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Measuring the effects of reduced snow cover on Australia's alpine arthropods

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Abstract

Snow is one of the most important factors in the ecology of alpine ecosystems. In Australia, both the depth and duration of snow cover have declined significantly in recent decades, and this trend is projected to continue with global warming. Many small arthropods remain active throughout the winter, within a space beneath the snowpack (subnivean) where the snow's insulation creates a thermally stable environment. Using field surveys and experimental manipulation of snow depth at two locations in the Australian alpine region, we explored the diversity of winter-active arthropods and their response to reduced snow. Individuals from 18 arthropod Orders were detected beneath the snow during winter, with the Collembola, Araneae, Acari and Coleoptera accounting for 95 – 98% of the individuals collected. The subnivean taxa represented a distinct subset of those active outside the winter months. Removal of the snow layer increased daily temperature fluctuations, increased the number of days below freezing and raised the mean surface temperatures. Community composition was altered by snow removal, driven by changes in the numbers of two abundant springtail taxa at each location. We found a strong reduction in the abundances of both taxa at one study site, and contrasting responses (one strong positive and one strong negative) to snow removal at the second study site. Subnivean arthropod communities in Australia thus appear sensitive to snow conditions at small spatial scales.

Keywords: Alpine, arthropods, climate change, snow, winter

Introduction

Snow is considered one of the most important factors governing the ecology of alpine ecosystems (Billings and Mooney 1968; Mani 1968). It determines the timing and length of the growing season, controls soil nutrient influxes and moderates local and regional hydrology (Blankinship and Hart 2012; Körner 2003; Vavrus 2007). The snow pack also creates a thermally stable subnivean microclimate, often close to 0°C, in which overwintering flora and fauna are buffered from freezing air temperatures and large daily temperature

fluctuations (Geiger *et al.* 1995; Pauli *et al.* 2013). The snow layer thus functions as a barrier between the cold, dry and variable atmospheric conditions and the relatively warm, humid and constant subnivean environment.

Snow, however, has an uncertain future. Since the late 1960s, global snow cover has decreased by 10% and many mountain regions have experienced declines in snow depth and duration (Lemke *et al.* 2007; Stewart 2009). This effect is particularly apparent at middle elevations (1500 – 2000m a.s.l.) and during the spring, when mean air temperatures are close to freezing and even a small rise in temperature causes a large increase in the proportion of precipitation falling as rain rather than snow (Brown and Mote 2009; Steger *et al.* 2013). As a consequence, a shorter snow season and earlier snowmelt are expected to be the first and largest effects of climate change across mountain systems (Brown and Mote 2009; Räisänen 2008).

For winter-active arthropods, snow creates three distinct habitats: the snow surface, the snow layer itself, and a space between the soil surface and the base of the snow pack (the “subnivean space”) (Aitchison 2001). Here we focus on the subnivean space, which forms when physical objects – such as vegetation – support freshly falling snow, and when latent heat from the soil melts the lowest layers of the snowpack (Marchand 2013). Many arthropods remain active within this space during winter, with Collembola (springtails), Acari (mites and ticks), Araneae (spiders), Diptera (flies) and Coleoptera (beetles) being particularly common (Aitchison 2001; Green 1997; Vanin and Turchetto 2007).

Predictions for the effects of reduced snow on alpine ecosystems fall into two broad categories. On the one hand, higher maximum temperatures and advanced snowmelt could increase productivity in alpine ecosystems (Billings and Bliss 1959). Alternatively, a shallow snow pack or early snowmelt, and consequent loss of the insulating layer, might expose alpine flora and fauna to the damaging effects of frost and a fluctuating thermal environment (Gerdol *et al.* 2013; Marshall and Sinclair 2012a; Wipf and Rixen 2010). Although several studies have experimentally tested the effects of reduced snow cover on alpine plants (reviewed: Wipf and Rixen 2010), only three have measured arthropod responses, all post-thaw (Adler *et al.* 2007; Leingärtner *et al.* 2014; Roy *et al.* 2004).

Laboratory and field experiments from the sub-Arctic, Arctic, and hardwood forests of North America suggest that changes to soil freeze-thaw dynamics can alter the composition

of soil arthropod communities (e.g. Konestabo *et al.* 2007; Sulkava and Huhta 2003). Springtails appear particularly responsive to small-scale climate manipulations. For example, supplementation of winter ice in the Arctic caused a 50% decline in springtail abundance (Coulson *et al.* 2000). Springtails are common in alpine habitats and many species remain active at temperatures near 0°C (Chapman 1954). They might therefore serve as sensitive indicators of changes in microhabitat conditions brought about by reduced snow cover (Convey *et al.* 2003; Greenslade 2013).

On the Australian mainland, snow seasonally covers an area of roughly 1675 km² for two or more months each year but, even at the highest elevations, the snowpack is marginal and daytime temperatures often exceed 0°C (Sanecki *et al.* 2006). Although Australian snow cover is naturally variable, the last 40 years have seen a large decline in mean spring snow depth (~40%) (Nicholls 2005), a reduction in total snow accumulation of nearly 10% (Fiddes *et al.* 2015), and shortening of the snow season by 18 – 22 days (Bhend *et al.* 2012; Sánchez-Bayo and Green 2013). Climate models predict further declines in both the depth and duration of snow cover on the Australian mainland (Hendrikx *et al.* 2013). In some areas, forecasts for maximum snow depths (0 – 30 cm) lie perilously close to the 20 cm depth threshold typically required to effectively insulate the subnivean environment from atmospheric temperature fluctuations (Bhend *et al.* 2012; Geiger *et al.* 1995).

With the exception of studies on the overwintering energetics of the iconic mountain pygmy possum (*Burramys parvus*) (Geiser and Broome 1993; Körtner and Geiser 1998) and seedling establishment in the snow gum (*Eucalyptus pauciflora*) (Ferrar *et al.* 1988), the effects of a changing winter snowpack on the Australian mountain biota are restricted to anecdotal reports. Green (1997), for example, ascribed a low number of arthropods in spring of one year to a late snowfall, while the numbers of *Kosciuscola* grasshoppers are apparently reduced following low-snow winters (Green and Osborne 2012). Recent summer warming experiments suggest that Australia's alpine arthropod communities are responsive to changes in environmental conditions (Nash *et al.* 2013), but there is little relevant information on which taxa are active during winter or their sensitivity to snow conditions.

This study focused on arthropod taxa that are active in the subnivean space. We focus on this group because arthropods are abundant in Australian alpine ecosystems (Green and Osborne 2012), they are typically responsive to changes in abiotic conditions (Chown & Nicolson 2004), and their small size allows experimental manipulations at ecologically

meaningful spatial scales (e.g. Nash *et al.* 2013). Our study had two primary goals. The first was to characterise Australia's winter-active subnivean arthropod fauna, adding to the sole published study of this ecosystem to-date (Green 1997). The second was to test the response of these taxa to reduced snow cover. With these goals in mind, we explored three key questions: (a) what arthropods are active in the subnivean space and are these distinct from those in the snow-free months?; (b) does the absence of a snowpack cause a shift in arthropod community composition?; and (c) do the numbers of dominant springtail taxa increase (predicted by warmer maximum temperatures) or decrease (colder minimum temperatures/greater thermal fluctuations) in response to reduced snow cover?

Methods

Study area

This study was carried out at two sites (Fig. 1) over four consecutive years (2013 – 2016). The first site, used in 2013 and 2015, was at Mt Stirling, Victoria, on the west-southwest-facing side of the summit, at 1700 m a.s.l. (37.12732°S, 146.49663°E). This site is within the Mt Stirling ski resort and the surrounding land is used for recreational activities throughout the year. The second site, used in 2014 and 2016, was on the eastern slopes of Mt Twynam, New South Wales, within the Western Fall Wilderness Area of Kosciuszko National Park, at 1700 m a.s.l. (36.39248°S, 148.35070°E). The two sites have similar vegetation structures of tall herbfield/grassland interspersed with low shrubs (McDougall and Walsh 2007).

The two sites experienced similar mean snow depths during the study, but there was considerable variation in snow depth and duration between years (Table 1, Appendix S1). Once snow began to accumulate, it persisted through to snowmelt in 2014 and 2015. However, the snow pack melted to less than 5 cm twice during the 2013 and 2016 winters. Sanecki *et al.* (2006) described Australian snow as “warm-temperate-tropical”, characterised by a snow-ground interface temperature between 0°C and 1°C, a high density (e.g. mean spring snow density is 0.4 g cm⁻³), rapid densification over winter, a weak vertical temperature gradient, and high inter-annual variability.

Subnivean arthropod communities

At each study site, one year was used only to monitor subnivean arthropod activity, while experimental treatments to test the effect of reduced snow cover on arthropod communities were imposed in the other year. New plots were established in each year.

Subnivean arthropod activity was recorded at Mt Stirling in 2013 and Mt Twynam in 2016. At each site, we established eight 1 m x 1 m plots and installed three pitfall traps (15 mm diameter glass test tubes, containing 5 mL of 1:1 propylene glycol:ethanol) within each plot (total 24 traps). Narrow traps were used to minimise the risk of vertebrate bycatch. Traps were activated during the autumn at Mt Stirling, and during the winter and spring at both sites (see Table 1). Winter traps were set in the subnivean space. These were installed and changed by means of an access tube installed prior to snowfall, which minimised disturbance (Appendix S2). Temperature loggers (Thermochron iButton DS1922L) were installed 1 cm above the soil surface in each of four plots (Mt Stirling) or every plot (Mt Twynam), and set to record temperature ($\pm 0.06^{\circ}\text{C}$) hourly.

Snow removal experiment

We tested the effects of reduced snow on subnivean arthropods by manual snow removal at Mt Twynam in 2014 and Mt Stirling in 2015 (Table 1). At both sites, we established blocks with one treatment and one control plot each. Within each block, the two 1 m x 1 m plots were separated by approximately 2 m and blocks were arranged 4 – 10 m apart. Three pitfall traps were installed within each plot, along with an access tube, and were changed every two – three weeks during the experimental period (Table 1). Over the winter, snow was manually cleared weekly from treatment plots, as well as a 50 cm margin around each plot. A 5 cm layer of snow was left undisturbed to prevent damage to vegetation. This snow depth is insufficient to provide thermal buffering effects (Geiger *et al.* 1995). We installed temperature loggers in both plots for five blocks (Twynam) or all blocks (Stirling).

Unusually heavy snowfall at the beginning of the 2014 winter, coupled with snowdrift, meant that half of the plots at Mt Twynam could not be accessed until later in the season so, within the experimental period, three treatment plots were kept snow-free for nine weeks and three for two weeks. In addition, differences in the timing of snowmelt among blocks (the first control plot melted on September 10th and the last on October 7th) meant that spring trapping at Mt Twynam continued for either five weeks (three blocks) or three weeks (two blocks). No spring data were obtained for one block, as snow did not melt within the experimental period. At Mt Stirling, trapping after September 19th was designated as “spring” for all blocks (Table 1).

Microclimate data analysis

Data from loggers were used to calculate summary temperature measures and the number of days where the minimum temperature was below 0°C (a proxy for the number of freeze-thaw cycles) for each year/site and trapping period. Snowmelt date was determined either from direct observation or from the temperature loggers. For the latter, snowmelt was defined as when the temperature first rose above 3°C at midday $\pm$ 2 h (Pickering and Green 2009).

Identification and pre-analysis data processing

All individuals in pitfall traps were counted and identified to Order under a stereo microscope (Leica M125). Three dominant winter-active groups (springtails, beetles, spiders) were identified to family level or below. Mites were abundant but, as approximately half of individuals were juveniles and could not be identified to family level, only adult Oribatida and Bdellidae were included in subsequent analyses. Including unidentified mites as a pooled group in the analyses did not qualitatively change the outcomes (results not shown). Identifications were made with the aid of relevant taxonomic keys, descriptive texts, and expert advice (P Greenslade, A Ślipiński, R Leschen, J Reid, M Rix).

For the multivariate analyses of experimental treatments in 2014 and 2015, we focused on taxa that accounted for at least 1% of the total sample. For Mt Twynam, the analysis included: nine springtail morphospecies from eight genera (*Paronellides*, *Pseudoparonella*, *Drepanura*, *Lepidophorella*, *Brachystomella*, *Triacanthella*, *Skadisotoma*, *Katianna*), two mite taxa (Bdellidae, Oribatida), and one spider family (Linyphiidae). For Mt Stirling, the taxa included were: five springtail morphospecies/species from five genera (*Acanthomurus*, *Katianna*, *Ceratophysella*, *Brachystomella*, *Tullbergia*), one mite family (Bdellidae), and two spider morphospecies (family Amphinectidae and family Micropholcommatidae, genus *Raveniella*).

Prior to analysis, data were pooled for the three traps within a plot. Traps that failed to catch any arthropods were deemed to be incorrectly installed, and were excluded from analysis (2014: 10/109 traps; 2015: 5/234 traps). Data were then standardised to number per trap-week. In 2014, counts within a plot were pooled for the whole winter period, as numbers were very low (with the exception of two common taxa, median number of individuals/trap-week = 3) and the number of sampling periods was uneven between blocks.

207 *Statistical analysis of snow removal experiment*

208 All analyses described below were carried out in R 3.2.2 (R Core Team 2015) and plots were
209 constructed with GGPLOT2 1.0.1 (Wickham 2009).

210 (1) Does the absence of a snowpack cause a shift in arthropod community composition?

211 We used non-metric multidimensional scaling (NMDS), implemented in VEGAN 2.3-0
212 (Oksanen *et al.* 2015), to visualise variation in community structure due to experimental
213 effects (Minchin 1987). These analyses were based on the restricted dataset of dominant taxa,
214 described above. NMDS was performed using a Bray-Curtis dissimilarity index (Bray and
215 Curtis 1957) to preserve rank order (Faith *et al.* 1987). Transformation (square-root) was
216 limited to particularly abundant groups (*Pseudoparonella*, *Paronellides* in 2014). We used
217 two (Twynam) or three (Stirling) dimensions and up to 20 random starts to avoid local
218 optima and find a stable solution with a stress0.1 (Clarke 1993). Principal components
219 were rotated and centred using VEGAN 2.3-0 (Oksanen *et al.* 2015), so that the variance of
220 points was maximised along the first axis and the origin was at the average of the axes. Axis
221 scores from the final run were used for subsequent exploratory analyses.

222 To test for an effect of treatment on axis score, we used either (a) paired t-tests
223 (Twynam, Stirling autumn, Stirling spring) or (b) linear mixed models with treatment (two
224 levels), trapping date (“time”, three levels), and a treatment-time interaction as fixed factors,
225 and block and plot as random factors to account for repeated sampling (Stirling winter). We
226 tested the significance of fixed factors using parametric bootstrap of the likelihood-ratio test
227 statistic, T , based on stepwise removal of factors. Bootstrapping was performed with 1000
228 simulations using PBKRTEST 0.4-2 (Halekoh and Højsgaard 2014), and mixed models were
229 implemented using LME4 1.1-9 (Bates *et al.* 2014).

230 To test the effects of (a) treatment (Twynam, Stirling autumn, Stirling spring) or (b)
231 treatment and trapping date (Stirling winter) on community composition, we used a
232 PERMANOVA (Anderson 2001) with a Bray-Curtis distance matrix. The Mt Stirling winter
233 data were analysed in a two-step process. First, the treatment and block factors were tested
234 using centroids for each plot (i.e. across the three trapping periods). Second, the effects of
235 trapping period and an interaction between treatment and trapping period were tested, with a
236 block-by-treatment factor included to remove between-plot variation from the residual error

term. PERMANOVA analyses were carried out with VEGAN 2.3-0 (Oksanen *et al.* 2015), using 999 permutations.

PERMANOVA is robust to heterogeneity in dispersion for balanced designs (Anderson and Walsh 2013). Nevertheless, we tested for differences in group dispersions (Anderson 2006) and a Bray-Curtis distance matrix. The average dissimilarity of an individual (e.g. plot) to the group (e.g. treatment) centroid can also be used to assess beta diversity (Anderson *et al.* 2006). We used 999 permutations with no restrictions for the Mt Twynam and Mt Stirling autumn/spring analyses. For Mt Stirling winter, permutations were permitted among trapping periods within plots (with a restriction that the same permutations were used across plots), and among plots within trapping periods. Permutations were defined using PERMUTE 0.8-4 (Simpson 2015).

(2) Do the numbers of dominant springtail taxa change in response to reduced snow cover?

An effect of snow removal was tested on two common springtail morphospecies at each site: *Paronellides* sp. and *Pseudoparonella* sp. at Mt Twynam, and *Brachystomella* sp. and *Ceratophysella pauciseta* at Mt Stirling. We used (a) paired Wilcoxon tests (Twynam, Stirling autumn, Stirling spring) or (b) a generalised linear mixed model with a negative binomial distribution (Stirling winter), implemented in LME4 1.1-9 (Bates *et al.* 2014). Treatment, trapping date, and their interaction were included as fixed factors with block and plot as random factors. The significance of fixed factors was tested using parametric bootstrap of the likelihood-ratio test statistic with 1000 simulations, using PBKRTEST 0.4-2 (Halekoh and Højsgaard 2014). Note that for Mt Twynam, the length of snow removal did not have a strong effect on either abundance or the treatment effect (see Results, and Appendix S3), so we did not include it in these analyses.

At Mt Stirling, snow removal plots were filled by fresh snow between one and three days after clearing during the early and mid-winter trapping periods (see Results). Only in the late winter (August 30th – September 19th) were snow removal plots snow-free for most/all of the trapping period. We therefore ran separate ordination, PERMANOVA, dispersion and abundance analyses for this trapping period.

For simplicity, we refer to the period during which the ground is snow-covered as “winter”. Unless otherwise stated, data are presented as mean $\pm$ s.d.

Results

Subnivean microclimates and abiotic effects of snow removal

Across sites and years, subnivean temperatures varied little (2013: $0.7 \pm 0.6^{\circ}\text{C}$, 2014: $0.5 \pm 0.3^{\circ}\text{C}$, 2015: $0.5 \pm 1.4^{\circ}\text{C}$, 2016: 0.4 ± 0.8) with snow almost completely buffering ground surface temperature fluctuations (Figs. 2, 3).

At Mt Twynam, snow removal plots were completely snow free an average five days before control plots, with mean melt-out dates of September 18th and September 23rd, respectively while at Mt Stirling, snow removal plots were snow-free an average four days before control plots, with mean melt-out dates of September 13th and September 17th, respectively.

Experimental snow removal plots experienced greater temperature fluctuations, more days with minimum temperatures below 0°C (Mt Twynam: 39 vs 0 days; Mt Stirling: 15 vs 3 days), higher maximum temperatures and, at Mt Twynam, warmer mean temperature (Figs. 2, 3; Appendix S1). These effects became more pronounced through the winter, as subnivean temperatures in control plots gradually decreased (Mt Twynam) or stayed constant (Mt Stirling) and maximum temperatures in snow removal plots increased (Figs. 2, 3).

Subnivean communities

A total of 32,106 individuals from 18 arthropod orders were caught across 956 trap-weeks in the four years of the study, with numbers consistently higher in spring than in autumn or winter (see Appendix S3 for details of taxa detected).

The subnivean fauna at both locations and in all years was numerically dominated by four taxa – springtails, mites, beetles, spiders – which together accounted for 96 – 98% of the individuals in winter pitfall traps (Fig. 4). These taxa were less dominant in the snow-free months, when they comprised 58 – 93% of the individuals detected. This difference was due in large part to the absence of ants (primarily *Iridomyrmex* sp.) during winters: ants were detected only when plots were snow-free for part or all of a trapping period, but were detected in 37 of 38 spring plots across the whole study, often in high numbers (94 ± 133 individuals in plots with at least 1 ant).

Of the 19 taxa collected at Mt Stirling during 2013 and 2015, five (Chilopoda, Orthoptera, Thysanoptera, Lepidoptera, Dermaptera) were found only when plots were snow-

free for at least some of the trapping period and one (Copepoda, family Canthocamptidae) was found solely during the winter (see Appendix S3 for details). Copepods were found in a single plot in 2013, where they were highly abundant in both July ($n = 2848$) and September ($n = 480$). At Mt Twynam, only 10 of the 18 taxa collected were represented by more than 2 individuals in a given year (Appendix S3). Three of these (Oligochaeta, Pseudoscorpionida, Symphyla) were detected only during the winter, in both years, but were rare.

The springtail fauna was consistent among years within a site but, whereas the fauna was dominated by Poduromorpha (families Brachystomellidae, Hypogastruridae, and Neanuridae) at Mt Stirling, the Mt Twynam springtails were primarily Entomobryomorpha (families Paronellidae, Isotomidae, Entomobryidae and Tomoceridae). These groups each accounted for over half of all the arthropods captured during winter at their respective locations and 77 – 89% of the springtails (82 – 99% of springtails in spring). At each site, two morphospecies were numerically dominant: *Brachystomella* sp. (33 – 78% of springtails within a trapping period) and *C. pauciseta* (12 – 58%) at Mt Stirling; *Pseudoparonella* sp. (20 – 68%) and *Paronellides* sp. (6 – 39%) at Mt Twynam.

Beetles were the most common insect in winter pitfall traps in all years but their composition differed between the mountains. At Mt Stirling, individuals from 19 families were detected throughout the study but only nine were found during winter. All of the nine families detected at Mt Twynam were present in both winter and spring. The most common families at Mt Stirling were, in order of abundance, Staphylinidae, Leiodidae, Carabidae and Curculionidae. By contrast, only four families (in order of abundance: Curculionidae, Carabidae, Staphylinidae, Latridiidae) were represented by more than one individual at Mt Twynam. Beetles were particularly scarce in 2016, with only nine individuals in winter traps.

Spiders from 14 families were detected at Mt Stirling across the two years, but individuals from only six families were found in subnivean traps (Appendix S3). Of these, the Amphinectidae (two morphospecies), Micropholcommatidae (one morphospecies, genus *Raveniella*), and Amaurobiidae were the most numerous. Seven spider families were detected in subnivean pitfall traps at Mt Twynam, with Linyphiidae the most common group (Appendix S3).

Effects of reduced snow on subnivean invertebrates

Mt Twynam

Snow removal altered the composition of arthropod communities during winter (Fig. 5), with treatment explaining 25% of the variation in community composition among plots ($F_{1,11}=1.17$, $p=0.296$; Appendix S3) and a significant treatment effect along axis 1 of the NMDS ($t=-5.45$, $p=0.006$) but not axis 2 ($t=-0.25$, $p=1$). Communities from snow removal plots also tended to be more variable (i.e. had higher beta-diversity) than those from control plots ($F_{1,10}=3.72$, $p=0.072$; Fig. 5). In spring, treatments were not separated along either of the NMDS axes (axis 1: $t=0.76$, $p=0.976$; axis 2: $t=0.46$, $p=1$; Fig. 5) and PERMANOVA indicated no difference in community composition among treatments ($F_{1,9}=0.48$, $p=0.229$). In addition, there was no detectable difference in dispersion among treatment groups ($F_{1,8}=0.05$, $p=0.806$).

Both *Pseudoparonella* sp. and *Paronellides* sp. were strongly affected by the snow removal treatment; snow removal plots had $95 \pm 4\%$ fewer individuals of *Pseudoparonella* sp. (Wilcoxon: $p=0.031$) and $91\% \pm 11.7\%$ fewer individuals of *Paronellides* sp. than control plots (Wilcoxon: $p=0.031$) (Fig. 6). This difference was not, however, detected in the spring (*Pseudoparonella* sp.: $p=0.178$; *Paronellides* sp.: $p=0.201$).

Mt Stirling

In autumn, prior to the experimental treatment, plots assigned to the two treatment groups showed similar community compositions (Table 2, Fig. 7) and beta diversity ($F_{1,14}=0.12$, $p=0.752$). Treatment groups also had similar numbers of *Brachystomella* sp. (Wilcoxon: $p=0.461$) and *C. pacusieta* ($p=0.945$).

In autumn, winter, and spring there was a strong tendency for plots within a block to share similar community compositions, with block accounting for most (53%, 64% and 60%, respectively) of the variation among plots (Table 2). Ordination showed considerable overlap among treatments over the winter period as a whole (Fig. 7). This was confirmed by the PERMANOVA, which indicated no significant treatment effect on community composition during the winter (Table 2). There was, however, a strong interaction between treatment and trapping period (Table 2). When the analysis was restricted to the late winter, in which snow removal had the strongest effect on abiotic conditions (Fig. 2), PERMANOVA indicated a significant treatment effect on community composition, which was also apparent in spring (Table 2, Fig. 7). In contrast to Mt Twynam, snow removal did not influence beta diversity,

when considering either the whole winter ($F_{1,46}=0.012$, $p=0.915$) or the late winter only ($F_{1,14}=2.82$, $p=0.122$).

Over the winter as a whole, there was no significant effect of treatment on the numbers of *Brachystomella* sp. ($F_{1,7}=0.69$, $p=0.456$) or *C. pauciseta* ($F_{1,7}=1.44$, $p=0.057$) in pitfall traps, but the effects of treatment differed among winter trapping periods (*Brachystomella* sp.: $F_{2,28}=3.43$, $p=0.011$; *C. pauciseta*: $F_{2,28}=1.85$, $p=0.011$). During the late winter, *C. pauciseta* was significantly more numerous in snow removal plots than in control plots (Wilcoxon: $p=0.008$) (Fig. 6). While the numbers of *Brachystomella* sp. tended to be lower in snow removal plots than in controls, this difference was marginally non-significant ($p = 0.055$; Fig. 6). Nevertheless, the contrasting shifts in relative abundances for these two taxa meant that, although *Brachystomella* sp. was significantly more common than *C. pauciseta* in control plots ($p=0.008$), they showed similar numbers in snow removal plots ($p=0.528$). By spring, there was no difference in the numbers of either taxon between treatments (*Brachystomella* sp.: $p=0.195$; *C. pauciseta*: $p=0.674$).

Discussion

Winter snow is a defining feature of alpine ecosystems but, despite continuing declines in its depth and persistence, tests of ecological responses to changing snow regimes are limited (Brown and Mote 2009). In this study, we found a winter-active subnivean arthropod community characterised by four arthropod groups, which was sensitive to changes in the snowpack.

Does Australia have a characteristic subnivean arthropod community?

The subnivean space is unique for the spatial and temporal homogeneity of abiotic conditions and contrasts with the high variability characteristic of alpine environments during the snow-free months (Geiger *et al.* 1995; Scherrer and Körner 2011). Springtails (Collembola), mites (Acari), spiders (Araneae) and beetles (Coleoptera) are the most common winter-active arthropods in seasonally snow-covered environments worldwide (Aitchison 1979a; b; c; Chapman 1954; Green 1997; Vanin and Turchetto 2007) and our results indicate that Australia is no exception. We suggest that the high relative abundances of these four taxa (> 95% of individuals in winter in all four years), the absence of several beetle and spider families (at least at Mt Stirling), and an almost complete absence of ants – which are highly abundant during snow-free months (Green and Osborne 2012; Nash *et al.* 2013; Slatyer 2015)

– defines a subnivean arthropod community that is a distinct subset of that active outside of the snow season. Greater sampling throughout the snow-free and winter months will allow a more refined definition of this community.

Despite similarity in order-level community composition at the two study sites, the arthropod communities at Mt Stirling and Mt Twynam differed considerably at lower taxonomic levels. These differences were apparent within the springtails (e.g. dominance of podurid forms at Mt Stirling versus elongate forms at Mt Twynam), spiders (e.g. dominance of Micropholcommatidae at Mt Stirling versus Linyphiidae at Mt Twynam), and beetles (e.g. presence of Leiodidae at Mt Stirling only) and were consistent across years, suggesting that between-site differences are due to geography (local/regional), rather than year-to-year variation. Such fine-scale variation is a feature of summer alpine arthropod communities (Nash *et al.* 2013) and is thus expected if winter communities represent a subset of the summer-active taxa.

Abiotic effects of reduced snow in an Australian context

Whereas most terrestrial ecosystems experience the effects of climate change directly, changes in winter precipitation and temperature regimes in alpine environments are mediated by the snowpack (Geiger *et al.* 1995). In most areas that receive winter snow, a reduction in snow cover below the hiemal threshold leads to increases in soil freezing and, on average, colder soil and surface temperatures (e.g. Austnes *et al.* 2008; Groffman *et al.* 2001; Petty *et al.* 2015). Logically, this situation should always occur where mean winter temperatures are below subnivean temperatures. In Australia, subnivean temperatures are just above 0°C (Sanecki *et al.* 2006; this study) and winter air temperatures are frequently above this threshold (BOM 2015). As a consequence, and in contrast to comparable studies from the northern hemisphere, snow removal could increase mean temperatures, as we recorded at Mt Twynam. Notably, this effect was most pronounced late in the season – the period when declines in the snowpack are likely to be strongest (Brown and Mote 2009; Räisänen 2008). If the physical effects of reduced snow cover vary among systems, then inferences regarding ecological effects will necessarily be region-specific. However, those that are mediated primarily by temperature extremes (e.g. frost damage: Gerdol *et al.* 2013) or snowmelt timing (e.g. phenology: Wipf and Rixen 2010) might be more comparable across geographic regions than those influenced by temperature averages or accumulated degree days (e.g. individual/population growth: Adler *et al.* 2007).

Ecological effects of reduced snow

Alpine organisms are uniquely adapted to winters beneath the snowpack and experimental manipulations of snow regimes can have rapid and pronounced effects on plant community structure (e.g. Gerdol *et al.* 2013). Over the two years of snow manipulation, we found short-term effects of snow removal on arthropod communities at a small spatial scale. When considering taxa in isolation, there was a strong negative effect of snow removal on three morphospecies, all of which are likely to be mountain endemics (P. Greenslade, personal communications), and a positive effect on one species (*C. pauciseta*). Notably, the genus *Ceratophysella* is typical of disturbed habitats and could be a recent introduction (Greenslade *et al.* 2014).

In cold climates, increasing mean temperatures should intuitively favour ectotherms by reducing cold stress, but higher rates of energy consumption and thermal fluctuations can also entail considerable fitness costs (e.g. Irwin and Lee 2003; Vasseur *et al.* 2014). Removal of the insulating snow layer increases temperature variability and the expected direction of effects is thus unclear (see Appendix S4 for an outline of potential pathways and mechanisms of response). We were not able to identify the mechanisms underlying community shifts and taxon-specific responses to snow removal in this study, but these could include movement of individuals into/out of the study plots if snow-free microclimates are more/less favourable (e.g. Hågvar 1995; Hugo *et al.* 2004), or changes in activity related to short-term temperature fluctuations and/or food availability (e.g. Hågvar and Klanderud 2009; Konestabo *et al.* 2007). Alternatively, the observed effects could be due to local mortality or recruitment (e.g. Colinet *et al.* 2015; Coulson *et al.* 2000; Marshall and Sinclair 2012b; Sulkava and Huhta 2003). Regardless of the mechanism, however, snow removal appears to create a less suitable environment for some taxa (i.e. *Pseudoparonella*, *Paronellides* and *Brachystomella* morphospecies) and a more suitable environment for others (i.e. *C. pauciseta*). A change in the abundance of one arthropod group could create a complex cascade of effects, particularly via trophic interactions (Lang *et al.* 2014). For example, winter-active spiders prey on springtails (Aitchison 1984) and direct effects of changes in snow conditions on springtail abundances might therefore have indirect effects on spiders, manifest as changes in body condition rather than (necessarily) abundance (e.g. Legault & Weis 2013).

The experimental method used in this study necessarily confounds the effects of reduced snow cover with disturbance, which could be a particular issue for small arthropods

that might inhabit the snow layer itself (Leinaas 1981). The results from Mt Stirling in 2015 in early/mid-winter suggest, however, that disturbance effects alone are unable to account for community shifts: when snow was cleared (i.e. inducing a disturbance) but re-accumulated rapidly such that microclimates were similar between treatments, there was no effect of treatment on community composition. It was only when snow removal induced differences in microclimate that treatment effects became apparent.

Conclusions

This study was a first step in assessing the responses of alpine arthropod taxa in the Australian alpine region to changes in snow cover and in characterising the diversity of subnivean arthropods in Australia. We found a distinct subnivean fauna, sensitive to changes in snow conditions, and differing among sampled sites. However, even within each study site, we detected only a subset of the subnivean faunal diversity (e.g. those taxa small enough to be caught in the pitfall traps) and the subnivean is only one aspect of the snow-associated habitat. Assessments of taxa utilising the snow surface and/or the snow layer itself, as well as winter-active soil-dwelling taxa, are therefore also needed.

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Supporting information

- Appendix S1. Summary of temperature and snow conditions at the study sites during the study period.
- Appendix S2. Schematic of the subnivean trapping apparatus.
- Appendix S3. Summary of taxa recorded during the study and supplementary data.
- Appendix S4. Potential effects of reduced snow on arthropods.

Tables

Table 1. Study details. For the snow removal experiment, plots were arranged in pairs (“blocks”) with one of each pair as an un-manipulated control and the other with snow removed manually. Three pitfall traps were installed in every plot, and activated at one- to three-week intervals. We defined three periods based on snowfall: “autumn” was before the date of first snowfall, “winter” was during the period of snow cover and “spring” was the period after snowmelt.

Location	Year	Snow removal experiment?	Snow duration (days)	Max snow depth (cm)	N plots	N plots with ibuttons	Season	Trapping start date	Length of trapping (weeks)
Mt Stirling	2013	No	64	75	8	4	Autumn	20-May	1
							Winter	9-Jul	2
								2-Sep	2
							Spring	8-Nov	1
	2015	Yes	77	100	16	16	Autumn	4-May	2
							Winter (early)	19-Jul	3
							(mid)	8-Aug	3
							(late)	30-Aug	3
							Spring	19-Sep	2
Mt Twynam	2014	Yes	95	130	12*	10	Winter	6-Jul	3
								22-Jul	3
								16-Aug	3
							Spring	6-Sep	3
								27-Sep	3
	2016	No	70	100	8	8	Winter	26-Jun	3
								17-Jul	3
								4-Aug	3

Spring	21-Aug	3
	11-Sep	3
	2-Oct	3
	23-Oct	2

*16 plots were initially established, but snow conditions meant that four of these could not be used for the experiment.

Table 2. Results from permutational analysis of variance testing the effects of experimental snow removal (treatment) on arthropod community composition at Mt Stirling in 2015 during autumn, winter, and spring. The analysis across the whole winter (three trapping periods) was carried out in two stages to test (1) the effects of treatment and block and (2) the effects of time and a treatment-time interaction.

Season/effect	df	SS	MSS	Pseudo- <i>F</i>	<i>p</i>
<i>Autumn</i>					
Block	7	1.32	0.19	1.22	0.295
Treatment	1	0.10	0.10	0.66	0.655
Residual	7	1.08	0.15		
Total	15	2.50			
<i>All winter</i>					
Block	7	1.12	0.16	2.16	0.017
Treatment	1	0.13	0.13	1.69	0.150
Residual	7	0.52	0.07		
Total	15	1.76			
Time	2	1.16	0.58	7.06	0.002
Treatment:Time	2	0.41	0.21	2.51	0.001
(Block:Treatment)	15				
Residuals	28	2.29	0.08		
Total	47	8.54			
<i>Late winter</i>					
Block	7	0.96	0.14	1.27	0.265
Treatment	1	0.48	0.48	4.38	0.014
Residual	7	0.76	0.11		
Total	15	2.20			
<i>Spring</i>					
Block	7	1.53	0.22	2.25	0.012
Treatment	1	0.32	0.32	3.33	0.013
Residual	7	0.68	0.10		
Total	15	2.54			

Figures legends

Figure 1. Location of the study sites within the Australian alpine region. Grey shading indicates areas above 1500 m and the study locations are indicated with white triangles.

Figure 2. The effect of snow removal on surface temperatures at (A) Mt Twynam in 2014 and (B) Mt Stirling in 2015. Hourly temperatures are shown for a pair of control (blue) and experimental snow removal (red) plots at each site. The horizontal black line is 0°C; vertical dashed lines indicate (from left to right) the date of first snowfall, the date when snow was first cleared, and the date of snowmelt at the control site. Grey shading indicates the snow depth at (A) the Snowy Hydro Deep Creek snow depth gauge, which was close to the average snow depth across plots at the Mt Twynam study site and (B) Mt Stirling upper trail average snow depth. For both, a smooth curve was fitted to weekly (Mt Twynam) or daily (Mt Stirling) snow depth data with a locally weighted regression ($\alpha = 0.3$). Equivalent figures for the remaining blocks are provided in Appendix S1.

Figure 3. Effects of snow removal on overall mean (Mean), mean daily minimum (Min), mean daily maximum (Max), and mean daily temperature fluctuation (DF) of surface temperatures at (A) Mt Twynam in 2014 and (B) and Mt Stirling in 2015. Error bars are ± 1 s.d. Control plots are shown as black squares and experimental snow removal plots are shown as white circles. Winter temperatures in (B) are shown only for late winter.

Figure 4. The percentage contribution (by numbers) of dominant taxa to the pitfall-trapped arthropod fauna at Mt Stirling and Mt Twynam over the four years of the study. Data for Mt Stirling in 2015 and Mt Twynam in 2014 are from control plots only and n is the total number of individuals collected in each sampling period. Percentage contributions for all taxa are provided in Appendix S3.

Figure 5. Non-metric multidimensional scaling ordination of 12 arthropod taxa sampled in (A) winter, from six experimental snow removal plots (filled squares) and six paired control plots (open circles), and (B) spring, from five experimental snow removal plots and five paired control plots, at Mt Twynam in 2014. Ellipses show the 95% confidence limits around the centroids for the two treatments (grey: snow removal, white: control). Axis scores for all taxa are provided in Appendix S3.

Figure 6. Mean ($\pm$ s.e.) number of individuals per trap-week for the two most common morphospecies at Mt Twynam (A, B) and Mt Stirling (C, D). For Mt Twynam, results are shown separately for blocks with snow removal for nine weeks (“long snow removal”, $n = 3$) or two weeks (“short snow removal”, $n = 3$) during the winter. Significant differences (Wilcoxon test, $p < 0.05$) among treatments (control vs snow removal) within a site/sampling period are indicated by a star.

Figure 7. Non-metric multidimensional scaling ordination of eight arthropod taxa sampled in (A) autumn, (B) early winter, (C) late winter and (D) spring from eight experimental snow removal plots (filled squares) and paired control plots (open circles) at Mt Stirling in 2015. Ellipses show the 95% confidence limits

around the centroids for the two treatments (grey: snow removal, white: control). Ordination was run for the winter as a whole, and (B) shows the early winter results for visualisation only. The late winter trapping period was also tested separately (C). For all ordinations, the first two axes (of three) are shown. Axis scores for all taxa are provided in Appendix S3.

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