# Australian Subalpine Soil Invertebrate Diversity and Abundance Under Simulated Drought

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# Abstract

The impact of climate change, notably more frequent and extreme drought, on soil invertebrate communities essential to the survival of the Australian subalpine ecosystem, remains a relatively unexplored concept. Using samples collected from the AMRF FutureClim site near Mt Perisher, we studied how a simulated drought environment influences soil invertebrate community composition, diversity and abundance, to predict what may occur in Kosciuszko National Park's near future. The significant decrease in overall abundance of soil invertebrates observed under drought conditions, coupled with variations in the composition of orders and feeding guilds suggests possible negative impacts of decreased moisture availability on these communities. Whilst only preliminary findings, this research is beneficial in raising awareness on how every aspect of the environment, whether as big as the trees or as small as the grains of soil, is a significant contributor toward the ecosystem's survival.

# Introduction

In terrestrial environments like the Australian Alps, soil invertebrates not only act as fundamental bioindicators of the overall health and abundance of the ecosystem (Lavelle et al., 2006), but also sustain essential biological processes that maintain the delicate balance of the biosphere (Goncharov et al., 2023). In nature, primary resources like carbon, nitrogen, phosphorous and energy are finite, and therefore must be recycled and reused. By regulating organic matter decomposition (Fitter et al., 2005; Yin et al., 2023), soil invertebrates facilitate the release of these resources back into the ecosystem, allowing the cycle to continue (Steinwandter et al., 2018; Gaven-Centol et al., 2023). Due to the various trophic levels involved in this process, it is only maintainable if a diverse soil invertebrate community is present in a high enough abundance to fulfill the demand of the ecosystem (Semeraro et al., 2022; Nash et al., 2013). This in turn influences the growth and productivity of native plant species (Wardle et al., 2004), and therefore the distribution of the fauna that rely on it (Figueroa et al., 2021). The importance of soil invertebrate community diversity has been previously documented by Decaëns et al. (2006) who found that an extreme abundance of herbivorous invertebrate negatively affected the surrounding flora, with subsequent impacts on

fauna species higher up the trophic chain (Decaëns et al, 2006). Predatory soil invertebrates help to reduce overgrazing by herbivores, with can disproportionately affect native species compared with invasives (Smith & Williams, 2022). Additionally, decomposers and detritovores aerate and redistribute nutrients throughout the soil, increasing water retention and reducing run-off erosion. This is one of the factors that enables the Kosciuszko National Park to contribute up to 30% of the water received annually by the Murray-Darling Basin (National Parks Association NSW, 2016).

The effects of climate change, including increased temperatures, altered precipitation, and increased atmospheric CO<sub>2</sub>, will have detrimental impacts on global ecosystem functions and lead to diversity losses (Masson-Delmotte et al., 2021; Hooper et al., 2012). These changes are likely to influence soil invertebrate community dynamics, and the essential services of litter decomposition, as well as carbon and nutrient cycling that they provide (Goncharov et al., 2023). Additionally, climate change will impact the frequency and intensity of extreme weather events such as droughts (Yuan et al., 2023), which have the potential to alter population dynamics and disturb ecosystem functions (Scheffer and Carpenter, 2003). Predictions for 2050 in Kosciuszko National Park indicate that temperatures will rise between 0.6°C – 2.9°C, precipitation rates will decrease, and the frequency and intensity of droughts will increase (Worboys et al., 2011). Furthermore, the alpine tree line will rise and decrease the habitat of endemic high-altitude flora and fauna, increasing competition pressures and augmenting ecosystem processes (Griffiths et al, 2021; Masson-Delmotte et al, 2021; Hooper et al, 2012). The unique environmental and cultural attributes of this region in Australia emphasise its significance for conservation and protection against climatechange induced diversity loss (Mansergh et al., 2004). Given limited research on soil invertebrates in this region, combined with their vital roles in supporting biodiversity and the environment, it is critical to prioritise research on their abundance, diversity, and response to extreme conditions, such as drought.

Existing literature on Australian soil invertebrates is sparse, and there is no consensus surrounding the responses of soil invertebrates to drought. Some research suggests that drought conditions will cause a decrease in soil invertebrate abundance due to reduced moisture availability, and a loss of carbon due to reduced photosynthesis by plants (Seeber et al, 2012; Kardol et al, 2011; Lindberg et al, 2002). Contrasting papers suggest the certain adaptations in behaviour will mitigate the effects of drought on soil invertebrates (Torode et al, 2016; Fitter et al, 2005). Changes in community composition of soil invertebrates as a result to drought are also documented by Kardol et al. (2011) and attributed to changes in the quantity and quality of available nutrients. A preceding study in the Australian Alps investigating arthropod community composition along a snowmelt gradient found that notably higher predator numbers were observed in late-melting zones characterised by low soil moisture availability (Green & Slatyer, 2020). The effect of temperature on soil invertebrates, and on invertebrate communities within the Northern Hemisphere is better documented. Figueroa et al. (2021) found that increased air temperatures resulted in slower leaf litter decomposition and decreased invertebrate abundance and diversity in Massachusetts, United States. Studies in Iceland investigating the effect of an increase in soil temperature on soil invertebrate abundance and diversity concluded similar results, with the caveat that certain species became more abundant at higher temperatures with implications to flora abundance and diversity (Robinson et al, 2018; Escribano-Alvarez et al, 2022).

In this study we seek to investigate the effect of a simulated drought on the diversity and abundance of orders present in soil invertebrate communities within the sub-alpine zone of Kosciuszko National Park. Additionally, we seek to understand the impact of drought on the abundance and diversity of feeding guilds to gain insight into functional changes in the soil ecosystem in response to reduced moisture availability. This research represents novel and

preliminary insights into the response of soil invertebrates to drought within the Australian subalpine zone.

We hypothesise that reduced moisture availability and the associated change in available nutrients in drought sites will reduce the overall abundance of soil invertebrates, as well as reduce abundance within orders and feeding guilds. Furthermore, we hypothesise that reduced moisture availability and differences in the abundance and quality of certain nutrients will cause a loss of diversity in both orders and feeding guild. This reflects the differences in the functionality, as well as adaptations and behavioural responses of different groupings to the environmental stress.

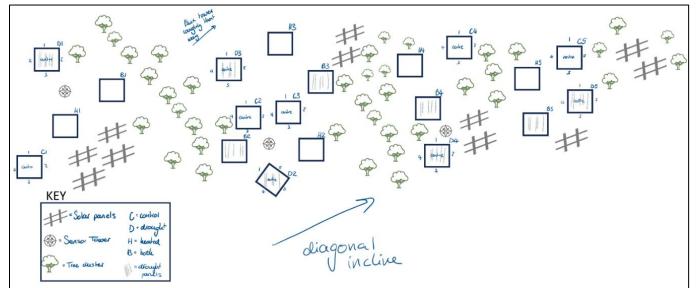
# Methods

## Study site

This study was conducted at the Australian Mountain Research Facility's FutureClim site, an alpine grassy herb field located near Mt Perisher in Kosciuszko National Park (elevation 1600m, 36° 22' 20.3803" S, 148° 25' 52.2516" E). Soil collection occurred on the morning of the 27th of November 2023, in clear conditions, following two days of intermittent rain.

The Aqueduct site contains 5 blocks of four "climate-controlled shelters" or treatment plots (approx. 4m<sup>2</sup> area): a control treatment, heat treatment (uses vertical heating tubes buried 70cm below the soil surface and clear polycarbonate walls to maintain a minimum temperature of +4°C), drought treatment (uses clear polycarbonate panels to block approximately 40% of rainfall) and a combined heat/drought treatment. The non-heated plots are bordered with gardening mesh to prevent disturbance from local fauna. Each plot also has a buffer zone indicated by wooden stakes; a 0.5m wide perimeter around the 2x2 working area. For this study, the control and drought treatment plots from each of the 5 blocks were used, totalling 10 test sites.

Figure 1 – Kosciuszko National Park; Australian Mountain Research Facility FutureClim Site Schematic with 5 labelled blocks each including a control (C), drought (D), heated (H), and heated drought (B) plot.



## Field methods

At each of the 10 sites, a soil volume of approximately 529cm<sup>3</sup> was taken from the lower perimeter of the site, within the buffer zone to minimise impacts on concurrent experiments. The soil was collected using a corer with a diameter of 7.4cm which went to a depth of approximately 12cm. The corer was hammered in with a mallet and then prised out using a trowel if necessary. The collected soil was placed in a labelled Ziploc bag for transport back to the laboratory.

A soil moisture probe was used to take measurements at 5 different points within each of the 10 plots providing average values for both control and drought treatments.

### Laboratory methods

Soil collected, segregated by site, was placed into Berlese funnels (10 in total). Each Berlese funnel consisted of a 15cm diameter plastic funnel above a glass jar containing approximately 25mL of 70% ethanol. The funnels featured two plastic mesh squares in the stem to prevent large soil aggregates entering the ethanol. The tops of the funnels were covered with aluminium foil, which was duct-taped around the opening of the jar to prevent invertebrates from escaping. The Berlese funnels were positioned 23cm below three 250W heating lamps in a random order and left under the heat for 17 hours.

After this period, the foil covering was removed, and the distance between the funnels and the heat lamps was reduced to 12cm. Simultaneously, the ethanol was replaced, allowing for examination of the contents that had been collected until that point. The collected ethanol was poured into small petri-dishes and viewed under a dissecting microscope. Paint brushes were used to isolate specimens from any soil sediment. This allowed for morphological identification of invertebrates to order, and family where possible, with the assistance of CSIRO insect identification keys (CSIRO, n.d.) and resource person, Kate Farkas.

The ethanol jars were inspected again 24 hours later, and then the soil within the Berlese funnels was carefully searched through for any larger organisms unaffected by the heat lamp or unable to pass through the mesh in the funnels' stem.

## Identification

The number of individuals and orders from each of the 10 plots were recorded. Individuals identified as worms (Order: Opisthopora) were not included in subsequent analysis due to uncertainty with their identification.

Invertebrates were separated into feeding guilds using a table (Table 1.) adapted from Andrew & Hughes (2005) and Simberloff & Dayan (2003). The order Coleoptera was further separated into 3 distinct families, Carabidae, Staphylinidae and Scarabidae (CSIRO, n.d) to reflect the different feeding guilds that they are a part of. Ants were designated to their own feeding guild due to the variety of functional roles they fulfil (Andersen, 1995) and their high relative abundance across the two treatments. The single larva that was observed could not be identified to order and was consequently included in the 'Various' guild.

Table 1: Soil invertebrate orders and feeding group used in analyses

Feeding guild	Orders included		
Predators	Coleoptera: Carabid, Staphylinidae		
Detritovores/ Scavengers	Collembola, Coleoptera: Scarabidae, Diplopoda		
Ants	Hymenoptera: Formicidae		
Various	Acari, Diplura, Phyllodocida, larvae		

## Data Analysis

Data analysis was completed in Excel (Version 16.78). Two sample T-tests ( $\alpha = 0.05$ ) assuming unequal variance were conducted to compare the soil moisture measurements between conditions, and for the comparing the overall abundance of individuals in each treatment. ANOVA tests ( $\alpha =$ 0.05) were conducted to compare the individual abundance within orders and feeding guilds between drought and control plots.

Relative abundance, also the proportion of individuals of one grouping out of the total number of individuals found per volume per plot, was calculated using the equation:

 $relative abundance = \frac{no. of individuals within grouping}{overall no. of individuals}$ 

Shannon's diversity Index (H') was calculated to compare the diversity of orders and feeding guilds between treatments. It was calculated using the equation:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

Where *p<sub>i</sub>* is the proportion of individuals of a grouping found divided by the total number of individuals found (relative abundance), *s* is the number of groupings, *ln* is the natural log and S is the sum of calculation.

## Results

A total of 43 invertebrates from 7 different orders (plus larvae that could not be identified to order) were recovered from the soil samples across the 10 sites. 32 of these individuals were found in the control plots with the remaining 11 found in drought plots.

6 orders of invertebrates were present in the control treatment whereas only 4 orders were present in the drought treatment. Only Hymenoptera and Coleoptera were present in samples from both treatments. The orders Collembola, Acari, Diplopoda and Diplura occurred exclusively in the control treatment, and Phyllodocida and the larvae only occurred in the drought treatment.

There were no incidences of orders designated to the feeding guild 'Scavengers/ detritovores' in the drought treatment.

	Control	Drought
Hymenoptera	14	5
Collembola	5	0
Acari	2	0
Coleoptera Staphylinidae	1	1
Larvae	0	1
Phyllodocida	0	1
Coleoptera Carabidae	2	4
Diplopoda	5	0
Diplura	2	0
Coleoptera Scarabidae	1	0

Table 2: Soil invertebrate order/ family incidence across control and drought treatments.

#### Soil Moisture

Soil moisture in the control shelters (mean = 3.88%m SE = 0.495, n = 15) was significantly higher (p=0.003) than in the drought shelters (mean = 2.30%, SE = 0.510, n = 15), confirming that the rain-exclusion panels effectively reduced soil moisture at the drought sites.

Effect of simulated drought on soil invertebrate abundance

There was a significant difference in the mean number of total individuals found in  $100 \text{ cm}^3$  of soil between the control (mean = 1.21, SE = 0.23, n=5) and drought sites (mean = 0.45, SE = 0.22, n=5) [t = 2.38, df = 8, P = 0.0222] (Figure 2.)

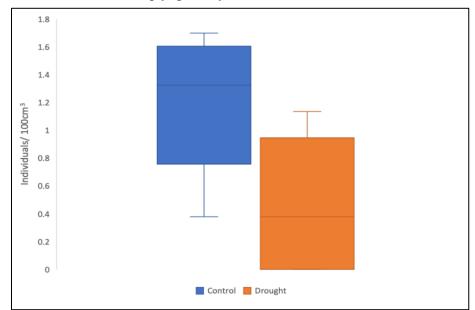


Figure 2. The mean number of individual invertebrates found in 100cm<sup>3</sup> of soil. Blue represents the control sites and orange represents the drought sites.

No significant difference (Table 3.) was found between mean number of individuals in each feeding guild per volume of the control and the drought sites. The feeding guild 'Ants' had the highest relative abundance across both treatments (Figure 3.). There was a higher abundance of individuals within the feeding guild 'Predators' in the drought treatment though this difference was not significant (Table 3.)

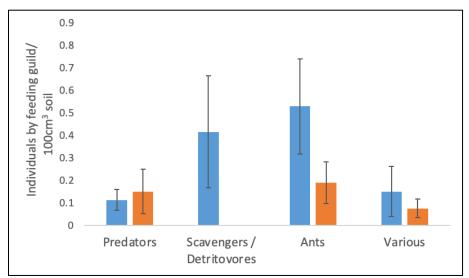


Figure 3i. Abundance as the mean number of individuals within a feeding guild per 100cm<sup>3</sup> of soil. Standard error shown by error bars. Blue represents the control sites; orange represents the drought sites.

Table 3: ANOVA test statistics comparing individuals within each feeding guild per 100cm<sup>3</sup> of control (C) and drought (D) soil.

<b>Feeding Guild</b>	Mean	Number	df	F-stat	P value
Predators	C: 0.11 D: 0.19	10	8	0.24	0.64
Scavengers	C: 0.42 D: 0	10	8	2.8	0.15
Ants	C: 0.53 D: 0.19	10	8	2.1	0.18
Various	C: 0.15 D: 0.076	10	8	0.4	0.54

Although different orders were present between the control and drought treatments, there were no significant differences (Table 4.) in abundance within orders across the treatments. Hymenoptera had the highest abundance in the control sites, and Hymenoptera and Coleoptera had the joint highest abundance in the drought treatment (Figure 4.).

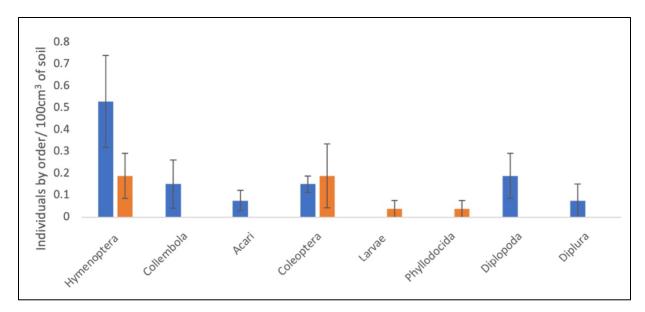


Figure 4. Abundance as the mean number of individuals within order grouping per 100cm<sup>3</sup> of soil. The error bars represent standard error. Blue represents the control plots and orange represents the drought plots.

Order	Mean	Number	df	F-stat	P value
Hymenoptera	C: 0.53	10	8	2.1	0.18
	D: 0.19				
Collembola	C: 0.9	10	8	2.5	0.15
	D: 0				
Acari	C: 0.075	10	8	2.7	0.14
	D: 0				
Coleoptera	C: 0.1	10	8	0.24	0.64
	D: 0.19				
Larvae	C: 0	10	8	1	0.35
	D: 0.038				
Phyllodocida	C: 0	10	8	1	0.35
	D: 0.038		2		
Diplopoda	C: 0.19	10	8	0.24	0.64
D: 1	D: 0	10	0	1	0.25
Diplura	C: 0.076 D:0	10	8	1	0.35

Table 4: ANOVA test statistics for individuals by order/ 100cm<sup>3</sup> of soil.

## Effect of simulated drought on diversity.

Figure 5. shows that the relative abundance of every feeding guild except 'Scavengers/ Detritovores' was higher in the drought treatment, however this pattern was not statistically significant (Table 5.). The value of Shannon's diversity index for feeding guilds in the control treatment was 1.32, and for the drought treatment was 1.03.

Feeding Guild	Mean	Number	df	F-stat	P value
Predators	C: 0.11	10	8	0.24	0.64
	D: 0.19				
Detritovores/	C: 0.42	10	8	2.8	0.13
Scavengers	D: 0				
Ants	C: 0.53	10	8	2.7	0.14
	D: 0.19				
Various	C: 0.15	10	8	0.4	0.54
	D: 0.076				

Table 5. ANOVA test statistics for individuals by feeding guild/ 100cm<sup>3</sup> of soil.

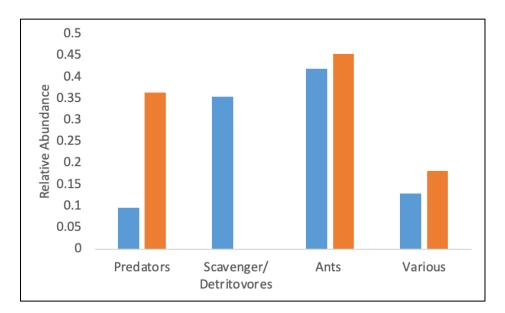


Figure 5. The relative abundance of feeding guilds in both the control (blue) and drought (orange) sites. Relative abundance was calculated by dividing the number of individuals within the feeding guild by the total number of individuals within each treatment.

The values of Shannon's diversity index for taxonomic diversity in the control treatment and drought treatments were 1.55 and 1.14 respectively. Figure 6 displays that for the control treatment, the order with the highest relative abundance was Hymenoptera, and the order with the lowest was Acari. For the drought treatment, Coleoptera had the highest relative abundance, with Phyllodocida and larvae had the lowest relative abundances.

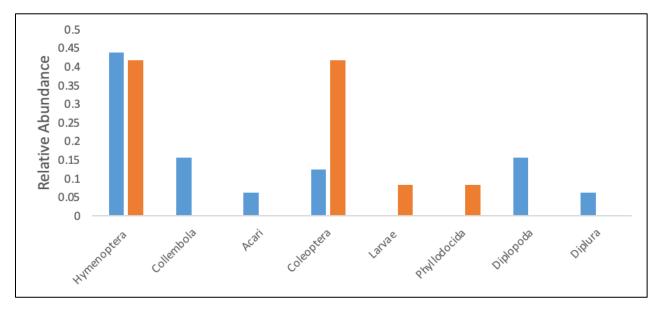


Figure 6. The relative abundance of orders in both the control (blue) and drought (orange) sites. Relative abundance was calculated by dividing the number of individuals within the order by the total number of individuals within the treatment.

## Discussion

This study investigated the impact of simulated drought on the abundance and diversity of soilinvertebrates in the Perisher sub-alpine zone of Kosciuszko National Park. After validating there was a drought effect, this experiment considered the effects on overall abundance, as well as the distribution of individuals across orders and feeding guilds. Furthermore, the study compared order diversity and feeding guild diversity between the control and drought treatments using Shannon's diversity index.

While the small number of soil samples collected and small sample sizes for soil invertebrates extracted means that statistical analysis is limited, the information gathered by the study suggests differences in abundance and diversity in the drought and control treatments. The initial hypothesis regarding a decrease in invertebrate abundance in drought conditions was partially supported by the results as there was a significant decrease in soil invertebrate abundance in the drought sites compared the control sites. However, the absence of significant changes in abundance within orders and feeding guilds did not support this hypothesis.

There is a mixed consensus in the literature for the responses of soil invertebrates to drought, with some studies reporting no change in abundance (Torode et al, 2016) and others reporting decreased abundance (Kardol et al, 2011; Seeber et al, 2012). Water availability both directly and indirectly influences soil invertebrates' abundance and activity, potentially causing deeper burrowing or evasion (Eisenhauer et al, 2012; Barnett & Facey 2016; Corbett, 2021). This behaviour can make drought-related changes in abundance difficult to discern, especially

considering the depth of sampling that occurred in this study. A further consideration is that within the subalpine area, an already extreme environment, minor perturbations like a moderate drought may not cause variation in abundance and diversity due to pre-existing selection for highly plastic traits (Figueroa et al, 2021). Similar results of significant overall changes in soil invertebrate abundance without significant changes in order or functional grouping abundance have previously be attributed to the notion that drought creates a uniform pressure across the broader ecosystem and effects individuals somewhat equally (Bessell-Koprek et al, 2023; Lindberg & Bengtsson, 2005).

The higher Shannon's diversity index value for feeding guilds in the control treatment would suggest that there is greater diversity in feeding guilds in communities existing outside of drought conditions, supporting the second hypothesis. However, the higher Shannon's diversity index value for orders in the drought treatment suggests more diversity in order under drought conditions. A change in order diversity or feeding guild diversity could represent a change to the stability of the ecosystem and impact the services provided by soil invertebrates. Existing literature suggests that invertebrate diversity will be reduced by drought, influenced by the reallocation of resources by plants (Dijkstra et al, 2012) leading to a cascade effect within food webs to higher trophic levels. Losses of phylogenetic and functional richness following drought have also been reported (Peguero et al, 2019). Interestingly, the result of a higher relative abundance of predator species within the control treatment, though not statistically validated, is similar to the results of Green & Slayter (2020) which saw a higher abundance of predators in areas of low water-availability.

The significant decrease in total abundance of soil invertebrates in the drought sites highlights the importance of conducting broader-scale research to ascertain the true extent of reduced soil moisture on these communities. Changes in diversity noted in the limited data further emphasise this need for continued research to elucidate the effects of drought on the function of soil invertebrate communities.

Invertebrates are underrepresented in ecological studies, particularly in the Southern Hemisphere and Australia (Green & Slatyer, 2020; Andrew & Hughes, 2005). By decomposing organic matter, creating porosity, influencing aggregation, regulating microbial communities, and influencing plant growth, the impact of soil invertebrate activities scales to a whole environment level (Lavelle et al, 2006). The importance of soil invertebrates to the landscape, especially in places of environmental and cultural significance like Kosciuszko National Park cannot be overstated. Any future research that investigates the effect of climatic perturbations on soil invertebrate abundance and diversity will help to better inform current and future land management and conservation.

Whilst this study only looked at changes in soil moisture content due to reduced incidence of rainfall as a potential cause for change in soil invertebrate communities, the importance of water relations in mediating above and below-ground interactions within the soil landscape has been indicated by several studies (Johnson et al, 2011; Torode et al, 2016). It is essential to consider a variety of different influences when investigating the response of soil invertebrates to drought. In conjunction with more frequent extreme weather events and reduced precipitation under climate change, temperatures are predicted to rise in Kosciuszko National Park (Worboys et al, 2011). The response of soil invertebrates to both drought and increased temperatures will provide valuable insights into how these communities might function in the future. Increased temperatures have been reported to impact the community composition of invertebrates and cause range increases in invasive species (Nash, 2013), as well as increase the abundance of invertebrate populations (Andrew & Hughes, 2005). Another avenue for future research in conjunction with soil moisture is the effect of fungal biomass on soil invertebrates. Fungivores were not a feeding guild explicitly

represented in this study, and previous literature suggests that alterations in fungi due to soil moisture may affect soil invertebrate community composition (Lindberg et al, 2002)

It is also important to note that there is a disparity between field-based studies and laboratory experiments investigating soil invertebrate communities. Studies like those by Figueroa et al. (2021) and Robinson et al. (2018) which occurred under strictly contained conditions do not have the capacity to reflect the natural variation of these communities in nature (Nash et al, 2013). Any future studies that occur in situ in the Australia alpine region would provide vital information about the functioning of soil invertebrates in this prominent cultural and environmental landscape.

## Limitations

Limitations of the study primarily revolve around the relatively low number of samples and small sample sizes of extracted invertebrates, which means that interpretation of our data and statistical analyses should be done with caution. A further implication of this was that calculating diversity indexes based on broad taxonomic or functional groups does not allow us to account for specific functional differences within those groups. Soil invertebrates often fill highly specialised roles in the ecosystem, particularly in carbon and nutrient recycling. We were unable to determine impacts of drought on specific species and their functional roles due to broad groupings used in analysis. Expanding the number of independent soil samples in our experiment would facilitate robust statistical tests to help discern the relationships between soil invertebrate abundance, diversity and drought. The relatively small difference in soil moisture between control and drought treatments, although significant, potentially buffered any changes in abundance or diversity within the drought treatment. Future studies should allow the Berlese funnels to stand for more time, to allow adequate passage of invertebrates into the ethanol trap, increasing the sample size of extracted individuals and preventing manual sifting.

# Conclusion

This study presents preliminary findings for the effects of simulated drought on soil invertebrate abundance and diversity in the sub-alpine zone of Kosciuszko National Park. The observed significant decrease in overall abundance of soil invertebrates within the drought treatment, along with discernible differences between in the composition of orders and feeding guilds points to possible adverse effects of reduced soil moisture on these communities. Changes to the abundance and composition of soil invertebrate communities are amplified across the broader ecosystem given their vital roles in nutrient cycling, maintaining soil health, and influencing plant growth. Investigations into the dynamics of soil invertebrate communities are underpinned by the need for further research to aid understanding of responses to different environmental stressors, and subsequent consequences of these responses to the rest of the ecosystem.

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# References

Andersen, A.N. (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* **22**. 15-29.

Andrew, N.R. & Hughes, L. (2005) Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change. *Austral Ecology* **30**. 281-297.

Barnett, K. & Facey, S. (2016) Grasslands, Invertebrates, and precipitation: a review of the effects of climate change. *Plant Science* **7**.

Bessell-Koprek, M., Andrews, O., Hibbert, E., Jaugietis, B., Walker, T., Miller, P., Mueller, I., Pay, L., Thomas, A. & Mceachern, A. (2023) The effects of drought on the leaf-litter invertebrates of an Australian wet tropics ecosystem: The Daintree rainforest. *Field Studies in Ecology* **4**.

Corbett, E. (2021) Response of a soil invertebrate community to a brief flood event. *Department of Biological Sciences* **101**. 43-52.

CSIRO (n.d.) Insects and their Allies, Key to the invertebrates, Commonwealth Scientific and Industrial Research Organisation, accessed November 2023 <u>https://www.ento.csiro.au/education/key/couplet\_01.html</u>

Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G.J. & Lavelle, P. (2006) The values of soil animals for conservation biology. *European Journal of Soil Biology* **42**. S23-S38.

Dijkstra, F.A., Pendall, E., Morgan, J.A., Blumenthal, D.M., Carrillo, Y., Lecain, D.R., Follett, R.F. & Williams, D.G. (2012) Climate change alters stoichiometry of phosphorous and nitrogen in a semiarid grassland. *Physiologia Plantarum* **196**. 807-815.

Eisenhauer, N., Cesarz, S., Koller, R., Worm, K. & Reich, P.B. (2012) Global change belowground: Impacts of elevated CO<sub>2</sub>, nitrogen, and summer drought on soil food webs and biodiversity. *Global Change Biology* **18**. 435-447. Escribano-Alvarez, P., Pertierra, L., Martinez, B., Chown, S. & Olalla-Tarraga, M. (2022) Half a century of thermal tolerance studies in springtails (Collembola): A review of metrics, spatial and temporal trends. *Current Research in Insect Science* **2**.

Figueroa, L.L., Maran, A. & Pelini, S.L. (2021) Increasing temperatures reduce invertebrate abundance and slow decomposition. *Ecology and Evolution* **16(11)**.

Fitter, A.H., Gilligan, C.A., Hollingworth, K., Kleczkowski, A., Twyman, R.M. & Pitchford, J.W. (2005) Biodiversity and ecosystem function in soil. *Functional Ecology* **19**. 369-377.

Goncharov, A., Leonov, V., Rozanova, O., Semenina, E., Tsurikov, S., Uvarov, A., Zuev, A. & Tiunov, A. (2023) A meta-analysis suggests climate change shifts structure of regional communities of soil invertebrates. *Soil Biology & Biochemistry* **181**.

Green, K. & Slatyer, R. (2019) Arthropod community composition along snowmelt gradients in snowbeds in the Snowy mountains of south-eastern Australia. *Austral Ecology* **45(2)**. 144-157.

Griffiths, H., Ashton, L., Parr, C.L. & Eggleton, P. (2021) The impact of invertebrate decomposers on plants and soil. *Journal of Ecology* **231(6)**. 2142-2149.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. & O'connor, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**. 105-108.

Johnson, S.N., Staley, J.T., Mcleod, F.L. & Hartley, S.E. (2011) Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions. *Journal of Ecology* **99**. 57-65.

Kardol, P., Reynolds, W.N., Norby, R.J. & Classen, A.T. (2011) Climate change effects on soil microarthropod abundance and community structure. *Applied Soil Ecology* **47**. 37-44.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. & Rossi, J.P. (2006) Soil invertebrates and ecosystem services. *European Journal of Soil Biology* **42**. S3-S15.

Lindberg, N. & Bengtsson, J. (2005) Population responses of oribatid mites and collembolans after drought. *Applied Soil Ecology* **28**. 163-174.

Lindberg, N., Bengtsson, J.B. & Persson, T. (2002) Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *Journal of Applied Ecology* **39**. 924-936.

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L. & Gomis, M. (2021) Climate Change 2021: The physical science basis. *Intergovernmental Panel on Climate Change*.

Nash, M.A. (2013) Alien invertebrates are invading the Australian Alps. *The Victorian Naturalist* **130**. 127-136.

Nash, M.A., Griffin, P.C. & Hoffmann, A.A. (2013) Inconsistent responses of alpine arthropod communities to experimental warming and thermal gradients. *Climate Research* **55(3)**. 227-237.

National Parks Association NSW (2016) A Plan to Protect Kosciuszko's Water Catchments.

Peguero, G., Sol, D., Arnedo, M., Petersen, H., Salmon, S., Ponge, J.F., Maspons, J., Emmet, B., Beier, C., Schmidt, I.K., Tietema, A., De Angelis, P., Kovács-Láng, E., Kröel-Dulay, G., Estiarte, M., Bartrons, M., Holmstrup, M., Janssens, I.A. & Peñuelas, J. (2019) Fast attrition of springtail communities by experimental drought and richness-decomposition relationships across Europe. *Global Change Biology* **25**. 2727-2738.

Robinson, S.I., McLaughlin, O.B., Marteinsdottir, B. & O'Gorman, E.J. (2018) Soil temperature effects on the structure and diversity of plant and invertebrate communities in a natural warming experiment. *Journal of Animal Ecology* **87(3)**. 634-646.

Scheffer, M. & Carpenter, S.R. (2003) Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution* **18**. 648-656.

Seeber, J., Rief, A., Richter, A., Traugott, M. & Bahn, M. (2012) Drought-induced reduction in uptake of recently photosynthesised carbon by springtails and mites in alpine grassland. *Soil Biology & Biochemistry* **55**. 37-39.

Semeraro, S., Kergunteuil, A., Sanchez-Moreno, S., Puissant, J., Goodall, T., Griffiths, R. & Rasmann, S. (2022) Relative contribution of high and low elevation soil microbes and nematodes to ecosystem functioning. *Functional Ecology* **36(4)**. 974-986.

Smith, L. & Williams, J. (2022) Plant and herbivorous insect communities respond in complex ways to rainfall manipulation in an oak savanna grassland. *Journal of Ecology* **111(3)**. 655-665.

Steinwandter, M., Rief, A., Scheu, S., Traugott, M. & Seeber, J. (2018) Structural and functional characteristics of high alpine soil macro-invertebrate communities. *European Journal of Soil Biology* **86**, 72-80.

Torode, M.D., Barnett, K.L., Facey, S.L., Nielson, U.N., Power, S.A. & Johnson, S.N. (2016) Altered precipitation impacts on above- and below-ground grassland invertebrates: Summer drought leads to outbreaks in spring. *Frontiers in Plant Science* **7**. 1468.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van Der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science* **304**. 1629-1633.

Worboys, G.L., Good, R.B. & Spate, A. (2011) Caring for our Australian alps catchments. *Australian Alps Liaison Committee, Department of Climate Change and Energy Efficiency*, Canberra.

Wyborn, C. (2009) Managing change or changing management: climate change and human use in Kosciuszko National Park. *Australasian Journal of Environmental Management* **16**.

Yin, R., Qin, W., Wang, X., Zhao, H., Zhang, Z. & Zhu, B. (2023) Warmer temperature promotes the contribution of invertebrate fauna to litter components release in an alpine meadow on Qinghai-Tibetan Plateau. *CATENA* **231**.

Yuan, X., Wang, Y., Ji, P., Wu, P., Sheffield, J. & Otkins, J.A. (2023) A global transition to flash droughts under climate change. *Science* **380**. 187-191.