Received: 26 November 2024 | Accepted: 29 August 2025

DOI: 10.1111/een.70015

ORIGINAL ARTICLE

Ecological Entomology

Combined heat and drought affect the abundance, composition and diversity of subalpine surface-active soil arthropod communities

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Funding information
Australian Research Council, Grant/Award Number: DP200101382

Associate Editor: Tali Reiner Brodetzki

Abstract

1. Alpine and subalpine ecosystems are predicted to have increased temperature and altered seasonal rainfall and snow cover duration as climate change progresses, potentially changing the communities of these ecosystems. Soil arthropods facilitate key environmental processes that determine ecosystem function and stability; however, little is known about how warming and drought conditions impact soil arthropod communities in the field.
2. This study aimed to assess the effects of soil warming and drought conditions on the abundance and diversity of soil arthropod communities. Climate-controlled shelters manipulated soil temperature and incoming precipitation in a factorial experiment (FutureClim) in a subalpine grassy herbfield in Australia. Surface-active arthropods were sampled from climate-controlled shelters using pitfall traps in January, March and April 2023 and were identified to order.
3. Abundance, diversity and community composition changed significantly across the sampling period. Diversity was lowest in all warming and drought treatments in April relative to control, while community composition was significantly driven by temperature and moisture but also was highly variable across the site.
4. The effects of warming and drought on abundance differed substantially between arthropod taxa, with opposing effects on mesofauna and macrofauna. Two Collembola orders, which comprised a large proportion of the arthropod community, were more abundant in heated shelters during the cooler months. In contrast, Hymenoptera (mostly driven by the dominant alpine ant *Iridomyrmex alpinus*), Hemiptera and Diptera were more abundant in drought and heat-drought conditions, but larvae were scarce in droughted treatments.
5. Collectively, this study suggests that the abundance, composition and possibly diversity of surface-active mesofauna and macrofauna will likely change in the future. Focus on phenological shifts of communities over both short and long

timescales, coupled with vegetation and soil changes, is needed to better understand potential ecological changes associated with soil warming and drying.

KEYWORDS
alpine, climate change, drought, pitfall traps, soil arthropods, soil community, soil invertebrates, subalpine, warming

INTRODUCTION

The effects of climate change on alpine and subalpine ecosystems have become more apparent in recent decades, yet the full extent of these consequences remains to be seen (Kotlarski et al., 2023; Schmeller et al., 2022; Seastedt & Oldfather, 2021). The Australian alpine zone is at a relatively lower elevation than other alpine zones globally, with its highest peak being Mt. Kosciuszko at 2228 m (NSW National Parks and Wildlife Service, 2003). As a result of its relatively low elevation, the effects of climate change are likely to be detected earlier in the Australian alpine and subalpine ecotones than in other comparable ecotones in the Southern Hemisphere (Thompson, 2016). Multiple climate prediction models for the Australian Alps predict an approximate 4°C increase in mean temperature and a 5%–20% reduction in mean annual precipitation by the end of the 21st century (Harris et al., 2016). These substantial climatic shifts will alter snow cover duration and seasonal patterns of precipitation, resulting in more severe droughts, which will challenge the resilience of high-elevation ecosystems (Love et al., 2019) and facilitate the movement of low-elevation flora and fauna to higher elevations (Auld et al., 2022; Richman et al., 2020). To plan conservation efforts and policies effectively, we first need to understand how future warmer and drier conditions might affect these more cryptic communities in the field (Praeg et al., 2025).

Soil ecosystem dynamics are essential, yet often neglected, when assessing ecological responses to future climate conditions. The decomposition of organic matter in the soil is an important stage in the carbon cycle and in ecosystem functioning, in which the activity and metabolism of soil organisms influence rates of respiration and nutrient cycling (Luo & Zhou, 2006). Soil arthropods facilitate and accelerate decomposition processes in the soil (Joly et al., 2020; Kitz et al., 2015; Semeraro et al., 2022). Detritivorous arthropods break down organic material by fragmenting and skeletonising plant material and via digestion. Soil detritivores typically only produce the enzymes required to break down simple organic molecules, leaving complex molecules including cellulose and lignin in a fragmented state to be digested by microbes (Scheu & Setälä, 2002). Arthropod taxa fragment and digest organic material differently depending on their movement patterns and digestive systems. For example, ants facilitate the movement of organic material across the soil surface, while detritivores fragment litter and deposit their faeces on the soil surface, and secondary detritivores digest it further (Kitz et al., 2015; Scheu & Setälä, 2002). The soil ecosystem is shaped by detritivore faeces, in which the shape and size of these faeces vary by taxa and influence soil porousness, permeability and the leaching of nutrients (Joly et al., 2020). Thus, functional diversity in soil arthropod communities facilitates and accelerates decomposition processes and is therefore essential for ecosystem functionality, stability and efficiency (Kitz et al., 2015).

As warmer and drier conditions become more prevalent, especially during the crucial growing seasons of spring and summer, the responses of soil arthropods may have major implications for decomposition, nutrient cycling and ecosystem stability. Warming increases the metabolic rates and activity levels of soil invertebrates and other microbiota (Praeg et al., 2020), which can cause rates of decomposition and soil respiration to accelerate in their environment (Thakur et al., 2018; Yin, Qin, Wang, Zhao, et al., 2023). Increases in decomposition and soil respiration rates in alpine ecosystems could potentially alter the carbon cycle and soil characteristics with cascading effects on vegetation and animal communities. There is relatively little research on community responses of alpine and subalpine soil arthropods to climate change (Praeg et al., 2025). Studies on the effects of snow cover persistence have shown that arthropod communities become more variable with reduced snow cover duration or snowpack depth, where responses vary between taxa (Slatyer et al., 2017), and these responses are sensitive to short-term changes in environmental conditions (Green & Slatyer, 2020). Warming in alpine and subalpine ecosystems of New Zealand influences the distributions of invertebrates, where low-elevation taxa have moved upwards in elevation as temperatures have increased, and high-elevation taxa have tracked the upwards movement of the snow line (Chinn & Chinn, 2020). Previous studies on soil invertebrate community composition have found that responses to temperature and moisture treatments are not consistent between taxa, due to divergent ecological requirements and tolerances (Chown et al., 2007; Janion-Scheepers et al., 2018; Luo et al., 2023; Nash et al., 2013). Detritivore activity is known to increase with temperature, but some detritivorous taxa (especially Collembola and Acari) are prone to desiccation in dry conditions (Hodkinson et al., 1998; Hopkin, 1997). Therefore, detritivore abundance may increase in warm and wet conditions but decrease when soil is relatively dry. Yet, herbivore abundance may increase in drought conditions as a secondary effect of drought increasing the availability of dead plant matter.

The effects of warming on soil arthropods are dependent on limits to their thermal tolerance and phenotypic responses to temperature, both of which are influenced by the microclimatic conditions of their habitat due to constraints on movement and dispersal. Further, within a landscape there will be a heterogeneous network of microhabitats that allow refugia (sheltered, cooler and/or wetter conditions) to persist, altering the realised microclimatic conditions for organisms

(Nowakowski et al., 2018). For example, habitat is one factor that determines how different Collembola species are affected by temperature. Collembola species that occupy the topsoil naturally experience greater fluctuation in daily temperatures than species occupying more thermally stable deep-soil layers. Thus, surface-dwelling species typically have broader heat tolerance and are better able to alter their lipid composition to acclimate to warmer temperatures than deep-soil-dwelling species (van Dooremalen et al., 2013). Specialisation also influences how different Collembola species respond to warming. Generalist and alien Collembola species tend to have greater thermal tolerances and capacity to acclimate to warmer conditions than specialist and native species (Chown et al., 2007; Deharveng, 1996; Janion-Scheepers et al., 2018). Thus, climate change could facilitate the success of invasive soil arthropod species (Chown et al., 2007) and the movement of low-elevation species up the elevation gradient. However, Nash et al. (2013) suggest that the latter prediction may be oversimplified because responses to changing temperatures are highly variable among taxa or dependent on interactions with other biotic and environmental factors. Some arthropods, notably ants, display behaviours that directly alter the microclimate of their habitat, buffering the negative effects of warming for themselves and the surrounding ecosystem (Luo et al., 2023).

Soil temperature is often interconnected with soil moisture, and Australian high elevation ecosystems are increasingly becoming both warmer and drier as the climate changes (Harris et al., 2016). While warmer and drier soil conditions can occur independently in the alpine and subalpine zones, they also occur in combination during extreme events, such as heatwaves. In a short-term laboratory study, Thakur et al. (2018) observed an increase in soil invertebrate feeding activity in warm and wet soils, but a decrease in feeding activity in warm and dry soils. However, very few field-based studies have investigated the combined effects of heat and drought on soil arthropods over an extended treatment duration.

Here we assessed the individual and combined effects of in situ (field) manipulations of increased soil temperature (hereafter, heat) and decreased soil moisture (hereafter, drought), which represent extreme future climate conditions, on surface-active soil arthropod community composition and diversity of an Australian subalpine grassy herbfield during the warm season. We hypothesised that some soil arthropod orders would benefit while others would suffer from heat and drought treatments compared to the control conditions (Nash et al., 2013; Yin, Qin, Wang, Xie, et al., 2023), resulting in inflated abundances and lower diversity in these treatments. We hypothesised that diversity would be lowest when heat and drought treatments were combined, as their combination can be detrimental to arthropods beyond that of either treatment alone (Thakur et al., 2018). We hypothesised that heat and drought conditions would significantly alter arthropod community composition similarly across the warm season, with largest treatment effects apparent in the warmest month. Finally, we expected that the responses to heat and drought conditions would vary substantially among taxa but would be more similar among taxa within mesofauna and macrofauna classes.

METHODS

Study site

This research was conducted using the established Australian Mountain Research Facility (AMRF; https://www.amrf.org.au/amrf-sites/) Aqueduct site located in Kosciuszko National Park, NSW, Australia (elevation = 1598–1610 m; 36°22′20.38″ S, 148°25′52.25″ E; Figure 1a). The FutureClim (https://prometheusprotocols.net/experimental-design-and-analysis/experimental-treatments/drought-treatments/futureclim-a-method-for-delivery-of-a-factorial-heat-and-drought-manipulation-in-remote-field-conditions-on-solar-or-mains/) experiment at this field site is an in situ, fully factorial, long-term field manipulation of temperature and precipitation using climate-controlled shelters to simulate the local climatic conditions that are projected during severe future droughts in 2070–2100 (Harris et al., 2016). The vegetation community of the study site is subalpine grassy herbfield, which is defined in NSW legislature as consisting of "low herbfields dominated by forbs and grasses with scattered shrubs in rocky sites" (NSW Office of Environment & Heritage, 2015). The FutureClim infrastructure was deployed in autumn 2022 and heat and drought treatments commenced continuous operation from October 2022 until June 2023. All sampling for the current study was completed within this operating window.

The climate-controlled shelters in the FutureClim experiment simulated the effects of warming and drying in a factorial experimental design by manipulating soil temperature directly and by reducing incident rainfall (Figure 1b). There were four types of shelters (i.e. treatments): control, heat, drought and heat-drought. The shelters were organised into five replicate blocks containing one shelter of each treatment (20 total shelters) to account for variation across the landscape (Figure 1a). The shelters covered a ground surface area of 3 × 3 m, which consisted of a 2 × 2 m working area surrounded by a 0.5-m wide buffer zone. Vegetation cover split into functional types (bare ground, graminoid, forb and shrub) within the working area of each shelter is shown in Figure S1. Control shelters were simply an external metal frame without any alterations of the environment within, and these served to represent current ambient conditions. Heat (and heat-drought) shelters simulated soil warming approximately 4°C above the ambient temperature during the warm season (calculated and controlled separately for each block by applying +4°C to the ambient soil temperatures of their corresponding control shelters). The heated shelters contained seven vertical heating tubes buried up to 70 cm below the soil surface and clear polycarbonate walls to retain warm air inside the shelters. The heating tubes used resistance wires within sand-filled metal housing to heat the soil directly and the air within the shelter indirectly. Drought shelters had clear polycarbonate panels over the top of the shelters to reduce precipitation and snowfall by approximately 80% year-round. The heat-drought shelters simulated both a 4°C temperature increase and an 80% precipitation reduction and contained heating tubes, polycarbonate sides and panelled roofs. Unheated shelters (control and drought) had gardening mesh walls to prevent large animals from disturbing the

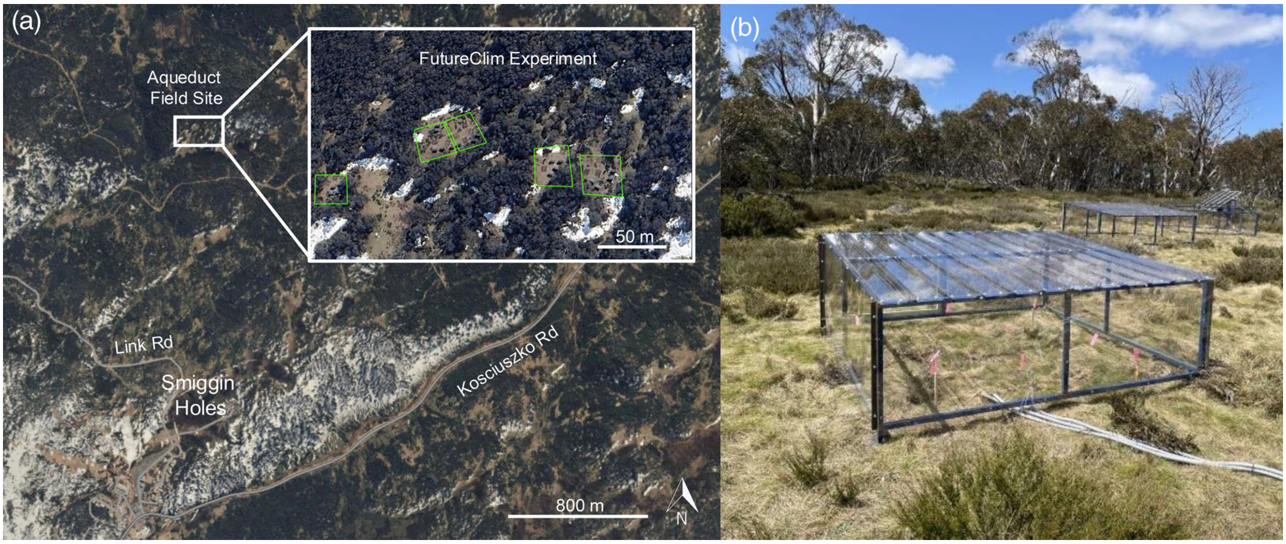

FIGURE 1 (a) Map of the FutureClim Experiment at the Aqueduct Field Site, Australian Mountain Research Facility (AMRF), Kosciuszko National Park, NSW, Australia. Inset shows the locations of the five blocks (green polygons, from left to right are blocks 1–5), which each contain four climate-controlled shelters. (b) Photo of a combined heat-drought shelter at the site, which includes a rainout shelter, side panels and embedded soil heating rods (credit: Thomas C. Hanley).

plots. Each shelter contained two soil probes (CS655, Campbell Scientific Australia Pty Ltd., QLD, Australia) – one at 0–15 cm below the surface and the other at 45–60 cm below the surface – that measured soil volumetric water content (VWC) and soil temperature at 5-min intervals. The temperature data from the deep-soil probes were used to control the heating tubes in the heated shelters.

Arthropod sampling

To assess the impact of the FutureClim treatments on soil arthropod communities, pitfall traps were used to capture samples of the ground surface and shallow-soil (upper 5 cm) dwelling arthropod communities present at each shelter. Three replicate pitfall traps were placed in set locations in each shelter (Figure S2). Trapping was conducted three times over the warm season of 2023 (12–19 January, 9–16 March and 18–25 April), in which traps were opened for 7-day intervals. In total, 180 samples were collected (20 shelters × 3 replicate traps × 3 sampling occasions). After field collection, samples were stored at 4°C to prevent degradation. The pitfall trap design (Figure S3) was based on Green and Slatyer (2020). The locations of the traps were permanently established by inserting PVC pipes (length = 100 mm, diameter = 50 mm) into the soil so that the top of the pipe was level with the soil surface. When the traps were in use, 70-mL sample containers (diameter = 46 mm, height = 55 mm) were filled with 20 mL of 30% ethylene glycol and placed inside the pipes. Plastic funnels (larger diameter = 50 mm, smaller diameter = 20 mm) directed falling arthropods into the containers, prevented captured arthropods from escaping and prevented vertebrate bycatch. Rain shelters were placed 30 mm above the soil surface over the traps to prevent them from filling with water. The pipes were covered with rubber plugs when not in use.

Arthropod identification

Arthropods were identified and sorted using a stereo microscope (M165C; Leica Microsystems Pty Ltd., NSW, Australia). All arthropod subphyla that were found (Chelicerata, Myriapoda, Crustacea and Hexapoda) were identified to the taxonomic level of order. Excluding orders belonging to the Holometabola, both adult and immature arthropods were identified and counted towards their respective orders. Since Holometabola larvae tend to have different ecological requirements to their adult forms, these were placed into their own group (hereafter, grouped as larvae). The very few specimens that could not be identified to order due to degradation were excluded from analyses. Hymenoptera were dominated by a single species of ant, *Iridomyrmex alpinus* (Heterick & Shattuck, 2011) and were therefore identified to that species, other Formicidae and other Hymenoptera. We acknowledge that identifying specimens to finer taxonomic resolution would permit more nuanced evaluations of the effects of the environmental treatments on specific feeding guilds and subgroups. Here, classifying most specimens to order was used as a "higher taxon approach" to reach taxonomic sufficiency (de Oliveira et al., 2020) while reducing costs and time required to identify the high quantity of arthropods (∼50,000) with limited information and resources available to identify the taxa to higher resolution. The results from our analyses are cautiously interpreted reflecting the limitation of this taxonomic resolution. Orders were also separated into mesofauna (typical body length <2 mm; Collembola, Diplura, Thysanoptera, Acari) and macrofauna (typical body length >2 mm; all other orders).

Statistical analyses

All analyses were conducted in R 4.3.1 (R Core Team, 2023). The three traps (per shelter) were pooled for analyses due to their proximity to one another. Overall abundance count data (excluding larvae and unidentified) was analysed with generalised linear mixed effects models (GLMM) using the *lme4* package (Bates et al., 2015). GLMMs with a Poisson distribution were fitted separately for mesofauna and macrofauna due to their obvious differences. Fixed effects included temperature (heat or no heat), moisture (drought or no drought), month (January, March, or April) and their interactions. A factor to account for temporal repeated measures (3 levels), as well as block and shelter, were included as nested random effects, in which shelter (4 levels) was nested in block (5 levels). We then conducted a type-III analyses of variance (ANOVA) on the GLMM to assess the significance of the treatment effects over the sampling periods and computed estimated marginal means for post hoc contrasts of treatments within each month that were adjusted using the “exact” multivariate-*t* method for robust inference using the *emmeans* package (Kotz & Nadarajah, 2004; Lenth, 2023).

To evaluate effects on diversity, the non-parametric Chao1 index (Chao & Shen, 2003) estimates total species richness while accounting for rare species by generating a ratio of singletons and doubletons. Chao1 was calculated for each of these pooled samples (excluding larvae and unidentified) as a robust measure of α-diversity using the *vegan* package (Oksanen et al., 2020). We fitted a GLMM with Gaussian residuals to Chao1 (log-transformed to meet homogeneity of variance assumptions) as the response variable to test the fixed effects of temperature (heat or no heat), moisture (drought or no drought), month (January, March, or April) and their interactions on taxonomic diversity. The structure of the random effects and the approach to significance and post hoc tests was identical to the GLMM for the overall abundance. Means and bootstrapped 95% confidence intervals from the *Hmisc* package (Harrell, 2019) are presented in visualisations of diversity data.

The effects of the treatments on arthropod community composition were analysed using non-metric multidimensional scaling (NMDS), conducted using the *vegan* package (Oksanen et al., 2020). Analyses were performed for each month separately to account for seasonal shifts in community composition. Bray–Curtis Dissimilarity Matrices (Bray & Curtis, 1957) were calculated using restricted datasets, in which orders that accounted for less than 0.1% of the monthly total number of arthropods were excluded. NMDS ordinations were generated from the Bray–Curtis Dissimilarity Matrices, using two dimensions and 250 random starts to find a stable solution with stress values below 0.2. Permutational multivariate analyses of variance (PERMANOVA) (Anderson, 2001) were then conducted using the Bray–Curtis Dissimilarity Matrices to test the effects of temperature, moisture and their interaction on community composition for each month. For PERMANOVA models, block was also included as a fixed effect (including interactions with moisture and temperature) to account for variation across the landscape. Permutations were restricted by block using the *permute* package (Simpson, 2022), and *p*-values were calculated using 10,000 permutations.

We also fitted GLMMs to test the effects of temperature, moisture and month on counts of individual arthropod orders. Count data for each taxon were pooled for the three traps within each shelter for each month and used as the response variables for the following GLMMs. All models included shelter nested within block as random effects to control for variation across the landscape and spatial differences among shelters, and all interactions between temperature, moisture and month as fixed factors. ANOVAs were conducted on the resulting GLMMs to clarify the significance of the treatment effects. When the GLMM included a three-way interaction, pairwise differences were calculated within months (i.e. comparisons were not made between groups belonging to different months). Separate GLMMs were fitted for Poduromorpha, Entomobryomorpha, Symphypleona, Acari, Coleoptera, Araneae, *I. alpinus*, Other Formicidae, Other Hymenoptera, Hemiptera, Diptera, Orthoptera and the larvae. Very rare taxa with large proportions of zero counts were not independently analysed.

RESULTS

Treatment differences in soil temperature and soil moisture

Shallow-soil temperature was clearly warmer in the heated shelters than in the non-heated shelters in all sampling periods (Figure 2a). The January sampling period was the warmest of the three sampling periods, where the average shallow-soil temperature (including daytime and night-time temperatures across the whole sampling period) in the heated shelters was 19.9 ± 0.39°C and in the non-heated shelters was 15.3 ± 0.27°C. Average shallow-soil temperatures in the March sampling period were cooler, where the heated shelters were 16.8 ± 0.27°C and the non-heated shelters were 12.2 ± 0.16°C. Average shallow-soil temperatures in the April sampling period were the coldest, where the heated shelters were 12.8 ± 0.28°C and the non-heated shelters were 8.3 ± 0.19°C. Mean soil moisture was lower in the drought shelters than in the non-drought shelters in all sampling periods (Figure 2b). In the January sampling period, the average shallow-soil volumetric water content (VWC; proportion) in the drought shelters was 0.10 ± 0.01 and in the non-drought shelters was 0.20 ± 0.01. In the March sampling period, the shallow-soil was slightly wetter, where the drought shelters were 0.11 ± 0.01 and the non-drought shelters were 0.21 ± 0.01. The April sampling period was the wettest of the three in both the drought and non-drought shelters, where the drought shelters were 0.25 ± 0.01 and the non-drought shelters were 0.30 ± 0.01. Moisture was also retained in the soil for longer post-rainfall in late March and April as compared to in January, when VWC would decrease relatively faster post-rainfall.

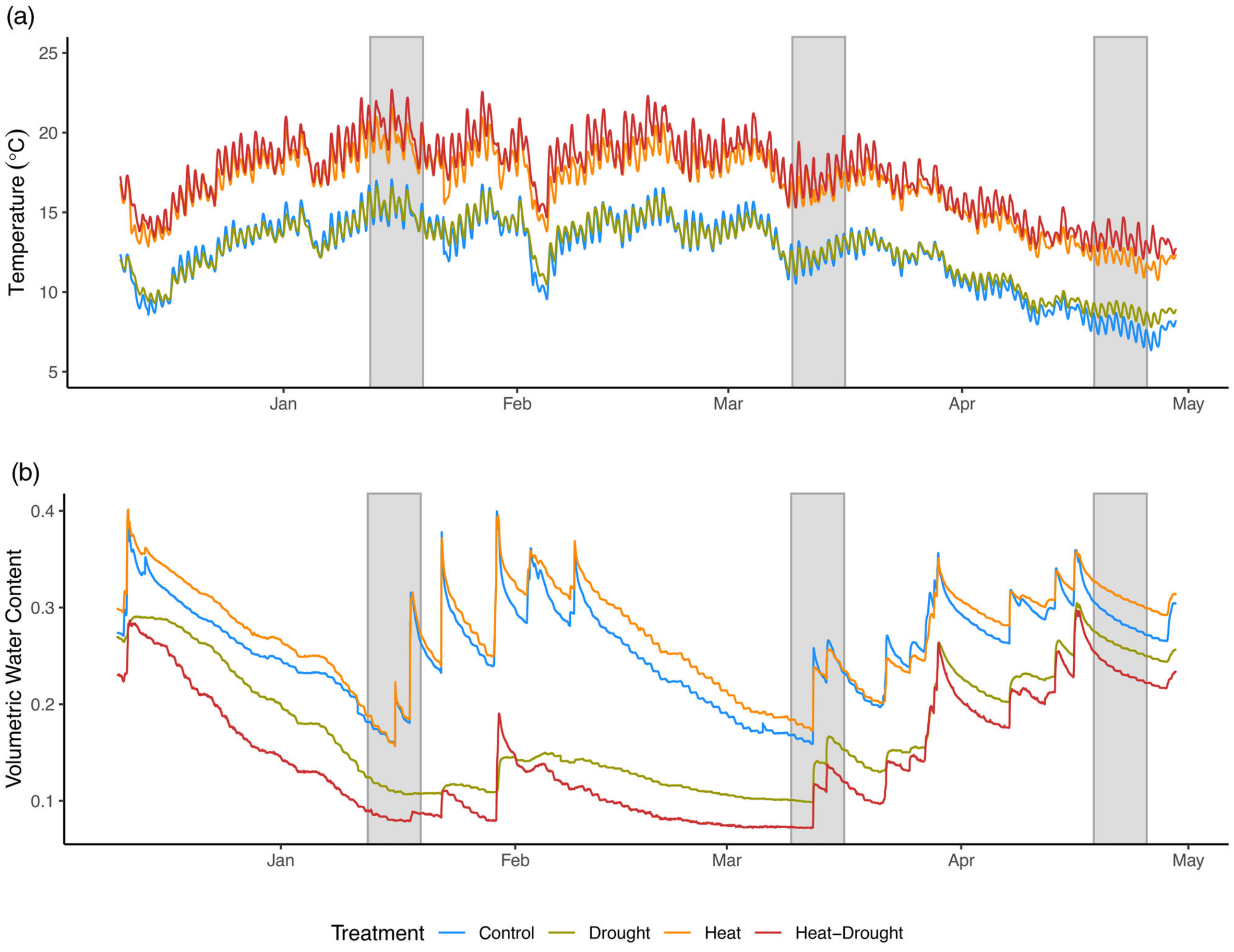

FIGURE 2 Environmental conditions in the FutureClim experiment treatments. (a) Temperature (°C) and (b) volumetric water content (VWC; proportion) over time in each treatment, averaged across blocks. Data were recorded in 5-minute intervals in each shelter at a soil depth of 0–15 cm. Of the four treatments (represented by colour), soil temperature was increased in the heat and heat-drought shelters, and incoming precipitation was reduced in the drought and heat-drought shelters. Grey bars indicate sampling periods when pitfall traps were set up in the shelters.

Overall abundance differed among treatments depending strongly on sampling month

We collected 49,794 arthropod specimens in total, spanning 21 orders (Figure 3; Table S1). The most specimens were captured in January (28,934 individuals), followed by March (15,694 individuals) and April (5166 individuals). The most abundant taxon was Collembola, which consisted of 48% of all specimens and was present in every pitfall trap. Of the three orders of Collembola present in the samples, Poduromorpha was the most abundant (29%), followed by Entomobryomorpha (14%) and Symphypleona (4%). The Hymenoptera was the next most abundant taxon, comprising 34% of the specimens and appearing in 93% of all the traps. Most Hymenopterans collected were identified as the alpine ant species *Iridomyrmex alpinus* (Heterick & Shattuck, 2011), which made up almost 33% of all specimens. The Acari made up 9% of the specimens, and they were found in almost all (99%) of the traps.

Mesofauna were far more abundant than macrofauna (Figure S4); however, the abundance of both fauna size classes responded similarly to treatments and through time, with significant effects of month, temperature × month, moisture × month and temperature × moisture × month (Table S2) indicating that temporal change both outweighs and influences the treatment effects. For both mesofauna and macrofauna, post hoc tests show that no treatment contrasts were significant in January. For mesofauna in March, the effect of drought in the absence of heat had a significant negative effect on abundance, while in both March and April heat in the absence of drought had a significant positive effect on abundance (Table S3). For macrofauna in March, there was a significant positive effect of heat-drought on abundance (which was similar but marginally not significant in April), and in April, there was a significant negative effect of heat (Table S3). The only difference introduced by excluding the dominant ant *I. alpinus* was the significant positive effect of heat-drought on abundance in April (Table S3). Thus, the effect of heat in April had

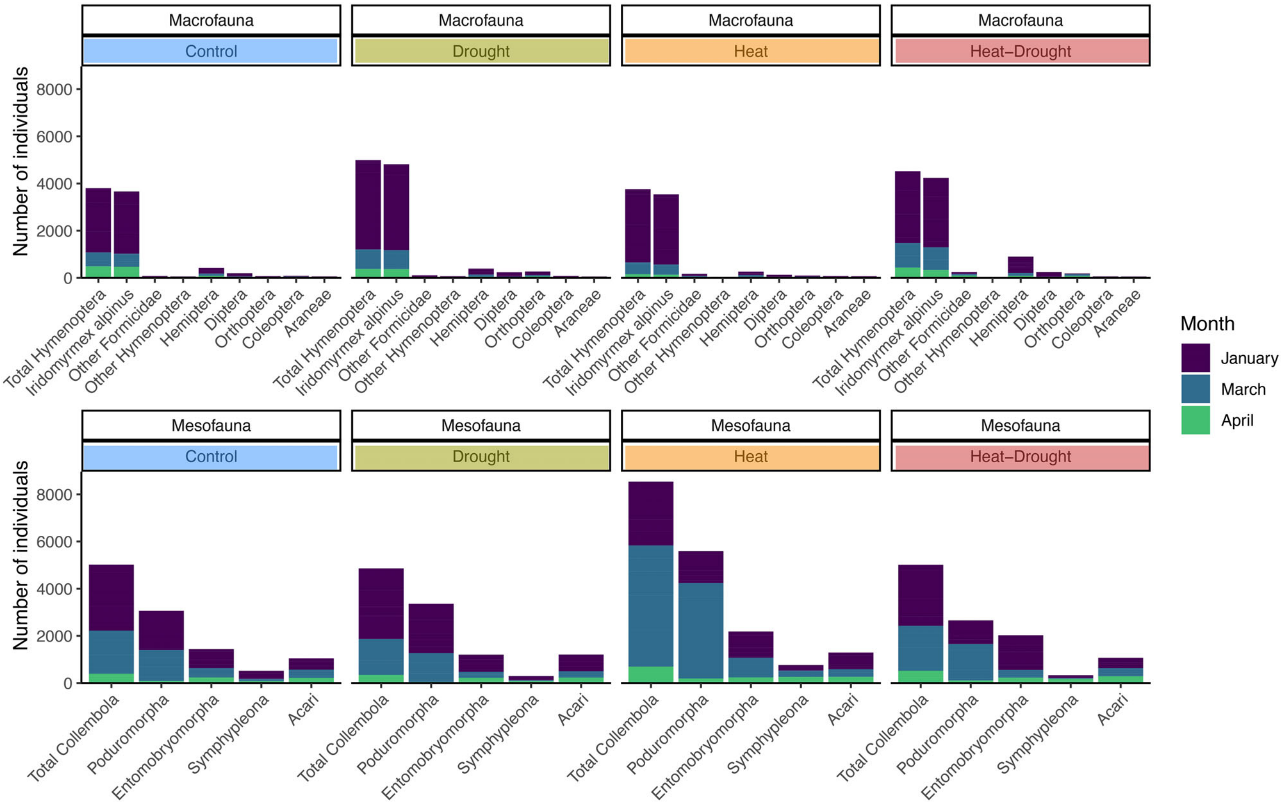

FIGURE 3 The total abundance of each soil arthropod group captured in 180 pitfall trap samples that were collected from the FutureClim experiment in January, March and April 2023. The top row of panels is macrofauna and the bottom row of panels is mesofauna. Each column of panels represents a treatment (coloured facet labels: control, heat, drought, heat-drought). There were 49,794 arthropods that were captured in total, spanning 21 orders—28,934 arthropods were caught in January; 15,694 in March; and 5166 in April. Labels indicate the total number of individuals captured for each taxonomic group across all months. "Total Collembola" is the sum of the three major orders of the Collembola subclasses: Poduromorpha, Entomobryomorpha and Symphypleona. "Total Hymenoptera" is the sum of the dominant ant species *Iridomyrmex alpinus*, "Other Formicidae" and "Other Hymenoptera". Table S1 includes rare taxa abundance, but for visual clarity, orders with relatively low numbers of individuals are not shown.

opposing effects on mesofauna and macrofauna abundance (Table S1). There were some large differences in abundance among blocks in macrofauna (driven by *I. alpinus*), where blocks 2 and 3 had much higher numbers (Figure S5).

Diversity differed temporally but only differed among treatments in April

We report GLMMs that exclude *I. alpinus*; however, both approaches indicated similar statistical significance of factors, and the results of analyses that include *I. alpinus* are presented in Table S4 and Figure S6. Chao1 α-diversity index was significantly affected by the three-way interaction of temperature × moisture × month ($F_{2,32} = 4.064$, $p = 0.027$), but no individual factor or two-way interaction was significant (Table S5). Diversity was highest in January, intermediate in March and lowest in April, while no treatment (temperature or moisture) had consistent effects on diversity (Figure 4). In January and in April, diversity was lower in all other treatments relative to the control, while heat-drought had the lowest diversity in March (Figure 4). Post hoc contrasts revealed that the only significant difference was between control and all other treatments in April (Table S6).

Community composition varied spatially and temporally

PERMANOVA revealed that temperature had statistically significant effects on the community composition of soil arthropods (excluding the dominant ant species *I. alpinus*) that was consistent in all 3 months (Table S7). Moisture was significant via an interaction with block in January, and alone in March, but was not significant in April (Table S7). There were no significant interaction effects between temperature and moisture in any month (Table S7). The community composition of soil arthropods was highly variable across the landscape, evidenced by the block effect, which represents and accounts for spatial variation across the study site. The effect of block on site dissimilarity was statistically significant in January and explained the most variation in community composition out of all the tested effects in January and April (Table S7). There were no distinct clusterings of

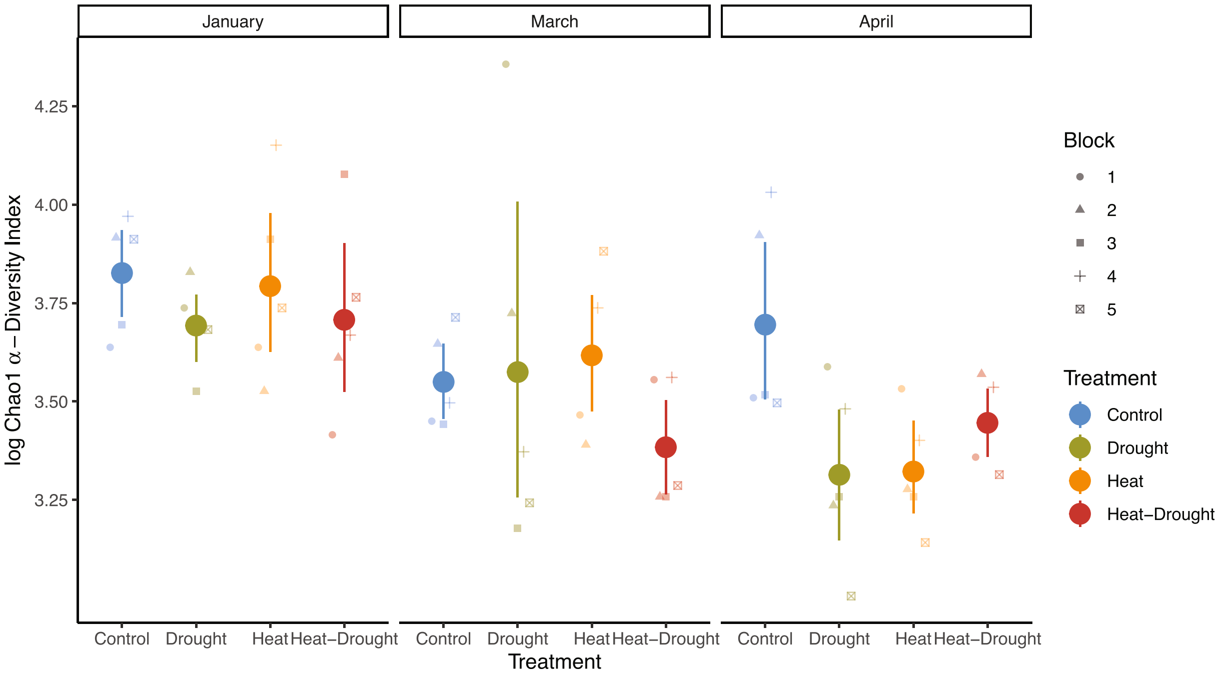

FIGURE 4 The effects of heat and drought treatments on the diversity (log Chao1 α-Diversity Index) of soil arthropod communities (excluding *I. alpinus*) in the FutureClim experiment over three sampling periods: January, March and April of 2023. Smaller points are the diversity for each of five blocks for each month, and larger points and error bars represent means with bootstrapped 95% confidence intervals.

points or ellipses by treatment in the NMDS ordinations; however, the ordinations for heat and heat-drought were somewhat separate from control and drought in January and March (Figure 5). When *I. alpinus* was included in PERMANOVA, the effects of temperature and moisture in March were dampened, but otherwise, results were similar (Table S8). Including *I. alpinus* in the NMDS analyses resulted in largely overlapping clustering by treatment, but greater separation among blocks, which indicates that the distribution of the dominant ant varied spatially across the landscape but was not dependent on treatment (Figure S7).

Taxon-specific abundances across time and treatments

The effects of temperature and moisture on abundance differed substantially across taxonomic groups. Out of the orders examined, the abundances of all except Diptera showed significant interactions among temperature, moisture and month, where month was a strongly significant factor in each analysis (Table S9). That is, abundances clearly changed over time, where they were generally higher in January. Abundance responses to the temperature and moisture treatments usually differed over time as well (Table S9).

The responses of Collembola to temperature and moisture were dependent on order. Abundance of Poduromorpha was affected by temperature in opposing directions in January and April, but the highest abundance was in the heated shelters without drought in March (Figure S8A). Entomobryomorpha had relatively higher abundances in both heated shelters in January, the heated shelters without drought in March, but was unaffected by temperature and moisture in April (Figure S8B). Symphypleona had lower abundances in drier conditions in March, while in January the heated (and wet) treatments had lower abundances, but in April these had higher abundances (Figure S8C). Acari were generally more abundant in January, but treatment effects were inconsistent within and between months (Figure S9). Coleoptera were less abundant in heat-drought conditions in March, but in April, abundance was dependent on an interaction between temperature and moisture (Figure S10). Araneae abundance was dependent on an interaction between temperature and moisture in January, but they were otherwise not consistently affected by the treatments (Figure S11). The abundance of *I. alpinus* was much higher in January than in March or April, but abundances in each treatment within month were not different among treatments (Figure S12). However, in March, there was a significant effect of moisture where abundance was higher in the drought treatments (Figure S12). Other Formicidae (excluding *I. alpinus*) showed a stronger response to temperature in March and April, where abundance increased in heated treatments, especially the heat-drought treatment in April (Figure S13). Other Hymenoptera (excluding all Formicidae) were affected by temperature and were generally more abundant in the unheated plots (Figure S14). Hemiptera abundance was much higher in the heat-drought treatment in January, but there were not significant differences among treatments in March or April (Figure S15). Abundance of Diptera was dependent on moisture, where they were more abundant in the drought and heat-drought treatments in January (Figure S16). Orthoptera were most abundant in

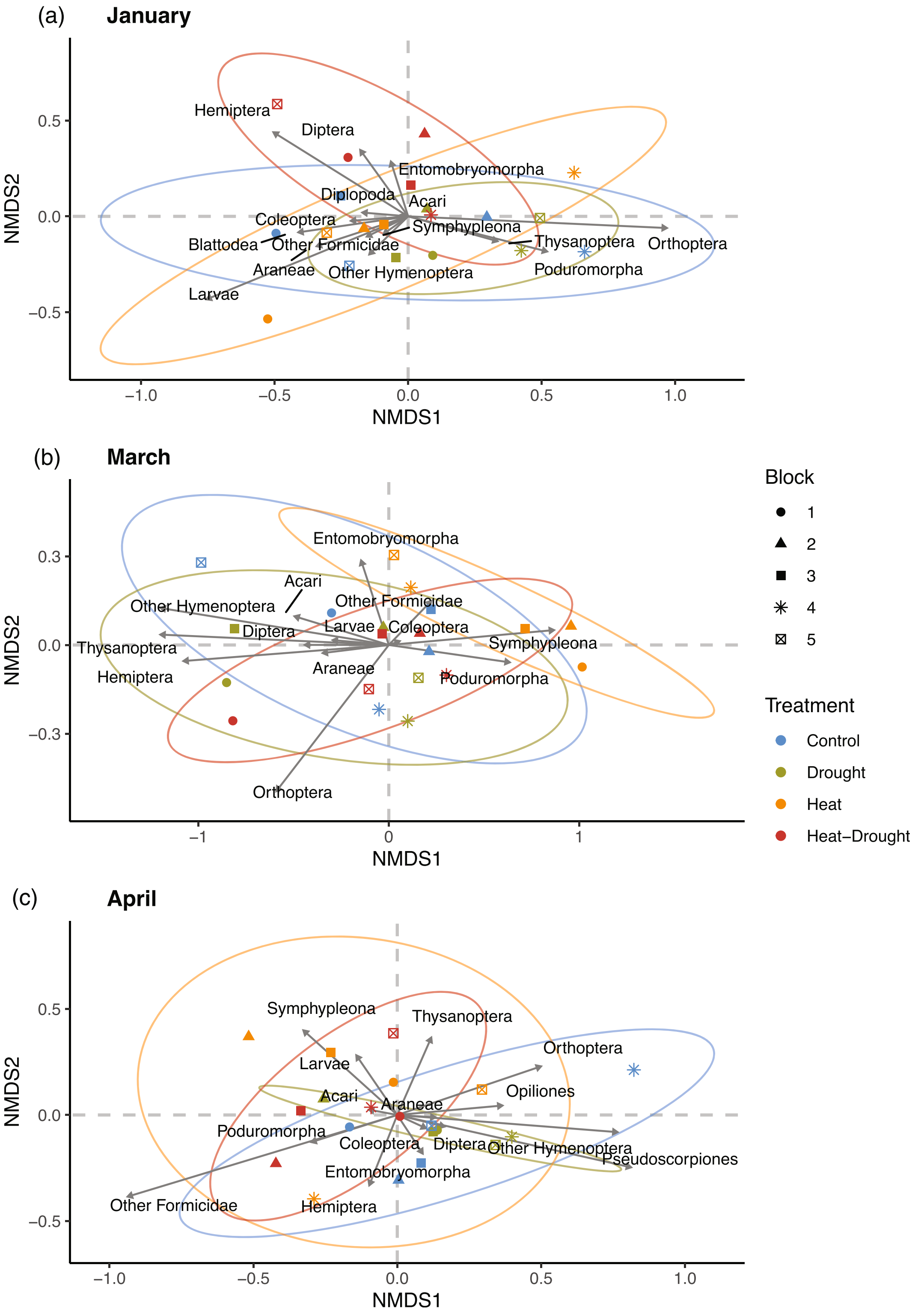

FIGURE 5 Non-metric multidimensional scaling (NMDS) ordination of soil arthropod orders (excluding *I. alpinus*) sampled from the FutureClim experiment. (a) Samples collected in January; stress = 0.121. (b) Samples collected in March; stress = 0.051. (c) Samples collected in April; stress = 0.142. Each point represents pooled values from three traps (within each block within each treatment). Treatment is indicated by point colour, and block is indicated by point shape. Arrows represent the correlation of a given taxon with the NMDS axes. Ellipses represent 95% confidence limited clusters grouped by treatment.

the drought treatment in January and had higher abundance in drought and heat-drought treatments than in the wetter conditions in both March (Figure S17). Larvae abundance was strongly dependent on moisture, where there were substantially fewer larvae in drought and heat-drought conditions than in control or heat conditions, especially in January and April (Figure S18).

DISCUSSION

By simulating potential future climate conditions directly in the field of an Australian subalpine ecosystem, we have shown that soil heating combined with drought treatments affected abundance and composition but had little overall or consistent effect on the diversity of surface-active soil arthropods through time. Our findings align with studies that observed significant changes in community composition and abundance, but generally not diversity (Cassagne et al., 2008; Roos et al., 2020). They do not support our initial hypothesis that diversity would be lower in heat and drought conditions and lowest when both heat and drought were combined, relative to the control (current conditions). Using a "higher taxon approach" limits the detail that diversity indices can capture (Grimbacher et al., 2008), but it is sufficient to begin to identify patterns in biodiversity shifts (de Oliveira et al., 2020).

We hypothesised that some soil arthropod orders would benefit while others would suffer from heat and drought treatments compared to the control conditions and that community composition would be most strongly affected by the treatments in the warmest month. Overall, temperature and moisture affected community composition significantly in all 3 months in which we took samples, which both supports our hypothesis and aligns with previous studies in alpine ecosystems in France (Cassagne et al., 2008) and Norway (Roos et al., 2020). Our study also found that several macrofauna orders: Hemiptera, Formicidae (excluding the ubiquitous alpine ant *I. alpinus*) and Orthoptera, were more abundant in heat-drought conditions, but only in some months, while larvae were consistently less abundant in the treatments with drought, as they are dependent on higher soil moisture. By March and April, the effects of the treatments over summer may have accumulated to change the soil conditions to exceed the tolerance limits of some taxa, while the conditions were more favourable for other taxa. Thus, the overall effect of heat was positive, and the effect of drought was negative for the less mobile mesofauna, which may be because the physiological trade-offs involved with acclimating to drier conditions were stressful or beyond the capacity of some mesofauna. Macrofauna were substantially less abundant in the heat treatment, but more abundant in the heat-drought treatment, implying that the warmer conditions were only beneficial when soil moisture was lower, perhaps increasing the susceptibility of some vegetation forms (e.g. forbs) to herbivory (Lemoine & Smith, 2019). Notably, while detritivores such as Collembola had much higher abundance, their biomass (and impact) may be lower than the rarer larger macrofauna detritivores (e.g. isopods, millipedes). To gain insights into the broader impacts of heat and drought manipulations on soil communities holistically, other types of traps and sampling regimes would be needed to also capture shallow and deep dwelling soil biota.

While there were clearly effects of soil warming and drought on the surface-active soil arthropod community composition, the effect of block shows that composition was highly variable across the landscape, which is consistent with studies from Australia (Nash et al., 2013) and the United Kingdom (Mitchell et al., 2016). In the current study, the large amount of community variation explained by block indicates that community composition was more likely driven by local-scale factors than by temperature or moisture. The vegetation communities at the FutureClim experiment site are spatially heterogeneous among the blocks (J.L. King et al., unpublished data), although the overall vegetation cover has relatively similar functional types (Figure S1). Nonetheless, vegetation can play a significant role in shaping the soil fauna community, especially macrofauna (Steinwandter et al., 2022), and it likely plays a role in driving the spatial differences we observed among arthropod communities. This influence of vegetation and landscape features extends beyond the FutureClim shelters themselves, and the presence of shrubs, proximity to trees, logs, or rocks may provide refugia or favourable habitats for more mobile macrofauna (e.g. Araneae, Hymenoptera) to move into or out of the shelters. Other local-scale factors that may have contributed to the substantial block effect include differences in nutrient availability (Hågvar & Klanderud, 2009), available plant biomass (Cassagne et al., 2008), litter content and quality (Seeber et al., 2008; Steinwandter et al., 2019; Steinwandter & Seeber, 2020) and microbial communities (Vestergård et al., 2015). We strongly encourage ongoing and future studies to measure local-scale factors (including edaphic, vegetation, nutrients and microbes) alongside temperature and moisture to increase explanatory power for detecting community changes.

Effects of heat and drought treatments on diversity were less clear. Diversity among treatments was generally similar in January and March but was significantly higher in the control compared to all other treatments in April. The treatment conditions in April were the mildest of all months; however, it is possible that the treatment effects accumulated over the summer and autumn months. If so, that would imply that heat, drought and their combination are all detrimental abiotic factors for surface-active soil arthropod diversity. Supporting this notion, a study in temperate grasslands in the USA manipulated precipitation treatments and found strong negative effects of drought on both arthropod abundance and diversity via reductions in soil moisture (Prather et al., 2020). However, both finer taxonomic resolution and additional sampling in the subsequent growing seasons would be necessary to make further inferences into the lasting effects of treatments on diversity.

Our results clearly show that the effects of heat and drought are variable even among taxa within mesofauna or macrofauna. In general, we expected that detritivorous mesofauna would be more abundant in the heated shelters in the absence of drought and would be less abundant in the drought shelters. This hypothesis was supported by the responses of Collembola, but not by Acari, likely because Acari includes different functional groups (predators, detritivores and omnivores). We also expected that herbivores would be more abundant in drought conditions, which was supported by Orthoptera. However, abundances of another herbivorous taxon, Hemiptera, were affected by an interaction between temperature and moisture, which demonstrates that heat and drought effects may not be generalisable across macrofauna.

The three Collembola orders all showed different responses to heat and drought conditions, and these responses varied across the season. The Poduromorpha and Symphypleona both showed positive responses to the heated shelters in the cooler months; however, these responses were more positive when soil moisture was higher. Our findings that heat (sometimes along with drought) had net positive effects on Collembola align with Nash et al. (2013) and another study from China (Yan et al., 2015). However, the effects of soil warming, and particularly drought, on Collembola populations more broadly are generally negative (Hågvar & Klanderud, 2009; Hodkinson et al., 1998; Kardol et al., 2011; Petersen, 2011; Vestergård et al., 2015). The ability of Collembola to acclimate to warmer temperatures is also often dependent on soil moisture availability, in which they cannot benefit from warmer temperatures in the presence of drought (Hodkinson et al., 1998). The differing responses between Collembola orders in our study highlight the need for further finer taxonomic resolution analyses on the effects of environmental change on Collembola. Since diets and trophic levels vary within Collembola (Potapov et al., 2016; Potapov et al., 2022), their differing responses to heat and drought may coincide with trophic changes within the detritivore community, which could have cascading effects on predator and microbial populations, and soil processes.

Collembola dominated the surface-active soil arthropod mesofauna community. Two Collembola orders had higher abundances in the heated shelters during the cooler months, which implies that detritivore feeding activity here will be extended into the cooler months of the year as the climate continues to warm on average. These findings align with a field manipulation study by Yin, Qin, Wang, Xie, et al. (2023) set in the Qinghai–Tibetan Plateau, in which soil fauna feeding activity increased by 20% in warmer conditions. Soil fauna feeding activity occurred earlier in spring (advanced phenology) and remained high long into autumn, thereby extending the season in which they can actively feed but leading to phenological mismatches between detritivores, soil microbes and plant growth. Higher levels of detritivore feeding activity in typically cooler months without corresponding phenological shifts in plant growth and microbial activity may enhance carbon loss from the soil (Yin, Qin, Wang, Xie, et al., 2023) and could expose Collembola to frost events. Soil moisture is likely a critical factor in the presence and activity of Collembola, particularly the surface-active species, and the co-occurrence of drought alongside warming may restrict detritivore feeding activity.

Acari were less negatively affected by heat and drought treatments than Collembola, which aligns with some previous studies (Hågvar & Klanderud, 2009; Nash et al., 2013) but not others (Cassagne et al., 2008; Roos et al., 2020). Acari have typically been more resilient to changes in soil temperature and moisture than Collembola (Vestergård et al., 2015). However, Acari occupy several functional feeding guilds (Potapov et al., 2022) and therefore have different ecological preferences. Different feeding guilds or subgroups of Acari could have shown divergent responses in our study, which resulted in a null net effect at the higher taxon level. Classifying Acari into feeding guilds is unreliable unless done at the genus or species level (Potapov et al., 2022), which was not feasible for this region due to lack of taxonomic descriptions and resources for identification. Use of emerging technology like DiversityScanner (Wührl et al., 2022) or functional trait-based methods to quantify arthropod communities is an emerging alternative to using taxonomic identification in ecological studies (Brousseau et al., 2018; Pey et al., 2014), which may be advantageous for poorly described taxonomic groups.

Larvae were clearly negatively impacted by drought conditions but unaffected by soil warming, whereas the adult forms of the larvae (largely Diptera and Coleoptera) were more strongly affected by the change in sampling month than specific treatments. Most larvae lack outer cuticles to conserve body water and therefore tend to occupy moist soil environments to prevent desiccation, unlike their adult forms. Larvae that live in the soil have limited movement capacity and are unable to easily relocate if the soil becomes too dry, which makes them highly susceptible to drying conditions. Soil warming is less likely to affect larval abundance than drought, but it could have a greater impact on larval development rate, adult emergence times and subsequent fitness. Given larvae are more sensitive to these conditions than adults, larval abundance may act as a reasonable ecological indicator for early signs of detrimental environmental change on soil arthropod communities (Menta & Remelli, 2020).

Hemiptera were far more abundant in the combined heat and drought treatment in January, compared to any other month or treatment. As phloem-feeders (Potapov et al., 2022), Hemiptera abundance is closely tied to the vegetation on which they feed. We hypothesise that vegetation in the combined heat and drought treatments could have been highly stressed, and therefore more susceptible to herbivory, which has been found across a range of climate change studies on plant–herbivore interactions (Hamann et al., 2021). Hymenoptera overall were largely unaffected by our soil warming or drought treatments. At our study site, Hymenoptera is dominated by an active alpine ant species, *Iridomyrmex alpinus* (Heterick & Shattuck, 2011), which is likely to be a soil ecosystem engineer (Jouquet et al., 2006; Lavelle et al., 2016). The distribution of ants across landscapes is rarely homogenous because they cluster to form trails, which can inflate and skew their apparent abundance when using pitfall traps (Green & Slatyer, 2020). Alpine ants are essential for soil organic matter turnover, and significant ant activity can accelerate decomposition (Luo et al., 2023). Other Formicidae species were more abundant in response to heat and heat–drought, so they benefit from warmer conditions and are not negatively affected by drier soils. As above, the most susceptible members of Formicidae populations to soil warming and drought are likely to be the larvae. Therefore, understanding the effects of soil warming and drought on the distribution of ant nests, rather than mobile adults, may reveal more about how these significant species will respond to climate change.

CONCLUSIONS

Our study using the FutureClim experiment investigated how both soil warming and drought alone and in combination affected in situ surface-active soil arthropod communities. We identified significant shifts in community composition in response to warming and drought throughout the season, with an interaction between soil temperature and moisture that was amplified in the warmest month in which we sampled. The responses of different arthropod orders to warming and drought were highly variable and cannot be generalised to the whole community over the course of a growing season. Detrimental effects of soil warming and drying may accumulate to affect soil arthropod community dynamics over multiple years, or soil arthropods may acclimate to the environmental conditions over time, thus long-term effects may differ from short-term effects. Changes to vegetation, soil carbon and nutrient cycling and microbial communities will likely be affected over both short (within a season) and long timescales (multiple years). We advocate that monitoring abundance, diversity and composition of soil mesofauna and macrofauna in field manipulation studies that are maintained and monitored long term is essential for understanding future ecosystem change.

AUTHOR CONTRIBUTIONS

Kate R. Farkas: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation. **Zachary A. Brown:** Methodology; project administration; data curation; resources. **James L. King:** Writing – review and editing; project administration; data curation; resources. **Adrienne B. Nicotra:** Conceptualization; funding acquisition; methodology; writing – review and editing; project administration; resources. **Megan L. Head:** Conceptualization; methodology; validation; writing – review and editing; formal analysis; project administration; supervision; resources. **Pieter A. Arnold:** Conceptualization; validation; visualization; writing – review and editing; formal analysis; project administration; supervision; resources.

ACKNOWLEDGEMENTS

We respectfully acknowledge the traditional custodians of the land from which our soil samples were collected and the land on which this research was conducted: the Ngunnawal, Ngambri, Ngarigo and Walgalu people. We sincerely thank Thomas Hanley, Laura Liersch and Tara Walker for their assistance with fieldwork. Soil samples were collected from Kosciuszko National Park under the NSW Department of Planning, Industry and Environment Scientific Licence SL102317. This work was supported by the use of Australian Mountain Research Facility (AMRF) infrastructure, a component of the Terrestrial Ecosystem Research Network (TERN), which is enabled by the Australian Government's National Collaborative Research Infrastructure Strategy (NCRIS). Open access publishing facilitated by Australian National University, as part of the Wiley - Australian National University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

Australian Research Council Project grant DP200101382.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.29434529.v1 (Farkas et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Vegetation cover in the FutureClim experiment.

Figure S2. The general layout of shelters within the FutureClim experiment.

Figure S3. The pitfall trap design used for this study.

Figure S4. The total abundance of each soil arthropod group by fauna size and month in this study.

Figure S5. The total abundance of each soil arthropod group by fauna size, block, and treatment in this study.

Figure S6. The effects of heat and drought on the diversity of soil arthropod communities (including *I. alpinus*).

Figure S7. Nonmetric multidimensional scaling (NMDS) ordination of arthropod orders (including *I. alpinus*).

Figure S8. The effects of heat and drought conditions on the abundance of Collembola.

Figure S9. The effects of heat and drought conditions on the abundance of Acari.

Figure S10. The effects of heat and drought conditions on the abundance of Coleoptera.

Figure S11. The effects of heat and drought conditions on the abundance of Araneae.

Figure S12. The effects of heat and drought conditions on the abundance of *I. alpinus*.

Figure S13. The effects of heat and drought conditions on the abundance of Other Formicidae.

Figure S14. The effects of heat and drought conditions on the abundance of Other Hymenoptera.

Figure S15. The effects of heat and drought conditions on the abundance of Hemiptera.

Figure S16. The effects of heat and drought conditions on the abundance of Diptera.

Figure S17. The effects of heat and drought conditions on the abundance of Orthoptera.

Figure S18. The effects of heat and drought conditions on the abundance of larvae.

Table S1. Overall abundance of each arthropod group in each treatment and sampling month.

Table S2. ANOVA outputs for effects of temperature, moisture, and month on abundance.

Table S3. Post-hoc contrasts for effects of temperature, moisture, and month on abundance.

Table S4. ANOVA output for effects of temperature, moisture, and month on diversity excluding *I. alpinus*.

Table S5. ANOVA output for effects of temperature, moisture, and month on diversity including *I. alpinus*.

Table S6. Post-hoc contrasts for effects of temperature, moisture, and month on diversity.

Table S7. PERMANOVA outputs for the effects of soil warming and drought conditions on composition (excluding *I. alpinus*).

Table S8. PERMANOVA outputs for the effects of soil warming and drought conditions on composition (including *I. alpinus*).

Table S9. ANOVA outputs for effects of temperature, moisture, and month on abundances of individual arthropod taxa.

How to cite this article: Farkas, K.R., Brown, Z.A., King, J.L., Nicotra, A.B., Head, M.L. & Arnold, P.A. (2025) Combined heat and drought affect the abundance, composition and diversity of subalpine surface-active soil arthropod communities. *Ecological Entomology*, 1–15. Available from: https://doi.org/10.1111/een.70015