Inconsistent responses of alpine arthropod communities to experimental warming and thermal gradients

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ABSTRACT: How alpine arthropods respond to climate warming is poorly understood. Empirical approaches to address this issue include experimental warming and characterizing changes in community composition across environmental gradients. Here we compare these short- and longer-term approaches in understanding the likely effects of warming on arthropods from grassland-heathland vegetation in the Australian sub-alpine zone. Arthropod communities showed relatively small changes in composition in response to passive experimental warming in open topped chambers (OTCs) under the ITEX (International Tundra Experiment) protocol. Collembola, Katiannidae (Collembola), *Australotomurus* nr. *barbatus* (Collembola; Entomobryidae) and Saprophytic Coleoptera increased in abundance; however, none of these patterns were evident when considering a similar range of natural temperature variation (11.3 to 13.6°C) associated with elevation (1676 to 1891 m). Thus, experimental warming using OTCs was a poor predictor of likely changes along natural gradients. Responses to OTCs appear to be associated with thermal extremes and secondary effects such as increases in resources. These findings suggest caution is required when extending results from experimental warming to likely shifts in arthropod abundance along elevation gradients.

KEY WORDS: Temperature change · Grassland · Elevation gradient · Invertebrate biodiversity · Open top chambers

1. INTRODUCTION

Projected temperature increases over the next 100 years have led to concerns about biodiversity loss and biological community change (Thomas et al. 2004). In Australia, anthropogenic climate change poses a particular threat to sub-alpine and alpine ecosystems (Hennessy et al. 2008), with their likely disappearance by 2100 (Williams et al. 2007). Mean annual temperature in this region has increased by an average of 0.02°C yr^{-1} over the last 35 yr, with total projected increases of 0.2–1°C by 2020 and 0.4–6.7°C by 2070 (CSIRO & BoM 2007).

In response to warming, communities are predicted to migrate to higher elevations, where macro-climatic temperatures are lower (McCain 2005). Sub-alpine vegetation is already following this prediction and is encroaching on current alpine vegetation (McDougall et al. 2005). Increased plant diversity (Grabherr et al. 1995) and earlier flowering in some Australian alpine species, based on data from long-term herbarium records (Gallagher et al. 2009) and experimental warming (Hoffmann et al. 2010), have also been linked to temperature increases.

Alpine communities may remain stable and persist under environmental change if key species demonstrate either resilience (by way of phenotypic plasticity and/or adaptation; Hoffmann & Sgrò 2011), or the ability to disperse in pace with the changing climate (Pearson 2006). Ecosystem functions may be

maintained if the food web is degenerate; that is, if resilient species can fulfil multiple functional roles (Petchey et al. 1999). A first step in evaluating species and community resilience is to monitor shifts in community composition over natural and experimental climatic ranges.

Although plant community responses to climate have been widely investigated, likely effects on arthropod communities are poorly understood. Arthropods are likely to be particularly responsive to warming, due to high intrinsic population growth rates under favourable conditions (Birch 1948). Temperature can directly impose a physiological limit on the elevation distribution of arthropod taxa (Addo-Bediako et al. 2000, Clarke & Gaston 2006), as well as affecting access to food resources (Sanders et al. 2007), and/or dispersal potential (Bale et al. 2002). Temperature provides cues that affect arthropod voltinism, diapause, relative growth rates and development rates (examples reviewed in Bale et al. 2002, Hodkinson 2005). Shifts in populations (Parmesan et al. 1999) and communities (Wilson et al. 2007, Hågvar & Klanderud 2009) have already been observed. These direct effects may be amplified up the food chain, such that predators are more sensitive to climatic changes compared to herbivores or plants, as demonstrated in grasslands (Voigt et al. 2003).

Arthropod abundance and richness generally decline with increased elevation; however, this relationship can vary among taxa (Lessard et al. 2010). The dominant high-elevation arthropod orders worldwide include Plecoptera, Coleoptera, Lepidoptera, Diptera and Collembola, with Hymenoptera and Orthoptera dominant in Australian mountains (Green & Osborne 1994). Coleoptera abundance tends to be relatively sensitive to temperature, and Collembola abundance often increases from low to high elevation (Chapin & Korner 1995). A number of different responses in both these groups have been reported around the world (Coulson et al. 1996, Dollery et al. 2006, Hågvar & Klanderud 2009, Molina-Montenegro et al. 2009).

The first aim of this study is to examine if unique Australian sub-alpine grassland arthropods respond to short-term warming in a way similar to Arctic and Northern Hemisphere arthropods. The second aim is to understand how Australian arthropod communities vary with elevation. To achieve these aims, passive experimental warming treatments based on the ITEX (International Tundra Experiment) protocol (Molau & Mølgaard 1996) were used to test arthropod responses to increased temperature. Secondly, studies were carried out along elevation gradients to examine potential local ecological determinants of community

structure (Lessard et al. 2010). Elevation gradients of 200 m spanned a range of average daily temperatures (Byars et al. 2007) equivalent to the range imposed experimentally under the ITEX protocol of 0.9 to 1.2°C (Jarrad et al. 2008, Hoffmann et al. 2010).

2. MATERIALS AND METHODS

2.1. Experimental warming

Following the ITEX protocol (Molau & Mølgaard 1996), hexagonal fibreglass open-top chambers (OTCs) were set up in 2003 at 4 locations within a 2 × 4.5 km area of the Bogong High Plains, Victoria, Australia, known as Rocky Knobs (36.90°S, 147.27°E) (Jarrad et al. 2008). In the summer of 2003, 2 locations were burnt by wildfire (ITEX 3 and 4), although vegetation has recovered following this disturbance (H. Wahren unpubl. data). The other 2 locations remained unburnt (ITEX 1 and 2). OTC and control plots (CTR), which lacked frames, have been monitored each snow-free season since November 2003 (Hoffmann et al. 2010). Within each of four 1 m^2 CTR and OTC plots at the unburnt sites and 2 CTR and OTC plots at the burnt sites, 3 sampling points were randomly chosen for sampling arthropods from November 2007. The same points were used each season. A 7 d sampling period was repeated 3 times during the snow-free season (October to April), to obtain the full range of organisms present, for 3 sample years (2007–08, 2008–09, 2009–10). Air temperature was recorded 50 mm above the surface with Onset Hobo data loggers (Onset Computer Corporation) in 8 plots (4 OTC, 4 CTL) per site (Hoffmann et al. 2010).

2.2. Thermal elevation transects

Along 2 elevation gradients on the Bogong High Plains, 15 locations were established in subalpine grassland-heathland mosaic considered ecologically similar (all plots contained a set of 16 common plant species): 10 locations were established on Mt. Nelse (lowest: 1676 m above sea level [a.s.l.] 36° 50′ 59″ S, 147° 21′ 5″ E; highest: 1891 m a.s.l., 36° 50′ 39″ S, 147° 20′ 24″ E) and 5 on Mt. Cope (lowest: 1674 m a.s.l., 36° 55′ 31″ S, 147° 17′ 46″ E; highest: 1840 m a.s.l., 36° 55′ 38″ S, 147° 16′ 53″ E). At each location, 10 sample points were arranged in a 5 × 2 m grid spaced 2 m apart. Arthropods were sampled in January 2010 for 7 d to coincide with peak activity and sampling at ITEX locations. Average hourly temper-

ature was recorded during the snow free period (14 November 2009 to 12 May 2010) at all 15 locations, using 2 temperature data loggers (DS1922 Thermochron®, Maxim Integrated Products) at each location. Both loggers were placed 50 mm above the soil surface, attached to a wooden stake (100 mm wide) and placed facing south, hence shaded.

Temperature records from the data loggers were used in analyses instead of elevation, to control for topographic and local vegetation effects. Each location had 2 loggers; where temperature data from 2 loggers were not within a 0.5°C range of each other, the data were excluded, consistent with procedures followed by the Australian Bureau of Meteorology. To expand this dataset, temperature data were also collected in the following growing season (20 November 2010 to 16 March 2011), but only from the northern area of the Bogong High Plains around Mt. Nelse at the original 10 locations with 4 extra locations included (14 in total).

2.3. Arthropod sampling

Ground-dwelling arthropods were collected in the same way at all sites using pitfall traps constructed from plastic sleeves, 22 × 150 mm diameter × depth, sunk 150 mm into the ground. A 20 × 120 mm diameter × depth glass test-tube containing 50 mm of propylene glycol and ethanol (1:1) was inserted into the sleeve so that the top of the trap was flush with the soil surface. Sleeves were sealed with foam plugs when test-tubes were not in place.

All collections were sorted using a stereo-microscope (Leica M50) at 6 to 40× magnification. Initial identification of some taxa involved mounting slides for examination at 400× magnification. Insects, spiders and Collembola were initially sorted to family level. Formicidae were sorted to species level using specific keys, with vouchers held at the University of Melbourne. Carabidae were sorted to species using descriptions and keys. Vouchers were verified against holotypes or paratypes; however some morphological exceptions were observed in long series (Roig-Junent pers comm.). Vouchers were lodged at the Australian National Insect Collection. Lycosidae, Micropholcommatidae, Pseudoscorpionida and Paradoxosomatidae were identified using specific keys and formally verified by Western Australian Museum staff, where specimens are lodged awaiting description of novel species. Juvenile Acarina and Araneae were not identified further and excluded from analyses. Due to taxonomic limitations, Acarina were identi-fied to order, except for abundant families and predatory Prostigmata. Taxonomic impediments restricted analysis to family level, but analyses of 4 dominant individual species were included.

2.4. Statistical analysis

For the OTCs and controls (24 in total), data were combined by pooling individual pitfall samples (3) collected within each season (3) at each experimental plot (i.e. pooled across 9 pitfalls). For each season (combined spring, summer and autumn samples), a mean value was calculated for each of the 3 yr of sampling (i.e. years were kept separate in this analysis; 24 × 3 data points). For the elevation data, individual data (10 pitfalls) were pooled for each location (15 in total), with mean values used. Samples from the January 2010 experimental locations were included in the elevation analysis by averaging data from all CTR plots for each of the 4 ITEX locations: for the unburnt ITEX 1 and 2, all 4 CTRs were pooled (12 pitfalls in total for each location); for burnt ITEX 3 and 4, both CTRs were pooled (6 pitfalls in total for each location).

2.4.1. Arthropod community ordination

Rare taxa (<3% of total abundance) were either removed or combined into groups of taxa (McCune & Grace 2002), except in the case of dominant families (see Table A1 & A2 in the Appendix). Standardization was limited to groups that were extremely abundant and/or showed skewed distributions. These groups included Collembola at ITEX 1 and Formicidae at ITEX 3. Outlier and ordination analyses were performed with PC-ORD version 5.0 (MjM Software). Sørensen's distance measure was always used to calculate distance between entities within matrices. Outliers were identified within taxa (columns) whose distance was >2 SD from the frequency distribution of the distances (McCune & Grace 2002). Identified outliers were relativized to the maximum value.

Nonmetric multidimensional scaling (NMDS) was used in ordinations. To avoid local minima, the best solution was calculated via a random starting configuration and 250 real data runs, involving up to 6 dimensions and stepping down in dimensionality. A Monte Carlo significance test based on 250 runs established final dimensionality (McCune & Grace 2002). Axis scores from the final run provided information on stress, instability and scores for subsequent exploratory analyses.

2.4.2. Environmental effects

Average hourly temperature data from 14 Nov 2009 to 12 May 2010, obtained at the experimental warming locations, were used in combination with data from elevation locations to assess direct responses of arthropod abundance to daily average temperature. Regression analysis (for elevation data), and *t*-tests (for experimental data) were used to test for trends/differences in average minimum and maximum, daily average, and periodic daily fluctuation (PDF) (Geiger et al. 2003) of temperature using the software PASW v.18.0.

Spearman correlations (r_s) were used in exploratory analysis to test associations between individual taxa and axis scores (see Table A1). Type III General Linear Models (GLMs) were run to test the significance of community response (as represented by axis scores from NMDS) to year, fire, location within fire and warming, including interactions between fire and warming, and between location within fire and warming. For elevation data, analyses focused on taxon- (see Table A2) and species-level associations with temperature from 14 locations sampled in Jan 2010, where concordant temperature data were recorded. Because these data met assumptions of normality, partial Pearson correlations (r_p) were used to correct for spatial association (Legendre & Legendre 1998). Subsequent community responses were tested with Distance-based Multivariate Analysis for Linear Models (DISTLMs) to look at the effect of multiple variables on beta diversity (Anderson 2001). DISTLM involves computing a test statistic (F) calculated directly from the distance measures to group centroids of the dissimilarity matrix with the significance value obtained using 4999 permutations (herein referred to as per*P*) using the software DISTLM v.5. The significance of location, burning (as categorical variables) and mean daily temperature (covariate in the model) on arthropod community diversity at locations sampled along the elevation gradient and experimental locations only sampled in January 2010. Association analysis and GLMs were run with PASW v.18.0.0.

2.4.3. Individual analysis of arthropod taxa

Based on the exploratory community analysis that identified several taxa potentially responding to OTC treatment, associations were examined further for those taxa that met GLM model assumptions. Means were calculated from the 3 trapping periods for each season for each plot to avoid zero counts. Transformations ($\mu' = \log_{10}[\mu + 1]$) were applied to minimise unequal vari-

ances between groups. Given the high number of taxa and the multivariate nature of assemblage composition, increasing the chance of Type 1 errors, Bonferroni corrections for multiple comparisons were applied.

3. RESULTS

3.1. Temperature

The average daily temperature decreased with elevation (Fig. 1). This was driven by the decreasing average daily maximum temperature, because the average daily
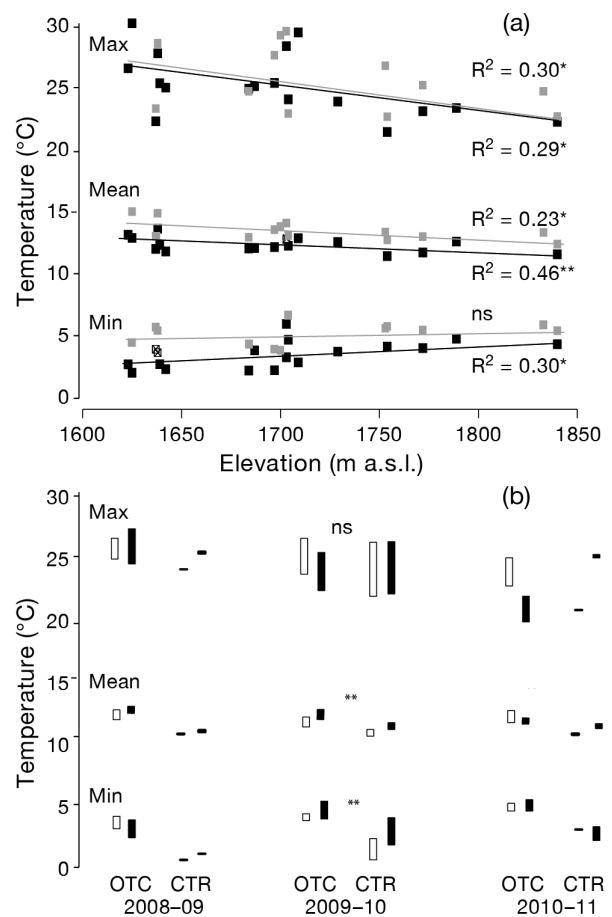

Fig. 1. (a) Mean daily temperatures (max., mean, min.) along the elevation gradient for the 2009–2010 (black, Nov–May) and 2010–2011 (grey, Nov–Mar) seasons. The 2009–2010 regressions include control plot means from ITEX locations as described in Section 2.1. R^2 values—lower: 2009–2010; upper: 2010–2011. *p < 0.05, **p < 0.01. (b) Mean daily temperatures (max., mean, min.) measured in the snow-free season from 1 Nov to 30 Apr for 3 yr on the experimental warmed (OTC) and control (CTR) plots. Bars: range recorded at unburnt ITEX 1 (white) and burnt ITEX 3 (black) locations. Solid line: single data point only. **p < 0.01 (1-sided *t*-test): OTC plots were significantly warmer than CTR plots (see text) in 2009–2010 season. ns: not significant

minimum temperature did not decrease significantly with elevation in either growing season (Fig. 1). Ascending the mountain, the overall temperature range decreased, resulting in the PDF declining significantly with increased elevation (PDF = 83.6 ± 18.8 to 0.035 ± 0.011 m a.s.l. [error 2.55]; $F_{1,15}$ = 10.65, p = 0.005).

In the OTCs (2009–10) the average minimum daily temperature was significantly (t_8 = 3.47, one-sided p = 0.006) warmer (4.68 ± 0.27°C) than in the control plots (2.68 ± 0.42°C), whereas there was no significant difference (t_8 = 0.788, one-sided p = 0.449) in the overall average maximum daily temperature (CTR 25.19 ± 0.97°C; OTC 25.35 ± 0.78°C). The average temperature inside the OTCs (12.64 ± 0.15°C) was significantly higher (t_8 = 3.70, one-sided p = 0.004) than in the controls (11.82 ± 0.12°C), concordant with previous data showing a 0.9 to 1.0°C increase (Jarrad et al. 2008). In contrast to the elevation sites, warming inside the OTCs was thus driven by an increase in minimum temperature.

3.2. Community response: OTCs

We collected 153126 ind. in total, assigned to taxa for analysis as shown in Table A1. The most abundant order was Collembola, in particular *Cryptopygus* sp. (Isotomidae) (104 855 ind.) collected only at ITEX Site 1. *Iridomyrmex mjobergi* Forel (10 085) and *Pheidole* morphospecies 1 (2,359)—2 species of Formicidae—were abundant. These were combined prior to analysis. *Amblyopone australis* Erichson and *Myrmecia pilosula* Smith—2 other species of Formicidae—were recorded, but excluded due to rarity (<3%). Only adult Coleoptera were included in analyses (see Table A1).

Ordination analysis of the experimental warming data at the taxon level produced a 3-dimensional solution (p = 0.004) with the lowest stress value of 12.4 requiring 240 iterations to reach the default instability of 10^{-4}. The 3 axes accounted for 88% of the variance, with axis 3 contributing 52% (Fig. 2). Communities varied between location and year (Fig. 2). Only results from NMDS axis 2 were significantly affected by warming, with location and year being a significant factor for all axes and fire associated with axis 1 (Table 1).

3.3. Community response: elevation data

There were 16 037 organisms recorded from the 15 elevation locations, with the addition of 39 628 ind.
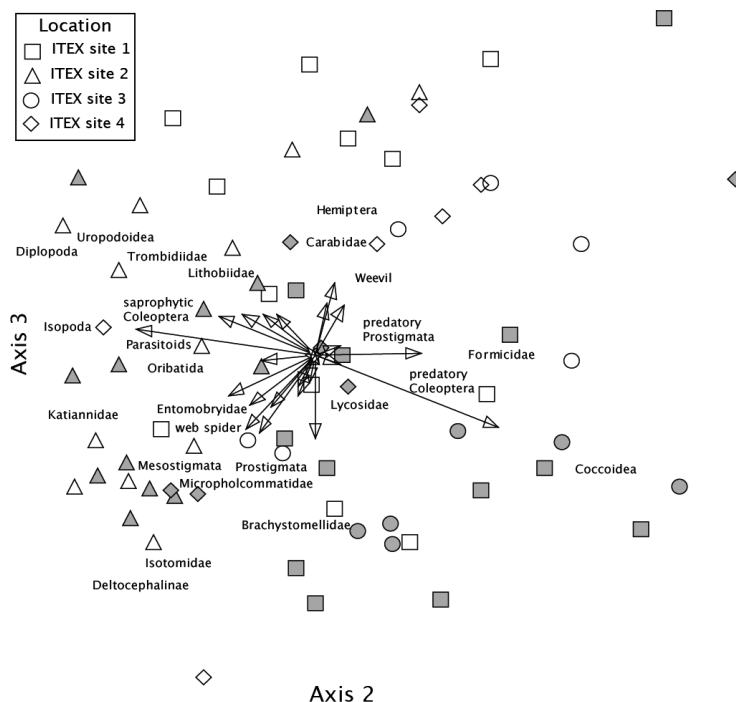

Fig. 2. Nonmetric multidimensional scaling ordination of arthropod families sampled from 4 experimental sites located at the Bogong High Plains, 2007–2010. Closed symbols: data from warming treatments (OTC). Axis scores that account for the greatest variance (Axis 3: 52%, Axis 2: 21%) are displayed and rotated to align Axis 2 with location

from the 4 ITEX locations. The distribution of organisms across taxa is given in Table A2. Over 30 000 *Cryptopygus* sp. were recorded swarming at ITEX 1. Because of this swarming, Isotomidae at 1 elevation location were relativised (McCune & Grace 2002). Ordination analysis of the data at family level indicated a 2-dimensional solution (p = 0.004) with lowest stress of 14.3, requiring 73 iterations. These 2 axes accounted for 84% of the variance (Fig. 3). From the variance in community composition, 15% was attributable to location (F = 3.80, per p = 0.003), highlighting the presence of local arthropod communities. In contrast burning was not found to be a significant factor affecting axes scores (F = 0.49, per p = 0.442).

3.4. Individual taxa response: OTCs

Relative abundance of taxa varied with year of sampling and location, while there were also minor effects of warming treatment, but responses varied between taxa (Fig. 4) (Table A1). Although this experiment was primarily aimed at investigating warming affects, one of the axes and 1 individual taxon (Lycosidae) showed a significant response to fires in

Table 1. Response of alpine arthropod taxa sampled in 4 locations across the Bogong High Plains between 2007 and 2010 to experimental warming (W), fire (F), location (L) within fire [L(F)] and year. Repeated measures Generalised Linear Models were used to assess significance of factors, and *F* ratios are presented. In all models the error df was 16. Significance: *p < 0.05, **p < 0.001, ***p < 0.001

Axis/Taxon	Factors				Interactions	
	Year (df 2)	W (df 1)	F (df 1)	L(F) (df 2)	F by W (df 1)	L (F*W) (df 1)
Axis 1	50.7***	<0.1	5.3*	10.4**	0.1	0.9
Axis 2	5.2*	8.6*	0.8	6.3*	<0.1	2.1
Axis 3	63.8***	1.7	0.8	11.0***	2.6	0.1
Orocladosoma kosciuskovagum	4.4*	0.9	3.1	10.9**	6.0*	0.2
Oribatida	1.6	3.1	0.2	17.3***a	6.7*	0.7
Mesostigmata	52.7***a	0.2	0.1	13.7***a	1.3	0.1
Trombidiidae	15.6***a	3.5	2.6	11.3***a	<0.1	0.8
Prostigmata	6.2*	1.3	1.1	4.7*	0.1	5.4*
Lycosidae	0.6	0.8	16.0***a	0.3	1.0	0.3
Collembola	23.8***a	24.6***a	0.1	16.9***a	0.6	1.0
Australotomurus nr. *barbatus*	7.2**a	13.5**a	<0.1	2.2	2.5	0.6
Katiannidae	1.8	8.7**	1.3	7.0**	0.3	5.2*
Carabidae	12.9***a	2.1	<0.1	6.1*	0.5	0.4
Percolestus blackburni	15.7***a	1.0	0.2	7.2**	0.5	0.3
Saprophytic Coleoptera	7.3*a	10.8**a	0.4	7.0**	5.0	0.2*
Iridomyrmex mjobergi	18.9***a	0.4	2.5	0.9	2.4	0.8
Parasitoids	5.5*	4.2	2.5	7.8**	0.5	1.2
Deltocephalinae	46.5***a	4.7*	1.9	0.4	1.0	0.3

aSignificant values after Bonferroni correction for multiple comparisons (p < 0.0033) when analysing individual taxa. Note significance is corrected (Greenhouse–Geiser) for the repeated within subject factor (year)
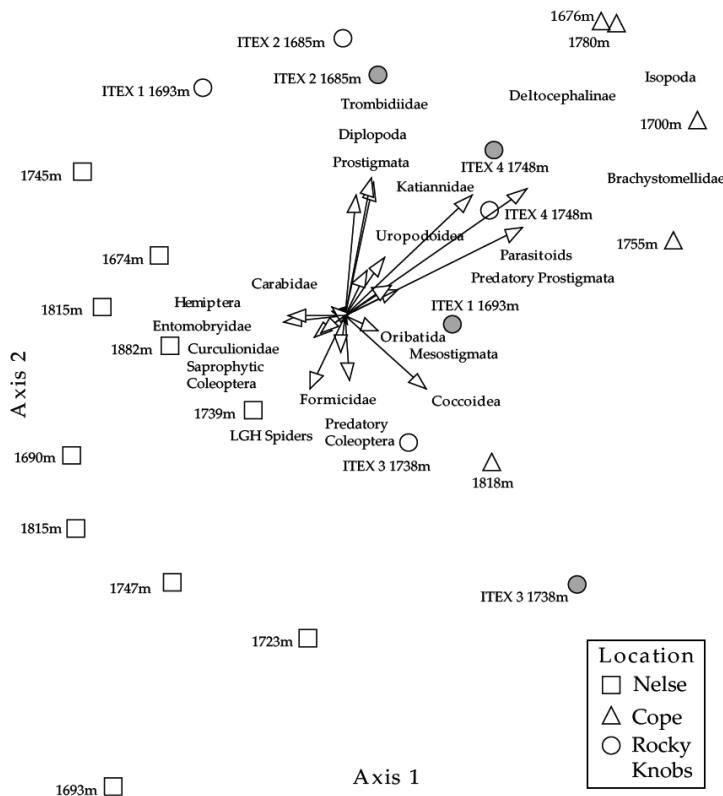

Fig. 3. Nonmetric multidimensional scaling ordination of arthropod families sampled from 19 locations across the Bogong High Plains, Jan 2010. Labels next to symbols: elevation (a.s.l.). Data are included from 4 experimental sites where warming treatments were included separately (closed symbols) (n = 23)

2003 (Fig. 4a, Table 1). The following were identified as dominant species in their taxa, hence analysed at the species level: 287 *Percolestus blackburni* Sloane (71% Carabidae), 2386 *Australotomurus* nr. *barbatus* (Entomobryidae) (10% Collembola), and 10 085 *Iridomyrmex mjobergi* Forel (81% Formicidae). The 2359 *Pheidole* morphospecies 1 (Formicidae) sampled were not analysed because this species varied markedly in abundance (9.6 ± 1.63 per pitfall at ITEX 1, 0.17 ± 0.13 elsewhere). Collembola were combined and analysed at the order level, excluding the over-abundant *Cryptopygus* species. A significant increase in relative abundance of this group was observed under OTC conditions. A similar trend was observed when analysis was at the individual species level (*A.* nr. *barbatus* also displayed a significant increase in overall abundance under OTCs (Fig. 4b, Table 1)) and at the family level (Katiannidae in Fig. 4c, but only at ITEX 2: $\mu_2 = 32.70 \pm 9.07$, p < 0.001). The overall trend was for plant feeding arthropods to show a positive response to the warming (OTC) treatment.

3.5. Individual taxa response: elevation data

Only 2 taxa showed direct associations with temperature along the elevation gradient. *Orocladosoma kosciuskovagum* displayed a positive association with temperature (Table A2), but this taxon was only re-
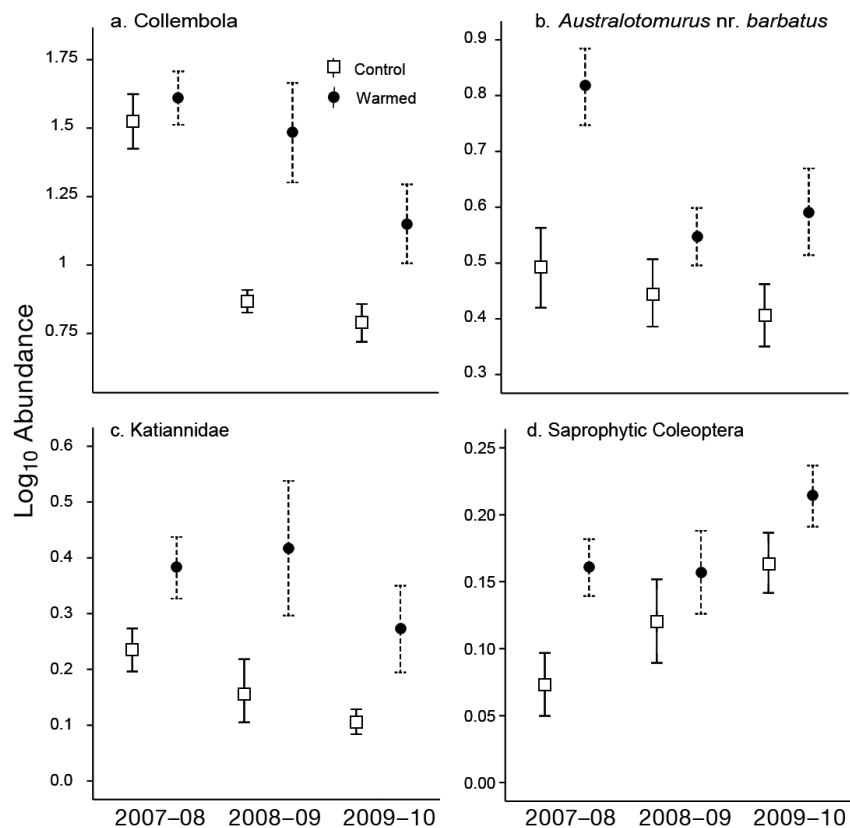
Fig. 4. Collembola, *Australotomurus* nr. *barbatus,* Katiannidae, Saprophytic Coleoptera. Log_{10} mean abundance of arthropod taxa (±SE) that displayed a significant (Table 1) response to experimental warming (OTC) over 3 yr of sampling. Control plots: open symbols, OTC: closed symbols. See Table 1 for corresponding significance values

corded at 6 of the 14 locations. Katiannidae showed a negative association (Table A2). The overall lack of response to elevation was consistent when taxa were combined or separated to lower taxonomic levels and analysed: e.g. Collembola at order level ($r_p = -0.038$, p = 0.908, n = 14) (Table A2), *Australotomurus barbatus* ($r_p = 0.250$, p = 0.433, n = 14), *Percolestus black-burni* ($r_p = -0.167$, p = 0.611, n = 14), and *Irido-myrmex mjobergi* ($r_p = 0.353$, p = 0.260, n = 14).

4. DISCUSSION

Poor knowledge of the Australian invertebrate fauna (Green & Osborne 1994) precluded a detailed species-level examination of temperature response; nevertheless, of the dominant species identified, one demonstrated a positive response to warming in the OTCs. Moreover, several taxa defined above the species level displayed positive responses to OTC conditions, particularly in plant feeding groups.

However, regardless of whether species or higher taxonomic levels were considered, patterns established in the OTCs were not consistent with those along the elevation gradient, in contrast with some other results (Dollery et al. 2006). Variation in abundance between years and between locations tended to be greater than differences produced by experimental warming, concordant with previous findings on arthropods (e.g. Coulson et al. 1996, Hodkinson 2005).

The lack of response to experimental warming in surface-active Orbatida was similar to results from the northern hemisphere (Coulson et al. 1996, Håg-var & Klanderud 2009) where communities remained nearly unchanged after 4 yr of warming. For Collembola, which were abundant and responded positively to OTCs when analysed at the order, combined family or species level, a mixture of negative and positive responses to increased temperatures has been recorded in arctic areas (Hågvar & Klanderud 2009). Large soil-active Collembola (e.g. *Hypogastrura tullbergi* and *Isotoma anglicana*) were less abundant in OTCs but *Folsomia bisetosa* was relatively more abundant (Dollery et al. 2006). Growth rates of some species are determined by food availability, not temperature (Addison & Parkinson 1978). The conflicting responses of Katiannidae to experimental warming and elevation may be due to availability of food, as voucher individuals collected in this study where this group was abundant were observed to have pollen in their guts.

One reason why the arthropod communities examined in this study responded in different ways to experimental warming and along elevation gradients is that mean temperatures are frequently used for both observational and predictive studies for climate change response, but patterns established from changes in mean temperatures do not necessarily capture variability in local thermal conditions (Geiger et al. 2003). The increase in minimum but not maximum temperatures inside OTCs recorded in this study is the opposite pattern to that observed along the natural elevation gradient (Fig. 1): that is, increased maximum and decreased minimum temperatures recorded at lower, 'warmer' elevations.

Apart from altering temperature, the OTCs may induce other microclimatic changes (Coulson et al. 1996), such as increased relative humidity, decreased soil moisture, changes in airflows and decreased radiation. It has been estimated that 52% of net surface energy is lost through evaporation, and this process is of primary importance (Geiger et al. 2003). OTCs may reduce air movement over the soil surface and minimize loss of water vapour. Heating the soil surface inside OTCs should also result in higher relative humidity and lower soil moisture. Another OTC study reported no change in relative humidity but reduced soil moisture (Bokhorst et al. 2008), as found previously for OTCs used here (Jarrad et al. 2008). In systems where air movement complicates microclimate, one might expect a loss of water vapour and more evaporation, thus less water available for growth. Air just above the ground interface is often drier on mountain peaks/slopes than in lower hollows due to movement of cold air to the lowest point (Geiger et al. 2003). Thus, an interplay of environmental factors controlling relative humidity and surface soil moisture may explain the difference in responses observed for some collembolan groups (Table 1), given their likely sensitivity to dry conditions at the soil surface. Increased herbivore populations (Fig. 4) inside OTC plots may also reflect a positive response to resources arising from an increase in plant biomass or change in vegetation composition, rather than a direct effect of microclimate (Hudson & Henry 2009).

Finally the experimental warming plots were designed to reflect short term responses to temperature whereas changes along elevation gradients involve a much longer timeframe and complex of abiotic and biotic factors and their interactions (Körner 1999). Nevertheless, comparison is important because recent changes in communities across elevations are often interpreted in terms of mean temperature, and OTCs are used to assess responses to mean temperature.

The only individual taxon to demonstrate a significant response to fire was Lycosidae. The lack of individual taxa response may reflect a lack of experimental power given that the design was nested and only 2 replicates were available for each of the 2 locations burnt in 2003. Because invertebrates are often quite mobile depending on fire intensity, frequency and extent, a high degree of variability might be expected in population recovery after fire (Swengel 2001). Although this experiment was primarily aimed at investigating warming affects, fire effects should be investigated further with an experimental design

that assesses populations prior to disturbance and with a higher level of replication.

The usefulness of these results for interpreting likely responses to climate change is questionable if arthropod abundance depends on extremes of temperature rather than mean values, moisture availability, and responses to plant growth. There is a moderation of temperature with increased elevation (Sanecki 2005), and lower minimum temperatures at lower elevations (frost hollows) may develop due to cold air drainage. Given projections of less snow cover and increased frost events (Hennessy et al. 2008), the expectation is that extremes may increase, favouring arthropods from lower elevations that tolerate extremes. Measures of resistance to thermal extremes and desiccation are needed for alpine arthropod communities to investigate if patterns of resistance can be linked to elevation gradients.

In summary, we have found that some taxa responded positively to increased temperatures in the OTCs used in this study. While patterns were not consistent with the survey carried out along elevation gradients, this may reflect the types of temperature changes seen in the OTCs and responses to biotic factors. The results caution against the simple prediction that communities under climate change, assessed as mean, will move to higher elevations, and instead suggest a potentially more complex response.

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APPENDIX 1.

Table A1. Arthropod families sampled from 4 experimental warming sites (n = 24 × 3 yr) located at the Bogong High Plains, 2007−2010. Correlations to axis scores from community ordinations are also presented. Spearman correlations (r_s) were used to test taxa correlations with axis scores derived from nonmetric multidimensional scaling ordination of the community data. Warming is associated with Axis 2 (see text for details). $^*p < 0.05$, $^{**}p < 0.01$

Taxonomic grouping	Taxon	Abundance	r_s to axis score (n)		
			1	2	3
Diplopoda	*Orocladosoma kosciuskovagum*	751	−0.531**[a]	0.622**[a]	0.287*
Chilopoda	Lithobiidae	52	−0.329**	0.268*	0.079
Astigmata	Uropodoidea	943	−0.479**[a]	0.571**[a]	0.078
Oribatida		742	−0.244*	0.263*	0.314**
Mesostigmata		1836	0.298*	−0.069	0.742**[a]
Trombidiidae	Trombidiidae	5120	−0.753**[a]	0.619**[a]	0.063
Prostigmata	Anystid	1197	0.297*	−0.142	0.107
Predatory Prostigmata	Bdellidae	181	−0.162	−0.008	−0.137
Ground-hunting spiders	Lycosidae, Miturgidae	427	0.175	−0.181	0.043
	Micropholcommatidae	224	0.285*	−0.065	0.372**[a]
Web-building spiders	Araneidae, Linyphiidae	322	0.469**[a]	−0.254*	0.381**[a]
Collembola	Brachystomellidae, Neanuridae	114 851	−0.225	−0.663**[a]	0.552**[a]
	Entomobryidae, Bourletiellidae	4115	0.115	−0.309**	0.492**[a]
	Hypogastruridae, Isotomidae, Tomoceridae	4543	0.524**[a]	−0.189	0.703**[a]
	Katiannidae	980	−0.026	0.012	0.629**[a]
Carabidae		243	−0.466**[a]	0.307**	−0.258*
Weevils	Curculionidae	163	−0.401**	0.196	−0.391**[a]
Predatory Coleoptera	Coccinellidae, Pselaphidae, Staphylinidae, Scydmaenidae	145	−0.178	−0.010	−0.147
Saprophytic Coleoptera	Anthicidae, Byrrhidae, Elateridae, Lathri-diidae, Scarabidae, Tenebrionidae	313	−0.356**	0.054	0.064
Ants	Formicidae	12 444	−0.273*	−0.413**[a]	−0.730**[a]
Parasitoids	Braconidae, Bethylidae, Chrysididae, Eulophidae, Mymaridae, Platygastridae	423	−0.190	0.072	−0.036
Hemiptera	Deltocephalinae	461	−0.261*	−0.274*	−0.264*
	Aphidae	104	0.498**[a]	−0.292*	0.609**[a]
	Lygaeidae, Miridae, Nabidae, Pentatomoidea	241	−0.402**[a]	0.238*	−0.345**
Slaters	Isopoda	68	−0.345**	0.318**	0.454**[a]

[a]Significant value after Bonferroni corrections for multiple comparisons (p < 0.002)

Table A2. Arthropod families sampled from 19 sites (4 controls from experimental plots, 15 elevation locations) located across the Bogong High Plains, January 2010. Correlations to site, daily mean temperature and axis scores from community ordinations are also presented. Spearman correlations (r_s) are used to test taxa correlations with axis scores derived from nonmetric multidimensional scaling ordination of the community data. To correct for location, partial Pearson correlations (r_p) were used to test taxa association with mean daily temperature for the period Nov 2009–May 2010. *p < 0.05, **p < 0.01

Taxonomic grouping	Taxon	Sites	Abundance	r_p to temperature	r_s to axis score (n) 1	2
Diplopoda	*Orocladosoma kosciuskovagum*	11	53	0.733**[a]	0.095	0.678**[a]
Astigmata	Uropodoidea	15	79	−0.352	0.224	0.253
Oribatida		18	305	−0.264	0.133	0.060
Mesostigmata		18	184	−0.496	0.341	−0.002
Trombidiidae	Trombidiidae	17	4173	0.215	0.166	0.885**[a]
Prostigmata		17	564	−0.202	0.128	0.725**[a]
Predatory Prostigmata	Anystid, Bdellidae	17	85	−0.014	0.361	0.142
	Lycosidae	19	162	−0.183	−0.085	−0.438*
Collembolla	Brachystomellidae, Neanuridae	12	32377	0.196	0.902**[a]	0.453*
	Entomobryidae, Bourletiellidae	19	1192	0.144	−0.509*	0.009
	Hypogastruridae, Isotomidae, Tomoceridae	14	4823	−0.229	0.431*	0.322
	Katiannidae	16	301	−0.739**[a]	0.305	0.375
Carabidae		19	233	−0.003	−0.164	0.023
Weevils	Curculionidae	19	203	−0.021	−0.262	−0.248
Predatory Coleoptera	Coccinellidae, Staphylinidae, Scydmaenidae	17	113	−0.247	0.056	−0.336
Saprophytic Coleoptera	Anthicidae, Byrrhidae, Elateridae, Lathridiidae, Scarabidae, Tenebrionidae	19	98	0.556	−0.263	−0.171
Ants	Formicidae	19	10006	0.259	−0.363	−0.829**[a]
Parasitoids	Braconidae, Bethylidae, Chrysididae, Eulophidae, Mymaridae, Platygastridae	19	247	0.102	0.699**[a]	0.327
Hemiptera	Deltocephalinae	13	70	−0.351	0.520*	0.456*
	Aphidae	10	98	0.445	0.033	0.018
	Lygaeidae, Miridae, Nabidae, Pentatomoidea	15	299	0.43	−0.336	−0.145

[a]Significant value after Bonferroni corrections for multiple comparisons (p < 0.0024)