteristics of High Arctic arthropods have focussed on relatively few groups, in particular the Hemiptera, Acari and Collembola (Block et al., 1994; Strathdee et al., 1995; Hayward et al., 2000; Holmstrup et al., 2002; Søvik and Leinaas 2003; Hodkinson and Bird 2004; Bahrndorff et al., 2007; Clark et al., 2009; Sørensen and Holmstrup, 2011), with a very limited amount of work on other groups such as nematodes (Carlsson et al., 2013). Documented field experiments are scarce (Strathdee and Bale, 1995; Coulson and Birkemoe, 2000; Coulson et al., 2000; Dollery et al., 2006; Ávila-Jiménez and Coulson, 2011).

Snow cover can insulate the ground against extreme low air temperatures (Davey et al., 1992; Coulson et al., 1995; Geiger et al., 2009; Morgner et al., 2010). This insulation can allow the survival of species not capable of tolerating the minima experienced in unprotected habitats (Convey and Block 1996; Danks, 2007; Ávila-Jiménez et al., 2010; Bale and Hayward, 2010; Hågvar and Hågvar, 2011; Marshall and Sinclair, 2012; Legault and Weis, 2013), and is a feature of the richer and more diverse Svalbard habitats. A reduction in snow cover, for example associated with elevated winter evaporation rates, winter thaws, or increased storminess and wind redistribution, will result in reduced soil temperatures and potentially increased frequency of repeated cold events that are appreciated to be stressful for the underlying ecosystems and their component species (Groffman et al., 2001; Isard et al., 2007; Kreyling and Henry, 2011; Marshall and Sinclair, 2012; Pauli et al., 2013). However, it is unclear how invertebrates, which are fundamental to soil processes including organic soil formation, decomposition and nutrient recycling (Bardgett, 2005; Brussard et al., 2007; Brussard, 2012) will respond to such changes.

Most low temperature studies have employed well-developed laboratory methodologies to assess cold tolerance, for example determining lower lethal temperatures and screening for supercooling

points using standard cooling rates. Such studies also tend to concentrate on focal species, rather than analysing all species within a community. However, while these techniques provide much useful and consistent information about the cold tolerance of the studied animals, placing this in the context of true field conditions is often difficult as the parameters investigated – in particular relating to rate of temperature manipulation, frequency of repeated cold events, duration of cold exposure, and survival – often differ greatly from the natural situation (e.g. Coulson and Bale, 1996; Convey and Worland, 2000; Worland and Convey, 2001; Marshall and Sinclair, 2012). Thus, laboratory-assessed cold tolerance characteristics do not automatically provide a good framework within which to predict or explain survival patterns under natural field conditions.

Here we report data from a simple field trial investigating the survival of the natural soil microarthropod community when exposed to the temperatures and fluctuations therein experienced under different levels of snow cover in the field over the course of a winter in High Arctic Svalbard. We hypothesised that, across natural diverse communities, some groups would be more vulnerable to low temperature extremes or other features of natural thermal regimes. We therefore set out to test a prediction arising from this hypothesis, that there would be evidence of greater and/or taxon-specific mortality in treatments exposed to lower winter temperature regimes. Our methodology involved comparing the impacts of different levels of snow cover – and hence thermal buffering - on terrestrial invertebrate survival in replicate natural soil and vegetation cores.

## **2. Materials and Methods**

### *2.1. Experimental design*

Thirty-two soil cores, nominally of 10×10 cm area and 5 cm depth and including surface vegetation, were cut with a sharp knife and carefully removed from a patch of *Dryas octopetala* tundra in Endalen (78° 11.1'N 015° 45.5'E) near to Longyearbyen, Svalbard, on 17 September 2012. Small (unquantified) differences were present between individual cores because of the presence of buried stones, etc, but these differences were minor and we do not consider they will have influenced the data obtained. Soil temperatures (1-2 cm depth) at this location typically range between +10°C in the summer and -10°C in the winter (Fig. 1a). Each sample was placed

in a plastic food freezer bag and sealed. Bags were carefully punctured with a single knife-cut slit (< 5cm length) to allow for gas exchange. The soil samples were then randomly assigned to one of four treatments. Eight samples were fixed to the ground by means of sheets of chicken wire pinned down with tent pegs in each of three locations known to accumulate different snow depths during the winter, on the same day as collection. The treatments were (a) No Snow (on the observation platform positioned on the roof of the Research Park, Longyearbyen), (b) Shallow Snow and (c) Deep Snow (both close to the Nordlystasjon in Adventdalen), and (d) maintenance at a constant +7°C in a controlled temperature room at the University Centre in Svalbard (UNIS).

## *2.2. Sample treatment*

To test the prediction of greater and/or taxon-specific mortality in treatments exposed to lower winter temperature extremes, four bags were retrieved from each treatment on 13 November 2012 and the remaining four on 4 March 2013. Samples were allowed to thaw for 24 h in the +7°C controlled temperature facility before being placed in Tullgren funnels (Burkard Scientific Ltd., Uxbridge, U.K.) and the soil arthropod fauna extracted into 96% alcohol until the soil was fully dry. As this method of extraction relies on the active movement of animals away from the source of light/heat, those animals extracted are assumed to have been living and active at the time of extraction, and this is generally also apparent from the undamaged morphology of the specimens obtained. Extracted invertebrates were classified into the higher taxonomic groups of Acari (Oribatida, Mesostigmata, Prostigmata), Collembola, Diptera (larvae of Nematocera), Coleoptera (Curculionidae) and Aranea (Linyphiidae). Recognising the well-known patchiness of soil faunal distribution in polar terrestrial habitats (Usher and Booth, 1984; Coulson et al., 2003; Hugo et al., 2004, Caruso et al., 2013; Seniczac et al., in press), 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.

## *2.3. Soil and air temperatures*

Soil temperatures were recorded with Tinytag loggers (TGP-4020, Gemini, Chichester, West Sussex, U.K.) fitted with PB-5009 thermister leads and set to record every hour. The thermistors were inserted approximately 1-2 cm into a soil core in each treatment. Data were downloaded at the end of the deployment in March 2013. Standard air temperature records were obtained for the

Norwegian Meteorological Station at Svalbard airport, downloaded from [www.eKlima.no](http://www.eKlima.no). The Endalen location from which the soil cores were obtained is also a site of long-term soil microclimate monitoring by UNIS.

#### *2.4. Statistics*

One-way ANOVA (SigmaPlot for Windows V.11, Systat Software Inc.) was performed to examine for significant differences between treatments in the November and March datasets after testing for normality (Shapiro-Wilk). Initial analysis demonstrated that the +7°C treatment was a strong outlier and significantly different from all the field treatments in both datasets, with the increased numbers of invertebrates extracted over time being consistent with activity and reproduction occurring under this treatment. In the subsequent inter-treatment comparisons the +7°C treatment was excluded.

### **3. Results**

#### *3.1. Temperature*

Winter air temperatures declined to -24°C in March 2013 (Fig. 1e, Table 1). Sample temperatures initially tracked air temperature closely during the autumn but, as snow accumulated, those at the Shallow and Deep Snow sites became increasingly uncoupled from air temperature (Fig. 1b-e, Table 2). There was no accumulation of snow other than a thin layer in November 2012. When the final samples were retrieved on 4 March 2013 there was a snow depth of 30 cm at the Shallow Snow site and of 120 cm at the Deep Snow site. There was no snow cover at the No Snow site and sample temperature under this treatment tracked air temperature closely throughout the experimental period. The Shallow Snow treatment most closely followed the natural snow depth and soil temperature situation at the location in Endalen where the soil cores were collected from (Fig. 1a). The uncoupling of soil temperatures from air temperatures resulted in mean winter soil temperatures of -3.2 and -1.5°C under Shallow Snow and Deep Snow, respectively, compared to a mean air temperature of -9.0°C during this period (Table 1).

Air temperature varied greatly during the study period, between +3.2 and -24°C (Fig. 1e, Table 1). On occasion, temperatures changed rapidly. For example, during the period 28-30 December

2012, air temperature rose from  $-18.3$  to  $+0.3^{\circ}\text{C}$  (Fig. 1e), an overall warming rate of  $0.28^{\circ}\text{C}$  per hour. The No Snow cores tracked this change closely over the same period, warming at a rate of  $0.27^{\circ}\text{C}$  per hour, from  $-19.7$  to  $-1.9^{\circ}\text{C}$  but cores under Shallow Snow and Deep Snow only warmed by  $0.8$  and  $0.1^{\circ}\text{C}$ , respectively, during the same period. Uncoupling of soil and air temperatures under snow cover was also reflected in the number of freeze-thaw events experienced (Table 2). Five freeze-thaw events were recorded in the No Snow samples during the period January to March 2013 (Fig. 1b), but the measurements from Shallow Snow and Deep Snow treatments revealed no such events (Figs. 1c, d).

### 3.2. Invertebrates

There were no clear differences in occurrence of the major taxonomic groups of invertebrates extracted from the field treatments between November 2012 and March 2013 (Figure 2) and thus no suggestion of snow depth promoting survival in any group. However, densities in the cores maintained at a constant  $+7^{\circ}\text{C}$  were consistently greater in both November 2012 and March 2013 than in the field treatments. Removing the constant  $+7^{\circ}\text{C}$  from the analysis revealed no significant differences in oribatid mite densities between the three field treatments at the end of the study in either November 2012 or March 2013 ( $F_{2,9}=1.703$ ,  $p=0.236$  and  $F_{2,9}=0.575$ ,  $p=0.582$ , respectively) or in Collembola densities in March 2013 ( $F_{2,9}=0.884$ ,  $p=0.446$ ; November data showed unequal variances). The densities of other groups retrieved in the extractions were too low to permit statistical analysis, but there was no suggestion of any differences between November or March samples (Figure 2) or, in particular, of lower survival in the more extreme No Snow exposure treatment. Survival of arthropods was seen in all the groups examined and in each treatment. This was despite a minimum temperature of  $-26.7^{\circ}\text{C}$  being experienced in the No Snow treatment, indicating that all these invertebrate groups have the ecophysiological ability to survive direct exposure to these low temperatures.

## 4. Discussion

Two central conclusions are apparent from the data obtained in this simple study, and do not support the prediction of differential mortality occurring under the contrasting thermal regimes generated by different levels of snow cover. First, there was no suggestion of either widespread or differential mortality in the soil invertebrate community generally, or the representatives of

any major taxonomic group specifically, under any of the exposure treatments. Second, the representatives of all the faunal groups obtained in the extractions were clearly capable of surviving exposure to extreme low temperature below  $-24^{\circ}\text{C}$  and to large and rapid fluctuations in temperature. The intentionally simple design of the study precludes detailed analyses of changes in community composition or structure over time, but points to a framework within which the work described here should be advanced. In particular, future studies should include quantification of invertebrate abundances at the point of initial core collection and, ideally, achieve greater taxonomic resolution on each sampling occasion within the major taxa quantified here.

The extractions here contained mixed communities of species many of which will not have been subjected to detailed ecophysiological study. The large majority of polar Acari and Collembola are known to employ the freeze avoidance tactic (Sinclair et al., 2003; Everatt et al. 2014). The use of the alternative cryoprotective dehydration strategy by the springtail *Megaphorura arctica*, a distinctive species not present in the current study, has also been documented (Worland et al., 1998). Sørensen and Holmstrup (2011) have suggested the use of this strategy may be more widespread, based on studies of temperate species. The data obtained here, with survival across the community of exposure to temperatures below  $-24^{\circ}\text{C}$ , suggest that most of these species are highly cold tolerant (*sensu* Bale, 1993).

The survival of 'higher' groups of arthropods (Coleoptera, Nematocera, Araneae) under these manipulations is notable. While small numbers of these groups were recovered, as would be typical in general extractions of this type on Svalbard, there was again no indication of systematic differences in their recovery between treatments. The cold tolerance abilities of species in these groups do not appear to have been studied previously on Svalbard or elsewhere in the High Arctic. Indeed surprisingly limited studies are available of the cold hardiness of High Arctic Insecta generally (Coleoptera Pythidae: Ring and Tesar, 1980; Lepidoptera Lymantriidae: Bennett et al., 2003). Beetles of the family Curculionidae are one of the dominant Coleoptera families in the High Arctic fauna (Coulson et al., 2014), as is also the case on the sub-Antarctic islands (Chown, 1992; Convey, 2007). These are freeze-avoiding, but in the latter region show relatively high critical thermal minima and limited survival below their freezing point (van der

Merwe et al., 1997; Klok and Chown, 2003), which reflect closely the stable cool climates of the sub-Antarctic islands. No comparable data are available for Arctic or other cold environment weevils from the Northern Hemisphere, although a recent study of woodland invasive weevils similarly reported a low extent of freezing tolerance (Coyle et al., 2011). The survival of temperatures as low as  $-24^{\circ}\text{C}$  in the current study therefore considerably extends the known lower thermal limits demonstrated in this beetle family.

Similarly, with the exception of a study on the occurrence of antifreeze proteins in a wide range of Alaskan insects and spiders (Duman et al., 2004), which did not itself document low temperature survival, no studies of High Arctic Araneae appear to be available. Aunaas et al. (1983) investigated physiological aspects of various Svalbard invertebrates including determining the supercooling points of summer animals. The available literature on cold tolerance of North American and European species generally indicates relatively limited tolerance of sub-zero temperatures (e.g. Duman, 1979; Bayram and Luff, 1993; Cramer and Mayright, 2008; Murphy et al., 2008). Their survival here of temperatures as low as  $-24^{\circ}\text{C}$ , and in the absence of any habitat protection through snow, was unexpected. Spiders, as with mites, are thought to be generally freeze-avoiding, and it has been noted that smaller temperate species such as the Linyphiidae have lower supercooling points than species from families where individuals are typically larger (Bayram and Luff, 1993). The Lyniphidae are the dominant spider family in Arctic terrestrial habitats (Coulson et al., 2014). Our confirmation of survival of direct exposure to at least  $-24^{\circ}\text{C}$  considerably extends the known tolerance to cold exposure of members of this family.

The data obtained suggest that the arthropod fauna of the soil habitat investigated, which is a typical habitat on High Arctic Svalbard, is relatively robust to changes in temperature and temperature variability that are likely to be a consequence of changes in patterns of snow fall and accumulation as predicted under current climate change scenarios. However, factors other than temperature are also likely to change under these scenarios, and future studies must include the quantification of additional stressors such as surface icing events (Coulson et al., 2000), as well as address the difficult challenge of incorporating assessment of fitness consequences of exposure to different winter stress regimes. This study also illustrates the difficulty of generalising from

laboratory experiments based on a small number of species and higher taxonomic groups to community-level responses to different patterns of exposure to low temperatures and, hence, the need for large-scale complementary field studies.

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### Figure captions

**Figure 1.** Soil (2cm) and air temperatures. a) Multi-year record from Endalen, the location from which the soil cores were obtained; b) No Snow, c) Shallow Snow, d) Deep Snow, and e) Air (Svalbard airport, Norwegian Meteorological Institute). 0°C reference indicated by horizontal broken line. Period of campaign indicated in 1a by vertical broken lines. Note differences in temperature and time scales between 1a and 1b-e.

**Figure 2.** Recovery of invertebrates at November and March sampling points (L to R in each panel: No Snow, Shallow Snow, Deep Snow, +7°C). Mean numbers of invertebrates extracted from cores recovered from under three different depths of snow or maintained at constant +7°C are presented. Error bars indicate standard error. N = 4 cores for each treatment and sampling date.

**Table 1.** Mean, maximum and minimum temperatures (°C) of the soil cores and air during autumn (18 Sept 2012 – 13 November 2012) and winter (14 November 2012 - 4 March 2013). Air temperature from the Norwegian Meteorological Institute station at Svalbard airport.

Treatment	Period					
	Autumn			Winter		
	mean	minimum	maximum	mean	minimum	maximum
No snow	-3.5	-21.2	+7.6	-10.7	-26.7	+0.8
Shallow snow	-2.0	-6.3	+1.7	-7.2	-12.3	-0.8
Deep snow	-1.4	-5.1	+5.5	-1.5	-2.2	-1.1
+7°C room	+7.5	+6.6	+9.4	+7.6	+7.4	+8.1
Air	-0.9	-16.9	+9.2	-9.0	-24.0	+3.2

**Table 2.** Frequency of freeze-thaw cycles (number of times temperature changed from negative to positive) in each month of the study.

	2012						
	September	October	November	December	January	February	March
No snow	1	3	1	1	2	0	0
Shallow snow	1	1	0	0	0	0	0
Deep snow	4	1	0	0	0	0	0
Air	3	8	3	4	4	4	0

## Highlights

- Overwintering survival of Arctic soil invertebrates in the natural environment
- With no snow cover soil temperatures dipped to below -26°C and fluctuated between 0 and -24°C
- Temperatures under deep snow were stable and close to 0°C
- No differences in invertebrate survival observed between snow depth manipulations
- Implications for interpretation of laboratory experiments and climate change responses



