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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 its 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 (30 cm) and Deep Snow (120 cm). 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 30 cm 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

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suggest that the studied polar soil invertebrate community may be robust to at least one important predicted consequence of projected 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 practise 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; Seniczak et al., 2014). It comprises a wide range of groups (Jensen and Christensen, 2003; Coulson and Refseth, 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., 2015). 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), and Everatt et al. (2015)). 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., 2003; 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, more rapid changes in temperature 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; Bokhorst et al., 2012; 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; Brussaard 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