

Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community

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The effect of patch size on the tolerance of the soil microarthropod population to an experimentally induced environmental catastrophe, a thick surface ice layer, was studied at a High Arctic site (78°55'N, 11°53'E). Such an ice layer currently occurs infrequently; however, climate change models suggest that the occurrence of such an ice layer is likely to increase in frequency. The experimental approach was a factorial design with two patch sizes, an icing treatment and controls. A thin layer of natural ice was present even in the controls and this was treated as a covariate in the analysis. The soil microarthropod fauna at the experimental site consisted of five species of Collembola and seven species of oribatid mite. The experimental surface ice layer reduced the total number of the soil microarthropods studied by 50%; however, mortality differed between mites and Collembola and species within the two taxonomic groups. Mites were very resistant and showed no significant change, Collembola more sensitive (the populations of *Hypogastrura tullbergi* declined by 56% and *Folsomia quadrioculata* by 54% in the iced treatment plots). The thin annual surface ice layer seemed to have an additional effect on *H. tullbergi* and the mite *Lauroppia translamellata*. That such a thin ice layer could reduce survival was unexpected and could play an important role in determining the extreme patchy distribution of arctic soil animals.

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The formation of a winter surface ice layer is a characteristic feature of Svalbard, an archipelago in the High Arctic, east of Greenland. The thickness of the ice layer varies both spatially and temporally and is dependent on brief thawing events or periods of freezing rain. Climate change models predict that arctic regions will experience a greater than global average increase in mean air temperatures, particularly in the winter when mean air temperatures are predicted to rise by ca 4.0°C by 2040 (Kattenberg et al. 1996). Furthermore, that there will also be an increase in the frequency and extent of severe climatic events, for example summer drought, temperature extremes and the thickness of the winter ground surface ice layer associated with freezing rain and/or brief thawing events during winter (Kattenberg et al. 1996).

Such icing events are suspected of having a deleterious effect on winter survival of arctic Collembola (Leinaas 1999). Species responses to such events are a result of complex interactions between the event, species specific life history traits and the habitat and are hence difficult to extrapolate from current ecological theory.

In tundra regions, a zone that covers 6% of the land area and contains 12% of the global soil carbon pool (Oechel and Vourlitis 1994), the soil microarthropod fauna has an enhanced importance in decomposition processes and soil formation due to the lack of annelid worms. The Collembola and mites also form the principal grazers of the cyanobacteria and hence may have a role in determining the growth rate and productivity of the cyanobacteria which form a conspicuous component

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of many High Arctic soil systems. The cyanobacteria fix atmospheric nitrogen and start plant succession (Dodds et al. 1995, Liengen and Olsen 1997), but, in addition, form a surface crust which stabilises the thin arctic soils and enables higher plant succession to commence (Tishkov 1986, Wynn-Williams 1993). By comparison with the more visible mammals and birds, very little is known about the soil fauna and how the soil system is likely to respond to climatic fluctuations.

The vegetation cover of the High Arctic is often incomplete, forming a naturally highly patchy landscape for the soil microarthropods (Coulson et al. 1993, Wookey et al. 1993, Hertzberg et al. 1994). Habitat patchiness is now recognised as a principal determinant in ecological and evolutionary processes from the level of the individual to communities (Formann 1995, Hansson et al. 1995, Hanski and Simberloff 1997). However, few studies have investigated the interaction of habitat patchiness and environmental stresses on ecological processes. This is somewhat surprising considering the importance of understanding such interactions, not only for general ecological theory (Mangel and Tier 1993), but also for conservation biology (Meffe and Carroll 1997) and evolutionary biology (Shorrocks and Swingland 1990).

Patch size potentially influences population dynamics through several processes. Larger patches are considered to have greater habitat heterogeneity and higher resource levels than small patches. The increased immigration rates to large patches, and reduced emigration compared to small patches (Stamps et al. 1987), combined with a smaller stochastic risk of population crashes, works to increase population performance and species diversity (Root 1973, Dooley and Bowers 1996). It is also predicted that populations inhabiting larger patches will be more robust against environmental catastrophes due to the increased habitat complexity of larger patches providing more refuges (Meffe and Carroll 1997). Empirical studies have often supported this prediction (Matter 1997, Marsh and Pearman 1997), but exceptions have also been reported (Robinson et al. 1992, Dooley and Bowers 1996, Forare and Solbreck 1997, Marsh and Pearman 1997, Eggleston et al. 1998). There is therefore a need to test and examine such theories and predictions using rigorous field experiments.

The use of soil microarthropods as model organisms for the experimental study of patch dynamics has many advantages which include, small size, precise patch manipulation, comparatively short generation time, range of different environmental requirements and often high local abundances (Gonzalez et al. 1998). In addition, the Arctic is a particularly suitable region to undertake such studies because the species diversity of the soil fauna of the Arctic is often reduced in comparison to more southerly latitudes, and the ecology is correspondingly simpler. Finally, patch manipulation experiments are applicable since the methodology only restructures a natural patchy habitat.

Here we report the results of a field experiment aimed at investigating the interaction between patch size and a naturally occurring environmental stress, a winter surface ice layer. The principal aim was to examine the interaction of patch size and climatic stress on the soil microarthropod population density (and assemblage diversity) and examine whether patch size had an effect on population response to an environmental stress. The results are discussed not only in relation to arctic soil biology but to ecological theory as a whole.

Materials and methods

In July 1997, we established 20 plots at Kolhaugen (78°55'N, 11°53'E), the crest of a raised ridge formed from glacial moraine, to the south of Ny-Ålesund, Svalbard. The patchy vegetation was dominated by *Dryas octopetala* and bryophytes, the *Luzula*/lichen heath zone (Anon. 1980). The soil had a depth of ca 3 cm and consisted of a thin organic layer overlying glacial moraine. Consequently the site was well drained and, in the absence of meltwater or precipitation, was relatively dry. The site was selected so as to be level with no obstructions. Hence there were no differences in the thickness of the uniform winter snow lie and summer soil water status across the site.

The 20 plots were subject to two experimental treatments; patch size and ice layer thickness in a randomised 2×2 factorial design. To create two patches of standard sizes, areas of suitable vegetation in each of the plots were marked out, either 12×12 cm or 30×30 cm (144 and 900 cm² respectively, hereafter referred to as “small” and “large” plots). These two areas were selected since they represented large and small patches of *D. octopetala* occurring naturally. The surface vegetation and soil was removed from around the outer edge to a distance of 30 cm in the previous summer. The removed soil was replaced by fine sand collected from an adjacent area. (The open ground thus forming “non-habitat” and restricting the immigration of animals from the “mainland” population).

The thickness of the winter surface ice layer was manipulated by erecting a metal frame around the 20 plots in August. These frames were constructed from sheet aluminium welded at the corners. Each was 25 cm high and so sized as to ensure a gap of 20 cm between the edges of the vegetation patch and the walls of the frame. On 8 January 1998 the frames enclosing five large and five small plots (randomly selected) were brimmed with water which froze during the following 24–48 h (air temperature ca -5 – -18°C).

The thickness of the naturally occurring ice layer was measured in all plots immediately prior to the treatment frames being filled with water in January. The same

measurement was repeated in mid-June 1998 to check that the 25 cm ice layer had been maintained in the experimental plots throughout the winter and to determine how much ice had accumulated within the control plots at the onset of the main spring thaw.

Tinytalk dataloggers were sited to record soil temperatures in the frames (large and small) and an unmanipulated control plot at a depth of 1 cm. Air temperatures were obtained from the Norwegian Meteorological Institute station in Ny-Ålesund.

The ground thawed in mid-late June. However, the samples were collected at the end of the growing season on 10 August. We were therefore able to observe the combined effects of immediate consequences of the icing treatment and the recovery in the subsequent growing season. One sample of 144 cm² and ca 2 cm deep was taken from each plot; i.e. the whole of the small plots and a proportion of the large. Hence the actual volume of extracted soil was equal for both the large and the small patches. The soil microarthropods were extracted at the Univ. of Oslo using a modified MacFadyen high gradient extractor (Leinaas 1978). After extraction the animals were stored, identified and measured in glycerol.

The Collembola and oribatid mites were identified to species. In all, five species of Collembola were identified at Kolhaugen: *Hypogastrura tullbergi* (Schäffer), *Folsomia quadrioculata* (Tullberg), *F. alpha* Grow and Christiansen, *Isotoma anglicana* Lubbock and *Anurida polaris* (Hammer). However, *H. tullbergi* and *F. quadrioculata*

dominated the species assemblage comprising 95% of the total Collembola sample. The juvenile stages of three species of mite, *Camisia anomia* Colloff, *Diapterobates notatus* (Thorell) and *Ceratoppia hoeli* Thor, were differentiated from the respective adults (proto, deuto and tritonymph, excluding larvae). Only adults of the remaining species *Lauroppia translamellata* (Willmann), *Tectocephus velatus* (Michael), *Ceratozetes spitsbergensis* Thor and *Ameronothrus lineatus* (Thorell) were considered. Body lengths of the Collembola were measured to the nearest unit using an eyepiece graticule (0.04 mm) at 25 × magnification. Subsequent analysis grouped the data to provide size classes of 0.08 mm. Body length was used as an indicator of age (Petersen 1971).

Both the populations of *F. quadrioculata* and *H. tullbergi* displayed a bimodal size distribution (Fig. 1). The sample specific distributions were pooled for all treatments and controls to set the appropriate midpoints between the modes (0.72 mm and 0.80 mm for *H. tullbergi* and *F. quadrioculata* respectively) to determine age/size classes for the two species.

Analysis

Log-linear models were fitted to the plot specific counts for each species. Starting from the most complex model which included the two experimental factors (patch size and ice treatment), thickness of natural ice preceding the ice treatment and all two-way interactions between these three main effects, insignificant terms were removed by backward elimination until the model contained only significant terms ($p < 0.05$). To test for eventual differences in the age/size structure in the various species as an effect of the experimental factors and natural ice binomial models were applied in the same manner to the proportion of small individuals/nymphs of the sample totals.

Results

Treatment effects

Of the five species of Collembola only *H. tullbergi* and *F. quadrioculata* had sample counts large enough (mean number of individuals per control sample 66.2 and 117.2 respectively) for robust analyses of treatment effects (Table 1). Of the eight species of mites only *D. notatus*, *C. anomia* and *L. translamellata* could be analysed.

The residual variability from the most complex log-linear model was considerably larger than expected from the Poisson distribution for all species. Residual deviance divided by residual degrees of freedom which is expected to be *1, ranged from 2.7 *D. notatus* to 61.1 in *F. quadrioculata*. Thus aggregated spatial distributions were indicated.

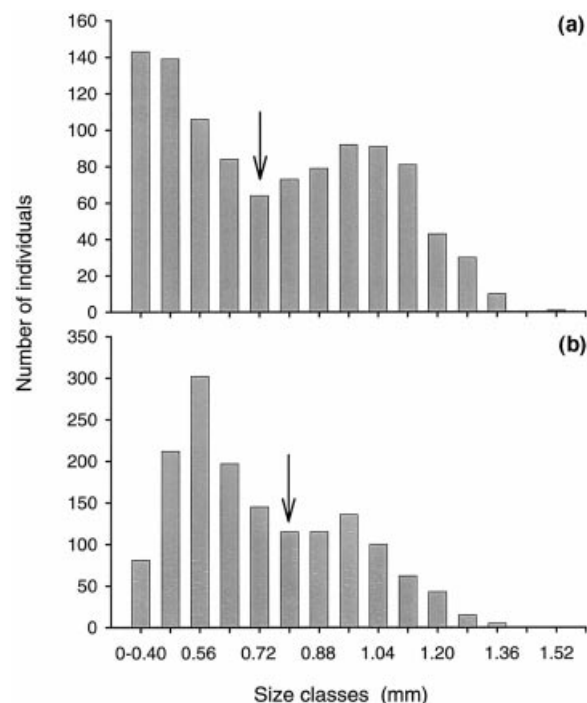


Fig. 1. The size distribution of *H. tullbergi* (a) and *F. quadrioculata* (b) pooled from control and treatment plots. Arrows indicate the midpoints selected (see text).

Table 1. The density of the Collembola and oribatid mite fauna sampled from the Kolhaugen plots (numbers m⁻²).

Species		Plot							
		Small	±SE	Large	±SE	Small-iced	±SE	Large-iced	±SE
<i>H. tullbergi</i>		4486	2006	1819	814	4708	2106	2264	1012
<i>F. quadrioculata</i>		8431	3770	2347	1050	7847	3509	3361	1503
<i>F. alpha</i>		569	255	347	155	236	106	153	68
<i>I. anglicana</i>		0	0	111	50	56	25	28	12
<i>A. polaris</i>		14	6	0	0	42	19	0	0
<i>C. borealis</i>	nymphs	264	264	139	62	931	416	97	43
	adults	194	87	153	68	472	211	69	31
<i>D. notatus</i>	nymphs	222	99	278	124	347	155	181	81
	adults	500	224	431	193	472	211	319	143
<i>C. hoeli</i>	nymphs	14	6	0	0	14	6	69	31
	adults	0	0	0	0	0	0	28	12
<i>A. lineatus</i>	nymphs	0	0	139	62	0	0	0	0
	adults	14	6	14	6	0	0	0	0
<i>L. translamellata</i>		167	75	861	385	681	304	486	217
<i>T. velatus</i>		14	6	0	0	139	62	56	25
<i>C. spitsbergensis</i>		42	19	0	0	0	0	0	0

For both Collembola species analysed ice treatment was significant (*F. quadrioculata*: $\chi^2 = 4.59$, $p = 0.032$, *H. tullbergi*: $\chi^2 = 4.46$, $p = 0.035$). The predicted number of individuals per sample was 2.59 times higher in control than in the ice treatment for *F. quadrioculata* and 2.08 times higher for *H. tullbergi* (Fig. 3). There was an additional effect of natural ice on *H. tullbergi* per sample ($\chi^2 = 4.62$, $p = 0.032$). The model predicted a 67% decrease in numbers from plots with no ice to plots with 60 mm of natural ice, but the scatter was considerable (Fig. 4). Neither patch size nor any of the interaction terms were significant in the log-linear models based on total counts.

For mites the only significant effect was that of natural ice on *L. translamellata* ($\chi^2 = 9.19$, $p = 0.002$). The predicted decrease from 0 to 60 mm natural ice was 82%, but again the scatter was considerable (Fig. 4).

There was no consistent variation in the size/age structure (proportion of small individuals or proportion of nymphs) among the samples for either Collembola or mites as tested by applying quasi-likelihood binomial models to the data.

Soil and air temperatures

The temperature records show no obvious differences between the treatments (Fig. 5). The soil was constantly frozen from 10 September until mid-June. Soil temperature in the small frame rose briefly when the frame was filled in January, but remained below 0°C. A soil minimum of -29.4°C was attained early in March. While there were a couple of freeze/thaw events in September, mean daily air temperature was constantly below 0°C from 6 October until the end of May.

Ice thickness

The thickness of the naturally occurring ice layer on all the plots in January varied from 0 to 60 mm. However, this ice had increased in thickness to between 90 and 150 mm by mid-June. This accumulation of ice must have occurred during the spring thaw in June as the air and soil temperatures were well below freezing between January and the end of May.

Discussion

The faunal assemblage at Kolhaugen was similar to that reported by other authors (Sendstad 1976, Wuthrich 1989, Coulson et al. 1996) for similar localities close to Ny-Ålesund, but poorer in terms of both total densities and species richness. Mean densities of Collembola and oribatid mites being ca 13000 and 1450 m² respectively (Fig. 2). This compares with mean figures of ca 50000 and 8000 for the Collembola and mites from a polar

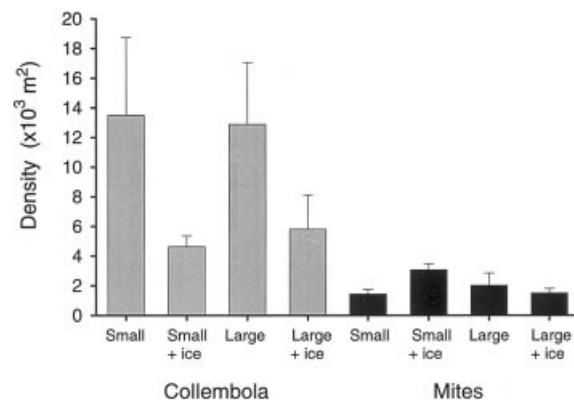


Fig. 2. Numbers of mites and Collembola in the four different plots: large/small, iced/control ($\pm$ SE).

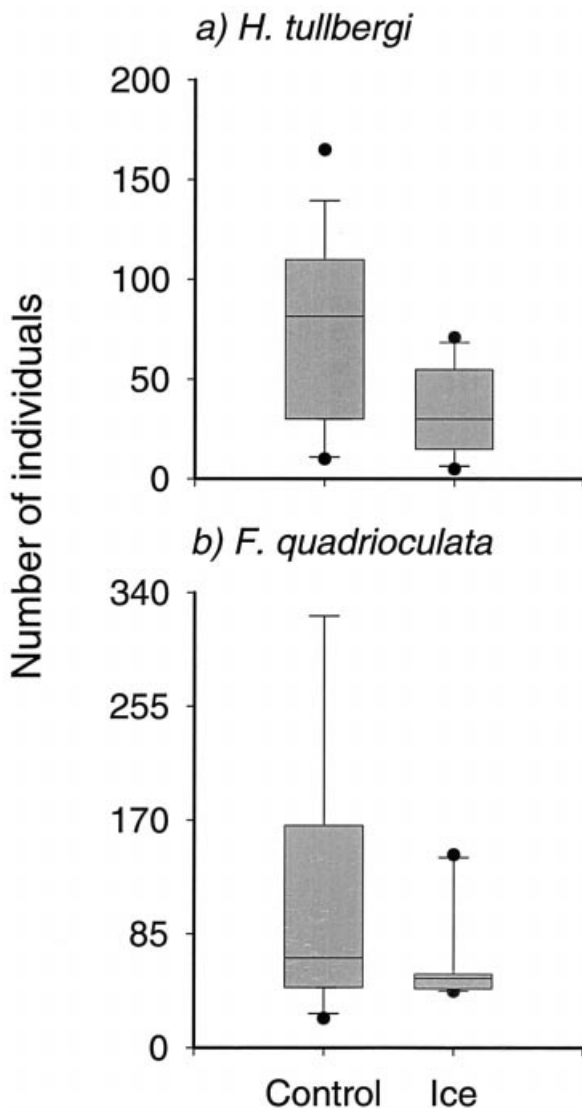


Fig. 3. Box plots showing the sample distributions of *H. tullbergi* (a) and *F. quadrioculata* (b) in the icing and control plots.

semi-desert site two kilometres to the west of Ny-Ålesund (Coulson et al. 1996). Coulson et al. identified eleven species of Collembola and six species of oribatid mite from the semi-polar desert site, compared to five species of Collembola and seven species of oribatid mite in the present study. Therefore despite possessing a greater vegetation cover than the polar semi-desert site, the Kolhaugen site appears to be a more extreme location. This may be due to either a combination of such factors as a more exposed position, thin soils and the risk of desiccation in the summer or a naturally regularly occurring surface ice layer.

Many studies have investigated the effects of either climate fluctuations and change (Strathdee et al. 1993, Wookey et al. 1993, Convey 1997, Hertzberg and Leinaas

1998) or landscape patchiness (Formann 1995, Dooley and Bowers 1996, Hill et al. 1996, Gonzalez et al. 1998), but few have investigated the interaction of both factors simultaneously on population processes. Since it is likely that many of these effects are synergistic, it is difficult, if not impossible, to predict many of the likely consequences from current theory.

The artificial surface ice layer had a dramatic impact on the microarthropod fauna, killing 50% of the total population. However, the mortality was restricted to the Collembola, the mites surviving the treatment relatively unaffected. Population decline in the two principal species, *H. tullbergi* and *F. quadrioculata*, was dramatic, > 54% for both species. However, the other Collembola species showed no such pattern although their numbers were too small to be analysed properly. It is unclear whether this is due to a genuinely greater tolerance to the icing treatment or that the low numbers of these species are masking the negative effects of the treatments.

Although the ice treatment killed a high proportion of the population, there were no differences in the effects between the two patch sizes. It is frequently argued that large patch sizes should support greater population densities than small patches (Root 1973, Stamps et al. 1987, Bowers and Dooley 1993, Ims 1995). It was therefore expected that, due to a combination of greater habitat complexity with the increased number of refuges, higher initial populations and the consequent reduction in the chance of stochastic population crashes, that the

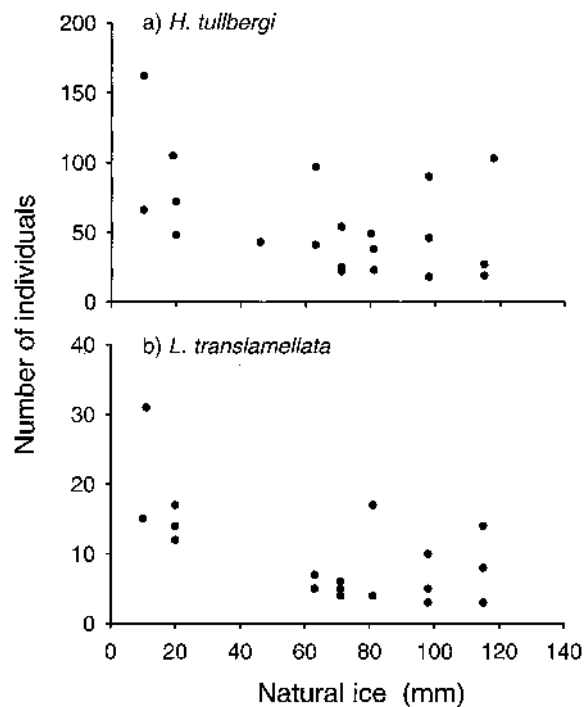


Fig. 4. Relation between the thickness of natural ice and numbers of *H. tullbergi* (a) and *L. translamellata* (b).

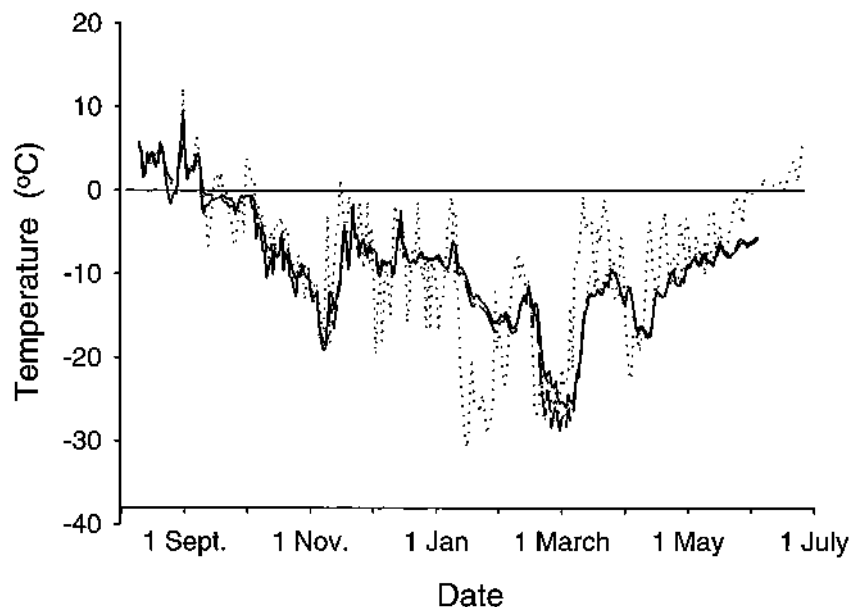


Fig. 5. Mean daily soil and air temperatures at Kolhaugen from August to June, 1997–1998. Soil temperature inside frames —; soil temperatures outside frames - - - - -; air temperature ·····.

microarthropod populations in the large patch sizes should be more robust against the icing treatment than those from the small patches. However, there was no indication of this. This does not necessarily mean that patch size is unimportant under natural conditions. The effect observed here was due to a combination of ice induced mortality and recovery during one growing season. Even if survival rate is unaffected, recovery may be size dependent through the effect of population size on growth rate and extinction risks. Such an effect might have been detected if different patch sizes had been selected. The patch sizes selected in the experiment were chosen so as to be representative of the naturally occurring patches at Kolhaugen and our study might indicate that habitat patchiness is not an important determinant of Collembola population performance in this habitat type. However, other systems have a higher degree of patchiness at differing scales (e.g. smaller tussocks) where an interaction between patch size and icing may be more important.

An unexpected finding was that the thin and variable cover of ice present in the area before the ice treatment had a significant and persistent effect on *H. tullbergi* and the mite *L. translamellata* throughout the study period. The importance of the thickness of the ice on these two species is also evident from the icing experiment which gave a marked effect on plots already covered with up to 50–60 mm of ice. However, the additive effect of natural and experimental icing also shows that the thickness of the ice is not the only important variable. If so, 250 mm of ice would have masked the effect of natural icing completely. Most likely, the results reflect a combined effect of thickness and duration of the ice cover. Judged from the temperature recordings, this ice layer must have been formed ca 3 months earlier, as no

prolonged period of thaw had occurred between 5 October and 30 May (Fig. 5). The effect of duration of ice cover is also indicated by the fact that all control frames were filled up with 90–150 mm of ice in late winter, without masking the effects of either early winter natural icing or of the experimental icing. Formation of an ice layer below the snow cover in late winter has been suggested as an important mortality factor in temperate soil dwelling collembolan species, and a reason why surface dwelling species tend to migrate up into the snowpack (Leinaas 1981, 1983).

It is quite surprising that the effects of a rather thin natural ice layer were so pronounced that it was still evident in two species towards the end of the following growing season. It is therefore important to stress the potential importance of a variable ice layer as a structuring factor in soil communities. The fact that *H. tullbergi* appeared more sensitive to a thin ice layer than *F. quadrioculata* may explain the differential winter mortality between these two species observed by Birkemoe and Sømme (1998). Icing has long been recognised as a mortality factor for microarthropods (Sømme and Conrad-Larsen 1977, Leinaas 1981, Leinaas and Sømme 1984), but no one has explicitly studied population consequences of the surface ice layer. This is in striking contrast to the extensively studied effects of factors such as soil moisture, exposure to winter cold and how species distribution is determined by their drought resistance and cold hardiness (for example, Salt 1936, 1961, Verhoef and van Selm 1983, Leinaas and Fjellberg 1985, Kennedy 1993, Block 1996, Hertzberg and Leinaas 1998, Hodkinson et al. 1999). In light of our results, it seems likely that the formation of a variable surface ice layer may explain some of the patchy distribution of arctic soil microarthropods. It additionally raises questions such as

does the soil microarthropod fauna actively or passively avoid areas with a high incidence of a relatively thick winter surface ice layer.

Only the abundance of *L. translamellata* among the mites was related to the natural winter ice layer. Here there was a population decline with increasing ice thickness, but the scatter is wide. As there was no treatment response observed it cannot be concluded that the mite was directly affected by ice thickness, rather that it may be the duration of icing that is more important for this mite species, than ice thickness per se. The lack of a response to the icing treatments amongst the remaining mite species agrees with earlier studies which have demonstrated the greater tolerance of the oribatid mite fauna to climatic extremes when compared with the Collembola (Worland and Block 1986, Danks 1992, Coulson et al. 1996, Hodkinson et al. 1996, Webb et al. 1998). High tolerance of environmental extremes would be a necessary adjunct to the extended life cycles observed for many species of polar and alpine mite which may span many years (Norton 1994, Convey 1994, 1997, Block and Convey 1995).

Hypogastrura tullbergi has a 2-yr life cycle (Birkemoe and Leinaas 1999). The group of large animals in our August sampling consisted of pre-reproductive adults that had survived the winter as juveniles. The juvenile peak, on the other hand, consisted of animals that hatched from eggs laid in early summer. Thus only one of the two cohorts in our autumn sample had been exposed to differential ice cover during the last winter, while the other one was indirectly affected by the icing via effects on their parents (survival and fecundity). The lack of a demographic difference between treatments indicates that there were no age specific effects of the treatments. *Folsomia quadrioculata* has a more extended reproductive period (Birkemoe and Sømme 1998) and some individuals may reproduce in their second summer, but the lack of treatment effects on demography again suggests that there were no dramatic differences in survival of juveniles and adults.

Conclusion

An environmental catastrophe was simulated by manipulating the thickness of the naturally occurring winter surface ice layer covering two standardised sizes of natural landscape patches. Patch size had no effect on the tolerance of the soil microarthropod fauna to the experimental stress. The overall effect of this catastrophic event was to reduce the Collembola populations by ca 54%, but there was no effect on the oribatid mite community. An unexpected observation was the great sensitivity of the Collembola fauna to the natural ice layer, which may be only a few centimetres indicating an interaction of duration of the ice layer with ice thickness.

With the predicted increased occurrence of such ice it is to be expected that the Collembola populations will experience more frequent population crashes. It is unknown how the warmer but dryer summers will act to mitigate or exacerbate the reduction in the populations. Various authors (for example Coulson et al. 1996, Webb et al. 1998) have demonstrated how hot dry summers at a similar site had a deleterious effect on Collembola numbers but less of an effect on the mite populations. The response of the soil fauna inhabiting a landscape with patches of different sizes to those selected in this experiment is unknown. As the soil fauna has such an important role in nutrient recycling in these (O'Lear and Seastedt 1994) and other soils (Lavelle et al. 1997, Rusek 1998, Sulkava and Veikko 1998), the knock-on effects to the general ecology of the system are also unclear.

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References

- Anon. 1980. Vegetasjonskart. Brøggerhalvøya, Svalbard. S10 V28H60 Ny-Alesund. – Det Norske Polarinstituttet, Oslo.
- Birkemoe, T. and Sømme, L. 1998. Population dynamics of two collembolan species in an Arctic tundra. – *Pedobiologia* 42: 131–145.
- Birkemoe, T. and Leinaas, H. P. 1999. Reproductive biology of the arctic collembolan *Hypogastrura tullbergi*. – *Ecography* 22: 31–39.
- Block, W. 1996. Cold or drought – the lesser of two evils for terrestrial arthropods? – *Eur. J. Entomol.* 93: 325–339.
- Block, W. and Convey, P. 1995. The biology, life-cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus*. – *J. Zool.* 236: 431–449.
- Bowers, M. L. and Dooley, J. L. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. – *Oecologia* 94: 247–254.
- Convey, P. 1994. Growth and survival strategy of the Antarctic mite *Alaskozetes antarcticus*. – *Ecography* 17: 97–107.
- Convey, P. 1997. How are the life history strategies of Antarctic terrestrial invertebrates influenced by extreme environmental conditions? – *J. Thermal Biol.* 22: 429–440.
- Coulson, S. J. et al. 1993. Simulated climate change: the interaction between vegetation type and microhabitat temperatures at Ny Alesund, Svalbard. – *Polar Biol.* 13: 67–70.
- Coulson, S. J. et al. 1996. Effects of experimental temperature elevation on High-Arctic soil microarthropod populations. – *Polar Biol.* 16: 147–153.
- Danks, H. V. 1992. Arctic insects as indicators of environmental change. – *Arctic* 45: 159–166.
- Dodds, W. K., Gudder, D. A. and Mollenhauer, D. 1995. The ecology of *Nostoc*. – *J. Phycol.* 31: 2–18.
- Dooley, J. L. and Bowers, M. A. 1996. Influences of patch size and microhabitat on the demography of two old-field rodents. – *Oikos* 75: 453–462.
- Eggleston, D. B., Hetherington, L. and Ward, E. 1998. Organisms response to habitat patchiness: species and habitat-dependent recruitment of a decapod crustacean. – *J. Exp. Mar. Biol. Ecol.* 223: 111–132.

- Forare, J. and Solbreck, C. 1997. Population structure of a monophagous moth in a patchy landscape. – *Ecol. Entomol.* 22: 256–263.
- Formann, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions. – Cambridge Univ. Press.
- Gonzalez, A. et al. 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. – *Science* 281: 2045–2047.
- Hanski, I. and Simberloff, D. 1997. The metapopulation approach, it's history, conceptual domain and application to conservation. – In: Hanski, I. and Gilpin, M. E. (eds), *Metapopulation biology, genetics and evolution*. Academic Press, pp. 5–26.
- Hansson, L., Fahrig, L. and Merriam, G. 1995. Mosaic landscapes and ecological processes. – Chapman and Hall.
- Hertzberg, K. and Leinaas, H. P. 1998. Drought stress as a mortality factor in two pairs of sympatric species of *Collembola* at Spitsbergen. – *Polar Biol.* 19: 302–306.
- Hertzberg, K., Leinaas, H. P. and Ims, R. A. 1994. Patterns of abundance and demography: *Collembola* in a habitat patch gradient. – *Ecography* 17: 349–359.
- Hill, J. K., Thomas, C. D. and Lewis, O. T. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. – *J. Anim. Ecol.* 65: 725–735.
- Hodkinson, I. D. et al. 1996. Can Arctic soil microarthropods survive elevated summer temperatures? – *Funct. Ecol.* 10: 314–321.
- Hodkinson, I. D. et al. 1999. Hydrology, water availability and tundra ecosystem function in a changing climate: the need for a closer integration of ideas? – *Global Change Biol.* 5: 359–369.
- Ims, R. A. 1995. Movement patterns in relation to landscape structures. – In: Hansson, L., Fahrig, L. and Merriam, G. (eds), *Mosaic landscapes and ecological processes*. Chapman and Hall, pp. 85–109.
- Kattenberg, A. et al. 1996. Climate models – projections of future climate. – In: Houghton, J. J. et al. (eds), *Climate change 1995: the science of climate change*. Contrib. of Working Group I to the Sec. Ass. Rep. of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, pp. 285–357.
- Kennedy, A. D. 1993. Water as limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. – *Arct. Alp. Res.* 25: 308–315.
- Lavelle, P. et al. 1997. Soil invertebrate function in a changing world: the role of invertebrate ecosystem engineers. – *Eur. J. Soil Biol.* 33: 159–193.
- Leinaas, H. P. 1978. Sampling of soil microarthropods from coniferous forest podzol. – *Norw. J. Entomol.* 25: 57–62.
- Leinaas, H. P. 1981. Activity of arthropods in snow within a coniferous forest, with special reference to *Collembola*. – *Holarct. Ecol.* 4: 127–138.
- Leinaas, H. P. 1983. Winter strategy of surface dwelling *Collembola*. – *Pedobiologia* 25: 235–240.
- Leinaas, H. P. 1999. *Collembola* in the Arctic. Adaption to and consequences of environmental change (*Collemboler i Arktis. Tilpasninger til og konsekvenser av miljøvariasjoner*). – In: Bengtson, S. A., Mehlum, F. and Severinson, T. (eds), *The terrestrial ecology of the Svalbard tundra* (Svalbardtundraens økologi). Norsk Polarinstitut, Tromsø, pp. 55–66.
- Leinaas, H. P. and Sømme, L. 1984. Adaptations in *Xenylla maritima* and *Anurophorus laticis* (*Collembola*) to lichen habitats on alpine rocks. – *Oikos* 43: 197–206.
- Leinaas, H. P. and Fjellberg, A. 1985. Habitat structure and life history strategies of two partly sympatric and closely related lichen feeding collembolan species. – *Oikos* 43: 448–458.
- Liengen, T. and Olsen, R. A. 1997. Seasonal and site specific variations in nitrogen fixation in a High Arctic area, Ny-Ålesund, Spitsbergen. – *Can. J. Microbiol.* 43: 759–769.
- Mangel, M. and Tier, C. 1993. Dynamics of metapopulations with demographic stochasticity and environmental catastrophes. – *Theor. Popul. Biol.* 44: 1–31.
- Marsh, D. M. and Pearman, P. B. 1997. Effects of habitat fragmentation on the abundance of two species of lepto-dactylid frogs in an Andean Montane forest. – *Conserv. Biol.* 11: 1323–1328.
- Matter, S. F. 1997. Population density and area: the role of between and within patch processes. – *Oecologia* 110: 533–538.
- Meffe, G. K. and Carroll, C. R. 1997. Principles of conservation biology. – Sinauer.
- Norton, R. A. 1994. Evolutionary aspects of oribatid mite life histories and consequences for the origin of the Astigmata. – In: Houck, M. A. (ed.), *Mites. Ecological and evolutionary analyses of life history patterns*. Chapman and Hall, pp. 99–135.
- Oechel, W. C. and Vourlitis, G. L. 1994. The effects of climate change on land-atmosphere feedbacks in Arctic tundra regions. – *Trends Ecol. Evol.* 9: 324–329.
- O'Lear, H. A. and Seastedt, T. R. 1994. Landscape patterns of litter decomposition in alpine tundra. – *Oecologia* 99: 95–101.
- Petersen, H. 1971. Methods for estimation of growth in *Collembola* in cultures and in the field, exemplified by preliminary results for *Onychiurus furcifer* (Börner). – *Annales de Zoologie, Ecologie Animale* 1971: 235–254.
- Robinson, G. R. D. et al. 1992. Diverse and contrasting effects of habitat fragmentation. – *Science* 257: 524–526.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). – *Ecol. Monogr.* 43: 95–124.
- Rusek, J. 1998. Biodiversity of *Collembola* and their functional role in the ecosystem. – *Biodiv. Conserv.* 7: 1207–1219.
- Salt, R. W. 1936. Studies on the freezing process in insects. – *Tech. Bull. Minnesota Agricult. Exp. Station* 116: 1–41.
- Salt, R. W. 1961. Principles of insect cold hardiness. – *Annu. Rev. Entomol.* 6: 55–74.
- Sendstad, E. 1976. Notes on the *Collembola* communities in some major plant-sociological associations at Spitsbergen, Svalbard. – *Norw. J. Entomol.* 23: 143–148.
- Shorrocks, B. and Swingland, I. R. (eds) 1990. *Living in a patchy environment*. – Oxford Univ. Press.
- Sømme, L. and Conradi-Larsen, E. M. 1977. Anaerobiosis in overwintering collembolans and oribatid mites from windswept mountain ridges. – *Oikos* 29: 127–132.
- Stamps, J. A., Buechener, M. and Krishnan, V. V. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. – *Am. Nat.* 129: 533–552.
- Strathdee, A. T. et al. 1993. Effects of temperature elevation on a field population of *Acyrtosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. – *Oecologia* 96: 457–465.
- Sulkava, P. and Veikko, H. 1998. Habitat patchiness affects decomposition and faunal diversity: a microcosm experiment on forest floor. – *Oecologia* 116: 390–396.
- Tishkov, A. A. 1986. Primary succession in Arctic tundra on the west coast of Spitsbergen (Svalbard). – *Polar Geography Geol.* 10: 148–156.
- Verhoef, H. and van Selm, A. J. 1983. Distribution and population dynamics of *Collembola* in relation to soil moisture. – *Holarct. Ecol.* 6: 387–394.
- Webb, N. R. et al. 1998. The effects of experimental temperature elevation on populations of cryptostigmatic mites in High Arctic soils. – *Pedobiologia* 42: 298–308.
- Wookey, P. A. et al. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in Sub-Arctic and High Arctic plants. – *Oikos* 67: 490–502.
- Worland, M. R. and Block, W. 1986. Survival and water loss in some Antarctic arthropods. – *J. Insect Physiol.* 32: 579–584.
- Wuthrich, C. 1989. Die Bodenfauna in der Arktischen Umwelt des Kongsfjords (Spitzbergen). – *Materialien zur Physiogeographie* 12 Basel.
- Wynn-Williams, D. D. 1993. Microbial processes and initial stabilization of fellfield soil. – In: Miles, J. and Walton, D. W. H. (eds), *Primary succession on land*. Blackwell, pp. 17–32.