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The Resilience of Polar Collembola (Springtails) in a Changing Climate

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ABSTRACT

Assessing the resilience of polar biota to climate change is essential for predicting the effects of changing environmental conditions for ecosystems. Collembola are abundant in terrestrial polar ecosystems and are integral to food-webs and soil nutrient cycling. Using available literature, we consider resistance (genetic diversity; behavioural avoidance and physiological tolerances; biotic interactions) and recovery potential for polar Collembola. Polar Collembola have high levels of genetic diversity, considerable capacity for behavioural avoidance, wide thermal tolerance ranges, physiological plasticity, generalist-opportunistic feeding habits and broad ecological niches. The biggest threats to the ongoing resistance of polar Collembola are increasing levels of dispersal (gene flow), increased mean and extreme temperatures, drought, changing biotic interactions, and the arrival and spread of invasive species. If resistance capacities are insufficient, numerous studies have highlighted that while some species can recover from disturbances quickly, complete community-level recovery is exceedingly slow. Species dwelling deeper in the soil profile may be less able to resist climate change and may not recover in ecologically realistic timescales given the current rate of climate change. Ultimately, diverse communities are more likely to have species or populations that are able to resist or recover from disturbances. While much of the Arctic has comparatively high levels of diversity and phenotypic plasticity; areas of Antarctica have extremely low levels of diversity and are potentially much more vulnerable to climate change.

1. Introduction

Polar regions are experiencing rapid and extreme climatic changes (Hogg and Wall, 2011; Convey and Peck, 2019; Siegert et al., 2019). These changes modify the abiotic environment and terrestrial habitats are already experiencing rising and increasingly variable temperatures (Convey et al., 2018; Koltz et al., 2018a; Clem et al., 2020). Concurrently, patterns of precipitation are changing, resulting in decreased winter snowpack with decreased insulation of soils, increased summer snow melt, and extended biologically active periods (Callaghan et al., 2011; Schmidt et al., 2019). Thawing permafrost and melting glaciers further modify summer water availability (Nielsen and Wall, 2013; Everatt et al., 2015). Glacial retreat will expose new habitat, with ice-free areas in Antarctica predicted to increase by 25 % above current levels by 2100 (Lee et al., 2017). Many of these changes, such as increased maximum temperatures, can cause physiological stress for polar inhabitants, as they exceed the parameters under which the biota has evolved, particularly in Antarctica. Conversely, some changes may

ameliorate abiotic stresses, for example by increasing liquid water availability (Convey and Peck, 2019).

Newly-exposed terrestrial habitats resulting from glacial retreat and snow melt will facilitate the colonisation and spread of both native and invasive species (Chown et al., 2012; Duffy and Lee, 2019). Different biogeographic factors constrain the endemic fauna in each polar region (Fig. 1; see also Meredith et al. 2019 for further definition of polar regions). The Antarctic terrestrial fauna has been isolated for over 28 Ma by the Southern Ocean and Circumpolar Current (Sinclair and Stevens, 2006; Pugh and Convey, 2008) with mites and Collembola the only known terrestrial arthropods present on the continent (Wise, 1967; Strandtmann, 1967; Wise, 1971). By contrast, the Arctic has remained largely contiguous with lower latitudes, allowing post-glacial migration and colonisation of arthropods from lower latitudes including Collembola, arachnids (spiders, mites, and pseudoscorpions), and a wide range of insects (Danks, 1990; Hodkinson et al., 2013). In the Antarctic, this limited diversity leads to a simple, short, food web (Adams et al., 2006). In the Arctic, the higher levels of arthropod diversity, abundance,

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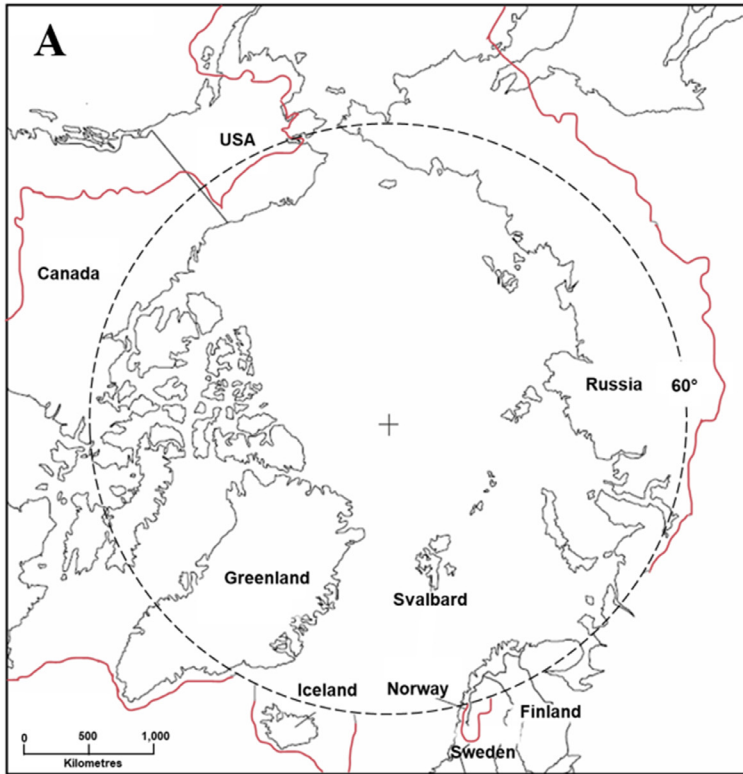
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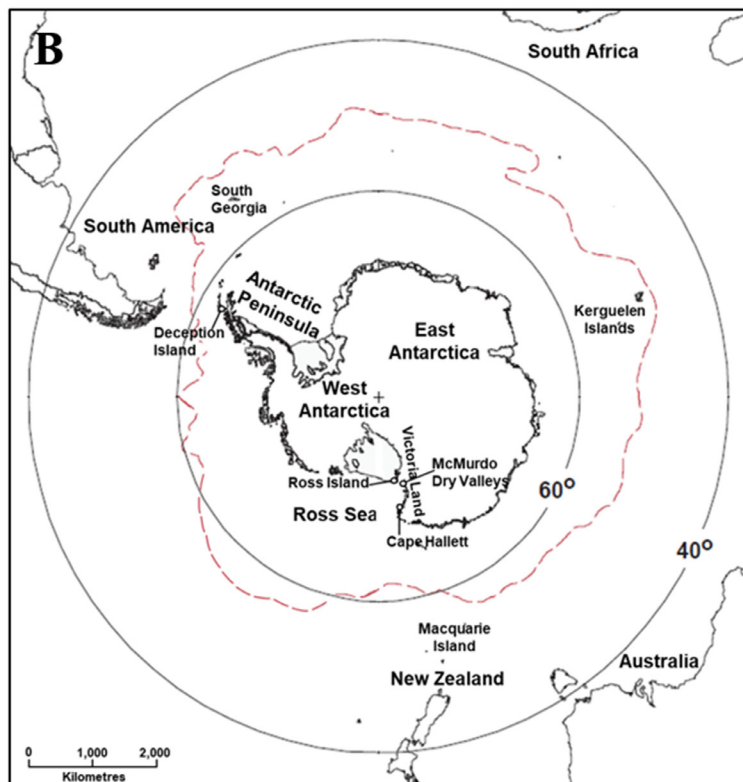
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ARCTIC

- >420 species of Collembola across Arctic, only 14 endemic
- Highly connected with lower latitudes
- Diverse multitrophic communities



ANTARCTICA

- 12 species of Collembola on the Continent, all endemic
- Continent isolated for >28 Ma
- Simple, short food-webs

Fig. 1. Arctic and Antarctic regions showing place names used in the manuscript. Key differences between the polar regions are highlighted in the boxes to the right of the maps: A) Map showing Arctic circle at 66°33'N (black-dashed circle) and the boundary for the Conservation of Arctic Flora and Fauna (red solid line); and B) Key regions of the Antarctic continent and Maritime Antarctic Islands. The approximate location of the Antarctic Polar Front is indicated by a red dashed line. Both poles are indicated by a + symbol. (Base maps sourced from https://d-maps.com/carte.php?num_car=3197&lang=en; and https://data.aad.gov.au/aadc/mapcat/display_map.cfm?map_id=13137).

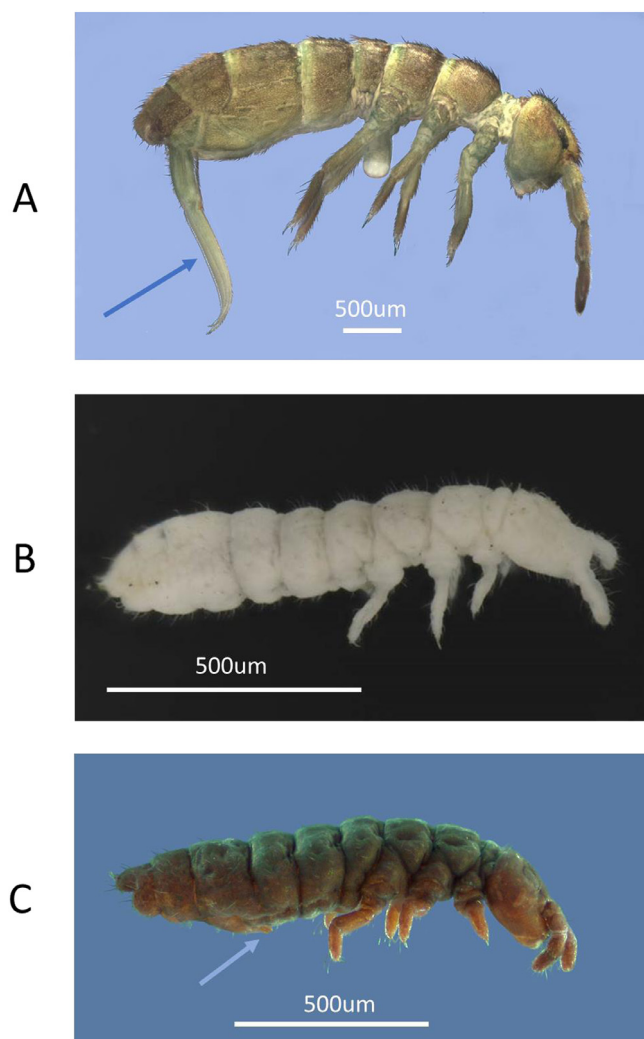


Fig. 2. Examples of: A) an epiedaphic (surface-dwelling) Collembola (*Isotomurus* sp. from the Canadian Arctic) showing elongated appendages including legs, antennae, furcula (indicated by blue arrow), and 'ventral tube' (collophore, visible between the second and third pairs of legs); B) an eudaphic taxon (*Tullbergia mediantarctica*) from the southern Transantarctic Mountains, showing lack of pigmentation or eye spots, short appendages and absence of a furcula; and C) an Antarctic hemiedaphic (intermediate soil profile) taxon from the Antarctic Dry Valleys (*Gomphiocephalus hodgsoni*), showing reduced appendages and furcula (indicated by blue arrow). Scale bars (500µm) are shown for each taxon. All images copyright University of Waikato.

and productivity support diverse multitrophic communities including migratory invertebrate-feeding birds (Hodkinson and Coulson, 2004; Wirta et al., 2015).

Collembola (springtails; Fig. 2) are among the most abundant and widely-distributed arthropods globally and are central to nutrient cycling in most soils, particularly in species-poor polar ecosystems (Danks, 1990; Krab et al., 2013; Hogg et al., 2014). There are 12 species of Collembola on the Antarctic continent, all of which are endemic (Wise, 1967; Wise, 1971). Higher species richness is found in the sub-Antarctic with 34 species on Macquarie Island alone (Phillips et al., 2017). The Arctic supports at least 420 species of Collembola (only 14 of which are known endemics; Danks, 1990; Hodkinson et al., 2013). Collembola have been considered as indicators of environmental change (Danks, 1992; Rusek 1998; Hopkin, 1997; Ponge et al. 2003), and are recognised bioindicators of overall soil health (Greenslade, 2007; Nakamori et al., 2010). Here, we consider the con-

sequences of climate change for polar Collembola which can also provide insights into the resilience of polar terrestrial ecosystems more generally.

Climate change is primarily a press perturbation (*sensu* Bender et al., 1984) and will result in a suite of potentially interacting stressors (Fig. 3). 'Resilience' is narrowly defined as the product of a species' ability to survive (its resistance) and its ability to recover from perturbation (see Box 1; Holling, 1973), and provides an holistic framework for determining how populations will respond to change (see review by Nimmo et al., 2015). Resilience can be influenced by both intrinsic and extrinsic factors (Nimmo et al., 2015). Intrinsic characteristics that promote resistance typically include physiological and behavioural traits (and their plasticity) at the individual level, whilst dispersal and recolonization abilities as well as population-level reproductive rates influence recovery potential (Nimmo et al., 2015; Hughes et al., 2019). Extrinsic factors such as the presence of vegetation or biotic interactions can moderate organismal responses to change, to produce contrasting responses among populations or species with otherwise similar resistance capacities (Nimmo et al., 2015). Understanding the factors that influence polar species' resistance and recovery capacities will allow for interpretation of potential responses within a resilience framework and could be used to inform management and conservation decisions (Oliver et al., 2015; Convey and Peck, 2019).

Studying (and ultimately predicting) organismal responses to environmental change in polar regions remains confounded by logistic constraints (e.g. seasonally-restricted access to sites), patchy baseline data - especially in the Arctic (Nielsen and Wall, 2013) - and limited research on the influence of extrinsic factors on resistance capacities of individual organisms. Extrinsic factors, such as biotic interactions (Hogg et al., 2006; Koltz, et al., 2018b; Caruso et al., 2019), natural variability in environmental conditions, and interacting stressors (Kaunisto et al., 2016) can all exacerbate, or ameliorate stress. However, few studies have explicitly compared the resistance capacities of Collembola, even for genetically isolated populations of broadly-distributed species (see Sengupta et al., 2016; 2017, for two notable exceptions).

Box 1. Definitions of key terms in resilience (after Ingrisch and Bahn, 2018).

Resistance: the capacity to limit the impact of a disturbance and maintain survival.

Recovery: the capacity to return to a pre-disturbance state or an alternative stable state.

Resilience: the capacity to resist disturbances and recover accordingly.

The genome encodes the physiological and behavioural responses of an individual and provides the raw material for evolution. A genetically-diverse population is therefore more likely to include individuals with genotypes that can respond to novel conditions, improving resistance (Somero, 2010). Overall, the capacity to evolve in natural systems within the timescales of climate changes depends on genetic variation within and among populations and the ability to buffer environmental changes through physiological and behavioural responses (Somero, 2010; Sunday et al., 2014; Marshall et al., 2020). Physiological and behavioural plasticity operate in concert and allow organisms to endure environmental extremes. Although polar marine organisms appear to lack such plasticity (Buckley and Somero, 2008), terrestrial organisms are usually physiologically plastic, and can change their environmental tolerances over scales of hours and days to seasons (Teets and Denlinger, 2013; Sinclair et al., 2015). Furthermore,

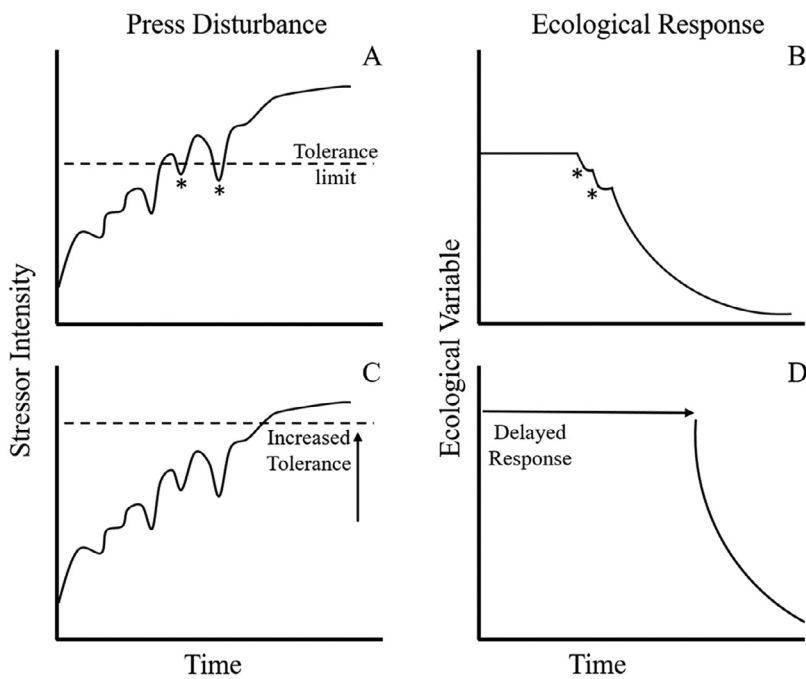


Fig. 3. Conceptual diagram showing a hypothetical and fluctuating press disturbance (A) and corresponding ecological response (B) resulting from climate change. Once maximal tolerance limits (maximum resistance capacity) are exceeded, steep declines in associated ecological responses such as fecundity or abundance are expected (B). Increased tolerance levels increases initial resistance (C), which may delay ecological responses (D). The fluctuating nature of almost all climates allow opportunities for recovery (*) which can influence resistance capacities.

mobile animals can modify their exposure to stress, or even avoid it altogether. Life forms of Collembola are often classified depending on where in the soil profile they reside, which impacts their exposure to stressors. Epiedaphic Collembola (Fig. 2A) are surface-dwelling; whereas euedaphic species (Fig. 2B) live deeper in the soil profile; and hemiedaphic species (Fig. 2C) are intermediate between these extremes (Christiansen, 1964; Hopkin 1997). However, beyond determining fine-scale distribution (e.g. Hertzberg et al., 1994; Hayward et al., 2004; Sinclair, et al., 2006a; Caruso et al. 2010), behavioural plasticity of polar arthropods, including the ability to avoid stress, has received less attention than other ecological characteristics (e.g. Krab et al., 2013; Sengupta et al., 2017; Koltz et al., 2018b).

Any recovery of polar biota following perturbation will depend on fecundity, life history and the likelihood of available habitat being recolonised (i.e. dispersal characteristics) (Hodkinson et al., 2004; Hågvær and Pedersen, 2015; Oliver et al., 2015). Recovery potential intersects with resistance to shape overall resilience (Fig. 3). For example, if populations have low resistance but high recovery potential then the risk of extinction is minimised (and overall resilience is increased). However, if populations have high resistance but low recovery potential, they may persist until a stress event occurs at the margins of tolerance, from which they cannot recover (decreased overall resilience) (Nimmo et al., 2015). Further, if genes underlying the ability to resist and recover from environmental changes are negatively correlated with each other, one strategy (resistance or recovery) may dominate at the expense of the other. It is therefore important to consider that if population size recovers to pre-disturbance levels but genetic variation is lost (i.e. a genetic bottleneck), the resistance and resilience of the population to continued and future environmental changes will likely decline (Oliver et al., 2015). One exception to this would be if a bottleneck event resulted in directional selection that increased resistance (e.g. selection for warm-adapted individuals in a warming climate, provided they can still survive cold winters).

We examine the potential resilience of polar Collembola to a changing climate and focus on three aspects that we think may drive resistance: 1) genetic diversity; 2) physiological tolerances and behavioural plasticity; and 3) biotic and ecological responses. We then discuss the recovery potential of polar Collembola. Together, this allows us to iden-

tify key traits underlying resistance and recovery potential as well as recommend profitable research avenues integrating this information to more fully understand resilience.

2. Genetic diversity and adaptive capacity

Genetic diversity provides the raw material for evolution and thus determines the probability that a population will persist by having genetic variants (individuals) capable of surviving an environmental perturbation (Hoffmann et al., 2003; Somero, 2010). Mutation is the ultimate source of that genetic variation (Sung et al., 2012). However, the rate of beneficial mutations is almost certainly too slow relative to the timescales of rapid climate change (Thomas et al., 2010; Sung et al., 2012; Lynch et al., 2016). Polar Collembola evolve and mutate more slowly than their temperate counterparts because they take longer to reach maturity and have lower reproductive rates (Convey, 1996; Thomas et al., 2010). Selection, meiotic recombination, and dispersal (gene flow) are therefore the main factors likely to maintain genetic variation of polar Collembola during rapid decadal climate changes. Selective responses to severe environmental changes can be rapid (<10 generations) in the laboratory (experiments using *Drosophila*: Gibbs et al., 1997; Gefen et al., 2006), and meiotic recombination facilitates the potential selection of individuals most suited to the local environment (Becks and Agrawal, 2010). Most Antarctic Collembola reproduce sexually (Janetschek, 1967; Wise, 1967; Peterson, 1971). However, soil-dwelling species are often asexual, which means that more taxa may be asexual in the Arctic where there is greater soil development and higher species diversity (Chernova et al., 2010; Bokhorst et al., 2018). If individuals can survive acute climate change effects, rising temperatures could shorten generation times leading to increased reproductive rates and accelerating local adaptation by increased mutation and potential selection (Birkemoe and Leinaas, 1999; Thomas et al., 2010; Sengupta et al., 2017). Assessing genetic diversity within and among populations can help to determine which populations have greater genetic variation and hence individuals with phenotypes potentially better able to respond to changing environmental conditions.

2.1. Current knowledge of genetic diversity in polar Collembola

Historical geological and glaciation events have structured the genetic diversity of polar Collembola (Ávila-Jiménez and Coulson, 2011; Collins et al., 2020). The long-term isolation of the Antarctic continent has elicited high levels of endemism (Pugh and Convey, 2008; McGaughran et al., 2010) in contrast to the Arctic which has a higher degree of physical connectivity with lower latitudes, and lower levels of endemism (Ávila-Jiménez and Coulson, 2011). Within Antarctica, large-scale geographic barriers such as glaciers and mountain ranges have prevented dispersal, resulting in highly-structured and genetically-differentiated populations (Nolan et al. 2006; McGaughran et al., 2008; Collins et al., 2019). Collembola are susceptible to desiccation and unlikely to routinely disperse aerially over long distances, although sporadic dispersal events can occur (Coulson et al. 2002a; Sinclair and Stevens, 2006; Hawes et al., 2007; Vega et al., 2020). Over long distances, Collembola likely disperse by rafting on the surface of inland and coastal waters (Hawes, 2011; McGaughran et al., 2011; Collins et al., 2020). Consequently, estimates of divergence times between populations of Antarctic species often correlate with periods of ice sheet collapse and open seaways (McGaughran et al., 2010; Bennett et al., 2016; Collins et al., 2020). The Arctic fauna has also been influenced by historical glacial cycles with ocean currents facilitating dispersal and recolonization (Ávila-Jiménez and Coulson, 2011).

Genetic variation is generally high in polar Collembola (Porco et al., 2014; Collins et al., 2019), and might confer greater resistance relative to less diverse populations (Hawes et al., 2010). Knowledge of genetic diversity for polar Collembola has been largely informed by variation in sequence fragments of the mitochondrial cytochrome c oxidase subunit I (COI) gene (Costa et al., 2013; Pentinsaari et al., 2020). COI data have been used to reconstruct phylogeographic patterns and infer historic levels of population connectivity (Stevens et al., 2007; McGaughran et al., 2011). COI data are available for all known continental Antarctic species including ten Ross Sea Region species (Beet et al., 2016; Collins et al., 2019; Collins et al., 2020), two from the Antarctic Peninsula (one of which has been recently re-described from *Friesea grisea* to *F. antarctica*) (McGaughran et al., 2010; Torricelli et al., 2010; Carapelli et al., 2020) and one from East Antarctica (Stevens and D'Haese, 2014). COI data indicate that genetic variation within some species may be high (greater than 2 % intraspecific pairwise divergence) with sequences differing by 1.7-14.7 % between populations of seven Antarctic species (Collins et al., 2019). By way of comparison COI sequencing of 33 species found across a 330 km range in temperate Estonia revealed that 57 % of species had intraspecific divergences of <2 %, and 81 % of species had divergences <5 % (Anslan and Tedersoo, 2015). Despite the prevalence of Holarctic Collembola, there are high levels of localised COI diversification and potential cryptic speciation in the Arctic (Hogg and Hebert, 2004; Porco et al., 2014; Pentinsaari et al., 2020). Genetic variation within the mitochondrial COI gene can also reflect genetic variation across the wider genome (Stevens and Hogg, 2003; Monsanto et al., 2019). For example, genome-wide single nucleotide polymorphisms (SNPs), were used to corroborate the three genetically distinct regional populations of *Cryptopygus antarcticus antarcticus* previously identified by COI sequencing (McGaughran et al., 2010; 2019). Thus, spatially explicit surveys using COI sequences likely provide an informative baseline for detecting climate change-induced alterations in diversity and distribution patterns.

2.2. Potential impacts of climate change on genetic diversity

Climate change will likely influence extant genetic diversity in four complex and interacting ways. First, changes in mean and maximum temperatures will likely increase mortality, directly leading to genetic bottlenecks (Convey et al., 2018). Second, increased population connectivity could simultaneously threaten the unique diversity borne of

isolation while increasing recovery and recolonisation following bottlenecks in the Antarctic and Arctic. Genetic bottlenecks can have persistent effects on population dynamics depending on the sex-ratios of surviving individuals with small populations more at risk of genetic drift and decreased fitness of individuals (the Allee effect, e.g. Courchamp et al. 2008), increasing the likelihood of localised extinctions (Oliver et al., 2015). Third, warmer temperatures may facilitate the spread of invasive species into areas of the sub-Antarctic, Antarctic Peninsula and High Arctic. These invasive species may outcompete local populations and decrease overall genetic diversity (Chown et al., 2012; Phillips et al., 2017; Hughes et al., 2020). Finally, altered connectivity arising from increased habitat availability (Lee et al., 2017) and enhanced dispersal opportunities (via meltwater and open seaways) (Collins et al., 2020) could directly affect existing genetic diversity (via altered rates of gene flow) and mediate the impacts of other processes including genetic bottlenecks.

Climate change is likely to decrease extant genetic diversity through more frequent genetic bottlenecks, increased competition, and homogenisation of divergent populations via increased connectivity (Collins and Hogg, 2016; Baird et al., 2019; 2020). Warmer conditions will increase the hydrological connectivity among habitats, enhancing dispersal opportunities (e.g. rafting) between sites in addition to human-mediated transfer of native and non-native species (Baird et al., 2020). Many genetically divergent Antarctic populations have been isolated for thousands to millions of years and are likely adapted to their local, and microscale, environment (Convey and Peck, 2019; Siegert et al., 2019; Collins et al., 2020). Increased gene flow from larger source populations could disrupt co-adapted gene complexes, purging unique genetic diversity, and decreasing the ability of populations to respond to future perturbations (Case and Taper, 2000; Convey and Peck, 2019; Siegert et al., 2019; Gutt et al., 2021). By contrast, increased connectivity between less-divergent populations could introduce new and favourable alleles to enhance individual fitness levels (Costa et al., 2013; Nielsen and Wall, 2013). Increased population connectivity could also improve recovery from bottlenecks by increasing population density and genetic diversity (Hertzberg et al., 1994; Jangjoo et al., 2016). Although data on polar Collembola are lacking, experiments on other invertebrates are beginning to reveal that low levels of gene flow can increase a population's adaptive potential while the hybridization of long-term isolated populations has only a limited or negative effect on adaptability (Swindell and Bouzat, 2006; Hudson et al., 2021; Hoffmann et al., 2021). Overall, an increase in connectivity and gene flow is only likely to negatively impact the adaptability of unique isolated Antarctic populations (Gutt et al., 2021).

Arctic Collembola are more connected at the landscape scale than their Antarctic counterparts. Consequently, many Arctic taxa have Holarctic distributions (Ávila-Jiménez and Coulson, 2011; Hodkinson et al., 2013). However, the effects of warming on heavily-glaciated Arctic regions such as Greenland are likely to be similar to those experienced in Antarctica. Much of the Arctic is already unglaciated and hydrologically connected, particularly in tundra areas where water has filled thermokarst (irregular pocked surface landscapes arising from frost heaving and melting permafrost) (Abnizova and Young, 2010). This increased connectivity has also disrupted soil structure and soil community stability stemming from permafrost degradation (Fraser et al., 2018; Farquharson et al., 2019). Available genetic data indicate low levels of population differentiation (high connectivity) for many species of Arctic Collembola (Hogg and Hebert, 2004; Porco et al., 2014). For example, low levels of population differentiation were observed for 38 of the 45 morphologically identified species in the Canadian sub-Arctic (Churchill, Manitoba) (Porco et al., 2014), and 17 of the 19 species found in the Canadian mid to high Arctic (Hogg and Hebert, 2004). This high level of population connectivity could mitigate the impacts of permafrost degradation and thermokarst expansion by increasing recolonisation rates (Nielsen and Wall, 2013; Fraser et al., 2018; Farquharson et al., 2019).

Intensive sampling and COI sequencing of Antarctic Collembola have revealed inherent levels of genetic variation, population connectivity and evolution. By contrast, although Arctic species and habitats are diverse, few Arctic Collembola have been sampled and sequenced. Improving baseline measures of Arctic genetic diversity and distribution will be critical for detecting future climate change impacts. Expanding knowledge of the genetic basis of key traits underlying the distributions of polar Collembola will help determine their ability to evolve and resist disturbance. In particular, mitogenome sequences currently exist for several Antarctic species (see Carapelli et al. 2019; Monsanto et al. 2019), and genome-wide studies are now tractable and affordable (Hohenlohe et al., 2021). These could be used to estimate the rates of evolution (and therefore adaptive potential) in polar populations (Faddeeva-Vakhrusheva et al., 2016, 2017; Wu et al., 2017) as well as identify the resistance potential of Collembola, for example by allowing sequence-level analysis of stress response genes such as heat shock proteins (Michaud et al. 2008; Cucini et al. 2021). Ultimately, connectivity, selection, and distribution need to be monitored temporally to understand the changing genetic diversity and resilience of polar Collembola.

3. Physiological tolerances and behavioural plasticity enable survival in extreme and highly variable environments

Polar Collembola are exposed to extreme environmental conditions, including winter temperatures below $-30\text{ }^{\circ}\text{C}$ (Coulson et al., 1995; Velasco-Castrillón et al., 2014), daily temperature fluctuations of $30\text{ }^{\circ}\text{C}$ or more (Worland and Convey, 2001; Sinclair et al., 2003), and surprisingly high microclimate temperatures in summer (Sinclair et al., 2006b; Convey et al., 2015; Convey et al., 2018). Arid polar desert conditions and high solar radiation further expose Collembola to intense ultraviolet light (Hawes et al., 2012; Beresford et al., 2013) and high desiccation stress (Sinclair et al., 2006b; Elnitsky et al., 2008; Holmstrup, 2018b). Collembola are soft-bodied and respire through a permeable exterior cuticle which makes them susceptible to desiccation, although susceptibility varies within and among species (Hertzberg and Leinaas, 1998; Worland and Block, 2003; Aupic-Samain et al., 2021). Determining how resistant polar Collembola will be to climate changes requires an integration of their exposure to extremes, the proximity of their physiological limits to current environmental extremes, and consideration of the effects of interacting environmental changes (Somero, 2010).

3.1. Behaviour and microhabitat occupation modifies exposure to environmental stressors

Environmental extremes only affect animals that are exposed to them. Thus, behavioural avoidance of environmental stressors is a key response to climate changes (Sunday et al., 2014; Kovacevic 2019). For example, Collembola can avoid exposure to a range of soil pollutants (Boiteau et al., 2006; Boiteau, Lynch, and MacKinley 2011; Zortéa et al., 2015), and the fine-scale distribution of Collembola in Antarctica is associated with soil moisture content (Hayward et al., 2004; Sinclair et al., 2006a). Unfortunately, not all environmental stressors can be easily avoided at the scale of an individual collembolan and the role of behaviour in mitigating natural environmental stressors is still poorly understood (Boiteau and MacKinley, 2013; Krab et al., 2013).

Collembola can generally evade stress by microhabitat selection, for example migrating deeper into the soil, or moving among surface microhabitats (Hertzberg et al., 1994; Sinclair et al., 2006a; Krab et al., 2013). Thus, effective behavioural avoidance requires an ability to move, and the availability of suitable habitat. Mobile surface-dwelling species (which may have longer limbs and furculae) can walk faster and “spring” away from disturbances, but may be unable to burrow effectively in the soil pack (Hopkin, 1997; Krab et al., 2013). Deeper-dwelling species are less mobile although they are inherently better buffered from environmental extremes and thus, initially, more resistant

to climate changes (Hopkin, 1997; Detsis, 2000; Ponge, 2000). Collembola that reside deeper in the soil profile tend to be less heat tolerant (Kovacevic, 2019), and may be killed when stressors penetrate deeper into the soil profile (Thakur et al., 2017).

In summer, migrating into the soil profile or under large rocks buffers temperature extremes (Huey et al., 1989; Huey et al., 2021), while simply moving into the shade is enough to mitigate UV, heat and desiccation stress (Hawes, Marshall, and Wharton 2012; Dahl et al., 2017; Asmus et al., 2018). Collembola clearly take advantage of microhabitat variation: in a mesocosm experiment involving sub-Antarctic Collembola, abundance in deeper soil layers increased by 75 % during a heat wave event, and this response was exacerbated by drought (Kovacevic, 2019). Experimental warming in a sub-Arctic peatland reduced collembolan densities at the soil surface, although downward migration of larger surface-dwelling species (e.g. see Fig. 2A) was not detected, perhaps due to difficulties of moving through the smaller soil pore sizes (and often waterlogging) found with increasing depth in many of these habitats (Krab et al., 2013).

Behavioural avoidance is easier for Collembola in the sub-Antarctic and Arctic where soils are more developed and vegetative communities are more abundant and diverse, providing greater variation in microhabitats (Coulson et al., 2003; Wilhelm et al., 2011; Boike et al., 2018). For example, temperatures exceeded $0\text{ }^{\circ}\text{C}$ only 74 times across the summer at a polar desert site in Svalbard, whereas nearby vegetated sites had more than 120 days above $0\text{ }^{\circ}\text{C}$ (Convey et al., 2018). Of course, more heavily vegetated sites also carry additional risks of competition and predation, demonstrating a trade-off that possibly drives occupation of the more extreme sites (Coulson et al., 2003; Convey et al., 2018). On the Antarctic continent and in High-Arctic polar deserts, vegetation is scarce and soil development is limited, with shallow top-soils (often only a few centimetres in depth) underlain by permafrost, which limits access to the soil column (Bockheim et al., 2007; Seppelt et al., 2010).

Capacity for behavioural avoidance is truncated in winter. At night (at sub-polar latitudes in the summer) and during the polar winter, there is no insolation to heat some microhabitats, and soil with shallow permafrost permits no downward escape from sub-freezing temperatures (Coulson et al., 1995; Sinclair and Sjørnsen 2001a). Over winter, snow cover provides considerable buffering from extreme air temperatures and the worst desiccation stress (Gooseff et al., 2003; Pauli et al., 2013). Snow also accumulates differentially by aspect or in patterned ground (e.g. Gooseff et al., 2003; Scott et al., 2008), which means that some microhabitat variation is still available. It is often assumed that polar Collembola are inactive and immobile over winter, where critical thermal minima can be below $-10\text{ }^{\circ}\text{C}$ (e.g. Sinclair et al., 2006b). However, Collembola are active under the snow in the (very cold) Canadian prairies (Aitchison, 1979), which suggests that there may be winter activity (and therefore capacity for microhabitat selection) in at least some polar environments.

Climate changes are introducing more extreme and variable fine-scale environmental stressors, and it is uncertain whether collembolan behaviour will be effective in avoiding these stressors or novel combinations thereof (Høye et al., 2021). Furthermore, there are complications in evaluating the relationship between microhabitat selection and physiological tolerances and plasticity (see Hawes et al. 2008). Surface-dwelling species are likely to have an advantage in behaviourally avoiding adverse environmental conditions associated with climate change due to an increase in vegetation/ microhabitats, improved mobility, and capacity to move between optimal microhabitats (see Kutcherov et al., 2020 for an example of habitat change rapidly modifying collembolan responses to temperature in Iceland). By comparison, deeper-dwelling species may be less exposed, initially, to changing temperature. However, they may also be exposed to large changes in hydrology and permafrost. Eventually, the full soil profile will change, challenging even the deeper-dwelling soil-taxa. Unfortunately, very little is known about behavioural responses to environmental conditions in Collembola, and almost nothing about the responses of polar soil-dwellers; filling these

gaps is essential for predicting the exposure to (and avoidance of) changing environmental conditions, and building a framework for interpreting resilience.

3.2. Tolerance of environmental extremes requires plasticity

Physiological tolerances determine survival when environmental extremes cannot be avoided. These tolerances are often divided into basal tolerances (the steady-state tolerance) and plasticity (the extension of those tolerances in response to changing environmental conditions; Somero, 2010). However, in nature, even basal tolerances change throughout the year (Cannon and Block, 1988) and extreme temperatures have been a significant evolutionary pressure on the evolution of Collembola (Zizzari and Ellers, 2014; Carapelli et al., 2019). As thermal variability and the frequency of extreme temperatures increases with climate change (Meredith et al., 2019), we expect that extreme thermal tolerances will remain key to resistance and resilience of polar spring-tails.

All Antarctic (and most Arctic) Collembola appear to be freeze-avoidant, keeping their body fluids liquid at sub-freezing temperatures via ice-binding (i.e. antifreeze) proteins (Sinclair and Sjørnsen 2001; Graham et al. 2020) and by accumulating small molecules such as glycerol (Cannon and Block, 1988; Sømme, 1999). Some Arctic species use cryoprotective dehydration, relying on external ice to remove body water, thereby concentrating the remaining body fluids and preventing them from freezing (Holmstrup and Sømme, 1998; Worland et al., 1998; Sørensen and Holmstrup, 2011; Holmstrup, 2018a). Cold tolerance strategies are not well studied except for a few species, so alternative strategies may yet be discovered. For example, freeze-tolerant mites – also previously presumed to be exclusively freeze-avoidant – have been reported from temperate Canada (Anthony and Sinclair, 2019). The lethal temperatures of cold-hardy, freeze-avoidant Collembola coincide with the supercooling point (SCP, the temperature at which they freeze). The SCPs of Antarctic Collembola can be very low – for example, a minimum of -38°C in early spring for *Gomphiocephalus hodgsoni* on Ross Island (Sinclair and Sjørnsen, 2001a). Thus, native Collembola appear well-equipped to survive the polar winter (Convey et al. 2015). Importantly, warm winters do not necessarily reduce cold-related mortality. Mid-winter snow melt exposes Collembola to extreme cold temperatures, which means that climatically warmer winters can increase cold stress (Coulson et al., 2000; Bokhorst et al., 2012; Williams et al., 2015).

In summer, polar collembolan SCPs are often bimodal, with a high group (putatively those with food in their guts; Sømme, 1986) whose SCPs can be as high as -2°C , and a low group (those moulting or with empty guts) with SCPs 10°C or more lower (e.g. Cannon and Block, 1988; Worland et al., 2006). Individual Collembola appear to be able to shift between these groups in a matter of hours (Worland and Convey, 2001; Sinclair et al., 2003; Worland, 2005). This plasticity is critical to allow feeding and also to ensure survival of low summer temperatures and freeze-thaw cycles (Coulson et al., 1995; Sinclair et al., 2003). The frequency of such freeze-thaw may increase with climate change (Nielsen and Wall, 2013). Collembola (particularly small deeper-dwelling individuals) are more sensitive to freeze-thaw cycles than mites which could lead to community level changes (Coulson et al., 2000; Bokhorst et al., 2012).

In summer, bare ground and (in some places) dark rocks in polar regions can capture a surprising amount of heat from the sun. Heat tolerances have been less-commonly measured, but reported high-temperature thresholds for polar Collembola range from 34 to 40°C (Hodkinson et al., 1996; Sinclair et al., 2006b; Everatt et al., 2013; Everatt et al. 2014). This suggests that many Collembola may have thermal tolerances similar to their non-polar counterparts: upper functional thermal limits of Australian and South African Collembola range from 30 – 45°C (Janion-Scheepers et al., 2018; Liu et al., 2020). Regardless, microclimate temperatures in some microhabitats at Cape Hallett, Antarc-

tica, regularly exceeded the critical thermal maximum of two of three Collembola species at the locality, highlighting their potential vulnerability to continued warming (Sinclair et al., 2006b). Further studies have also suggested that there is little plasticity and acclimation capacity in heat tolerances (Slabber et al., 2007; Everatt et al., 2013; Janion-Scheepers et al., 2018; Phillips et al., 2020). High temperature tolerance can decline rapidly in dry conditions or during long exposures (Hertzberg and Leinaas, 1998), suggesting that these acute measures probably underestimate the risk of high temperature exposure. Climate change is expected to yield longer periods of more extreme temperatures in both the Arctic and Antarctic (Meredith et al., 2019), although at the highest latitudes, changes in cloud cover (increasing cloudiness, particularly over areas of sea ice retreat) will likely have the greatest impact on surface temperatures (Morrison et al., 2018; Meredith et al., 2019). Even sub-lethal warming could increase the time spent above optimum temperatures for growth and corresponding reductions in fecundity (Sweeney and Vannote, 1978).

Collembola can rapidly increase their heat tolerance through the heat shock response, largely mediated by heat shock proteins (Escribano-Álvarez et al., 2022; Sørensen et al., 2003). For example, heat survival of *Orchesella cincta* increases by $>60\%$ after only an hour at 35°C (Bahndorff et al., 2009). This improved thermotolerance can persist for two days, thereby improving resistance to future thermal extremes and stochasticity (Bahndorff et al., 2009). However, the heat shock response is energetically expensive and can reduce subsequent activity, foraging, reproduction and development (Zizzari and Ellers, 2011; Klepsatel et al., 2016). Thus, induction of heat shock at sub-lethal temperatures, and repeated and fluctuating temperatures (Marshall and Sinclair, 2012; Colinet et al., 2015; Dillon et al., 2016), could have long term consequences on individual performance and population dynamics. Understanding the performance implications of real-world temperature regimes remains a challenge for any ectotherm (Dillon et al., 2016), and is especially relevant for contextualising existing thermal tolerance data in a resilience framework.

3.3. Water balance is critical for polar Collembola

Desiccation susceptibility determines microhabitat selection and local distribution in both the Antarctic (Hayward et al., 2004; Sinclair et al., 2006a; 2006b) and Arctic (Hertzberg and Leinaas, 1998). Surface-dwelling Collembola are generally more resistant to desiccation and exhibit a lower water loss rate (Kærsgaard et al. 2004; Lindberg and Bengtsson, 2005; Makkonen et al., 2011). By comparison, soil-dwelling species usually have more permeable integuments and are less resistant to desiccating conditions (Aupic-Samain et al., 2021). Under experimental conditions, exposing Collembola to dry air, smaller individuals tended to be more sensitive to desiccation stress due to their larger surface area to volume ratios (Hertzberg and Leinaas, 1998). However, dry air is not necessarily representative of drought conditions within soils. For example, Hilligsø and Holmstrup (2003), found that drought conditions within a simulated soil environment did not have a disproportionate effect on (temperate) *Folsomia candida* juveniles or smaller individuals. Experimentally reducing water availability considerably reduced collembolan density in both the sub-Arctic (Makkonen et al., 2011) and sub-Antarctic (McGeoch et al., 2006; but see, e.g. Aupic-Samain et al., 2021 and Holmstrup et al., 2013 for equivocal responses in temperate regions). Like most other traits, collembolan desiccation tolerance is plastic. For example, pre-exposure of Antarctic *Cryptopygus antarcticus* to mild desiccating conditions improved desiccation survival by 35% (Elnitsky et al., 2008), and the Arctic *Megaphorura arctica* (formerly *Onychiurus arcticus*) is inherently desiccation tolerant (Hodkinson et al., 1994; Worland 1996; Holmstrup and Sømme, 1998). While desiccation survival can be high in natural conditions, collembolan reproduction can be highly sensitive to declines in soil water potential (Wang et al. 2022). Given its clear importance in determining distribution, influencing reproduction, and responses to climate change, the mechanisms un-

derlying variation in water balance and desiccation susceptibility must be a priority for future physiological investigations in polar Collembola.

Modelling the impacts of large-scale climate changes on local-scale soil moisture levels is critical to predicting the resilience of polar Collembola. Precipitation models are complex and highly variable on several spatial scales with predictions involving both increases and decreases in snowfall and precipitation depending on the region and landscape dynamics (see review by Box et al., 2019). In the Arctic, an increase in desiccation stress is likely to arise in areas with permafrost degradation (thaw increases soil drainage and drying) and where increased soil evaporation (from warmer temperatures) is not offset by rates of precipitation (Box et al., 2019). Furthermore, winter warming (Arctic winter temperatures have risen by 3.1 °C since 1971; Box et al., 2019) is contributing to declines in snowpack accumulation which impacts not only summer soil moisture levels but the thermal buffering of overwintering Collembola (Box et al., 2019; Høye et al., 2021). In the Antarctic, soil moisture will predominantly be influenced by winter snow accumulation and increased glacial melt (Convey and Peck, 2019). Snow cover itself varies considerably with microtopography at a scale that directly influences soil moisture and Collembola distribution (Sinclair and Sjørnsen, 2001b; Sinclair et al., 2006a). Thus, it is very challenging to translate global- or regional-scale changes in precipitation to population-level impacts. Polar areas with intermediate warming and sufficient soil moisture are likely to see dramatic increases in Collembola abundance (Convey and Peck, 2019)

3.4. Environmental stressors interact in nature and vary among populations

In nature, environmental stressors interact with one another to either exacerbate or mitigate the stress (Todgham and Stillman, 2013). Understanding these interactions requires extensive multifactorial experiments (e.g. Brennan and Collins, 2015). Although frameworks exist to predict the outcome of interactions among stressors *a priori* based on shared mechanisms in a comparative phylogenetic context (e.g. Kaunisto et al., 2016), they remain to be applied in a polar context. We can, however, identify clear interactions based on our existing knowledge, and at least take them into account when considering Collembola responses to climate change.

For example, desiccation co-occurs and interacts with responses to other stresses. At high temperatures, vapour pressure deficit and therefore water loss rates increase, and cuticular hydrocarbons can melt further exacerbating cuticular water loss (Chown and Nicholson, 2004). Thus, high temperature mortality in terrestrial arthropods is often a product of thermal stress *per se* and water loss (Chown et al., 2011). In Antarctic Collembola, more heat-tolerant species are often also more desiccation resistant (Sinclair et al., 2006b), although the mechanistic links have not been explored. At low temperatures, some of the mechanisms of desiccation stress and cold stress – particularly loss of ion homeostasis – appear to overlap in chill-susceptible insects (Sinclair et al., 2013), and ice in the environment can dehydrate permeable, unfrozen Collembola (Holmstrup et al., 2002). Some soil-dwelling Collembola in moist Arctic habitats exploit this in a strategy termed cryoprotective dehydration (Holmstrup et al., 2002; Sørensen and Holmstrup, 2011). The Antarctic *Cryptopygus antarcticus* shows responses to dehydration consistent with the capacity for cryoprotective dehydration (Elnitsky et al., 2008). Thus, water availability could directly impact collembolan survival and also modify resistance to thermal stressors in ways that are currently poorly understood.

A less well-explored potential interaction among stressors traverses the boundary between the changes to the physical environment wrought by climate change with the all-pervasive pollution output of human activities. Based on work using Collembola as an ecotoxicological model, we know that they are susceptible to pollution (Hopkin, 1997; Mooney et al. 2019) and at least some pollutants modify responses to other environmental stressors in temperate Collembola. For example, some detergents and polycyclic aromatic hydrocarbons reduce desicca-

tion and high temperature tolerance (Sjørnsen et al., 2001; Sørensen and Holmstrup, 2005; Mikkelsen et al., 2019), mercury reduces cold tolerance (Holmstrup et al., 2008), and microplastics perturb the gut microbiota (Ju et al., 2019). Conversely, increased temperatures make Collembola more susceptible to copper toxicity (Callahan et al., 2019). Many of these experiments rely on high concentrations of pollutants that are not environmentally realistic. However, there is significant pollution associated with human activities at the local scale in both the Arctic and Antarctic (Errington et al., 2018; Ferguson et al., 2020; Rudnicka-Kępa and Zaborska, 2021). Pollutants generated elsewhere are also deposited into polar soils, including persistent organic pollutants (e.g. pesticides Ma et al., 2011), heavy metals (Chu et al., 2019), black carbon (Schacht et al., 2019), nitrogen (Stewart et al., 2014) nanoparticles (Kumar et al., 2012), and microplastics (Obbard, 2018; González-Pleiter et al. 2021). In addition to the increased deposition of many of these pollutants, warming can exacerbate their impacts. For example, newly-active organic matter in melting permafrost mobilises methylmercury (Yang et al., 2016; Obrist et al., 2017), while warming coupled with atmospheric nitrogen deposition increases currently limited plant productivity (Stewart et al., 2014). Experiments using lower, more realistic levels of pollutants will be needed to properly evaluate their potential influence. The longer-term implications of these pollutants in determining the resistance or recovery potential of polar Collembola are currently unknown and require urgent attention.

Polar Collembola can display remarkable physiological tolerances to extreme conditions with individuals in some cases tolerating temperatures below -30 °C and above +30 °C. Research-to-date has also highlighted high levels of physiological plasticity and acclimation capacity, particularly in cold tolerance (Sinclair and Sjørnsen 2001a; Sinclair et al. 2003; Worland and Convey 2008; Bahrndorff et al. 2007). The impacts of winter warming is largely unknown owing to the inherent logistical constraints of studying polar Collembola in winter. However, summer abundances of Collembola in Greenland have declined in response to warmer winters, with impacts more pronounced in drier habitats (Koltz et al., 2018a). This reinforces the need to better study the impacts of multiple interacting stressors, particularly in natural communities. Stressors can further prompt transgenerational and multigenerational impacts in Collembola (Hafer et al., 2011; Szabó et al., 2019), although this has not been investigated in polar species. Future physiological studies should explicitly account for size and developmental stages to assess levels of intraspecific variation in thermal tolerances. Disproportionate effects on juveniles are likely to result in high mortality (low resistance), and fewer individuals reaching maturity would also limit recovery (Franken et al., 2018; Widenfalk et al., 2018). A few Arctic studies have begun comparing physiological tolerances of species with widely distributed populations (e.g. Bahrndorff et al., 2007; Sørensen and Holmstrup, 2013; Sengupta et al., 2016; Sengupta et al., 2017). No such study has been conducted in the Antarctic despite the high levels of genetic differentiation documented among populations (Collins et al., 2019). Until recently, the links between physiology and genetics had not been explored for Collembola and available studies include only a few genes and proteins (e.g. heat shock proteins, aquaporins, Faddeeva et al., 2015; Faddeeva-Vakhrusheva et al., 2016; Cucini et al., 2021). A broader investigation of the molecular responses to environmental stressors and interacting stressors would help determine whether polar Collembola have the genetic capacity and physiological adaptability to survive climate changes.

4. Biotic interactions and resistance to climate change

Polar Collembola often live in biologically simple systems with limited trophic structure (Hodkinson and Coulson, 2004; Hogg et al., 2006). In Antarctica, biotic interactions are particularly limited and abiotic conditions are largely thought to regulate populations (Hogg et al., 2006;

Caruso et al., 2019; Lee et al., 2019). By contrast, terrestrial Arctic food-webs are more complex, with higher levels of trophic structure, competition, predation (e.g. by spiders, mites) and a wider range of available trophic niches (Danks, 1990; Post et al., 2009; Koltz et al., 2018b). Climate change is likely to disrupt terrestrial food-webs as biota across trophic levels exhibit differential responses. For example, flowering periods may no longer coincide with peak availability/activity of pollinators (Urbanowicz et al., 2018; Tiusanen et al., 2019). Predicting the potential biotic responses of lower trophic level taxa is therefore critical for understanding ecosystem resilience.

4.1. Collembola mediate complex soil decomposition interactions

Collembola are omnivorous detritivores with diets of bacteria, fungi, and plant and animal material (Hopkin, 1997). Current understanding of polar collembolan diets is largely based on dissection and morphological identification of gut contents (Broady, 1979; Hodkinson et al., 1994; Davidson and Broady, 1996). Such studies indicate considerable flexibility in feeding habits and that the studied species can readily exploit a wide range of available food resources (Broady, 1979; Davidson and Broady, 1996; Bokhorst et al., 2007). In a changing environment, a generalist opportunistic diet should confer a high level of resilience for individual taxa.

Collembola tend to have the greatest influence on soil decomposition when feeding on microbial communities dominated by fungi (Wardle et al., 2004; A'Bear et al., 2014). In Alaska, Koltz et al. (2018c) found that 99.6 % of carbon cycled by invertebrates originated from detrital matter and was primarily cycled by fungal consumers such as Collembola. Collembolan grazing pressures on bacteria and fungi also limit the ability of microbes to compete with plants for available nutrients (Chauvat and Forey, 2021). Accordingly, any changes to Collembola feeding habits are likely to strongly influence soil nutrient cycling (Koltz et al., 2018c), although species-specific, and/or ontogenetic shifts in food preferences are currently unknown. Under warming conditions, Collembola abundances will increase thus increasing community-level detritivory. Higher temperatures can also increase rates of metabolism and potentially rates of compensatory feeding, particularly if food quality declines (Sweeney and Vannote, 1978; Verberk et al., 2021). Together these processes will increase rates of decomposition and nutrient cycling in polar ecosystems provided they are not limited by water availability or by increased predation (Thakur et al., 2017).

4.2. Increased habitat complexity will alter food-web structure

Warmer air temperatures are resulting in the greening of both polar regions which increases habitat complexity (Parnikoza et al., 2009; Myers-Smith et al., 2020; Peng et al., 2020). Warming is also aiding the survival and spread of non-native plant species (Chown et al., 2012; Hughes et al., 2015; Newman et al., 2018). The establishment of non-native plants modifies local abiotic conditions, including increased shading, soil moisture, and organic matter as well as increasing available trophic niches (Coulson et al., 2003; Convey and Peck, 2019). Collembola are often the dominant arthropods in simple soil ecosystems (Collins et al., 2019; Collins et al., 2019). However, as polar systems increase in biotic complexity, additional arthropod taxa, including non-native species are likely to establish (Coulson et al., 2003; Convey and Peck, 2019). While increased niche diversity may foster an associated increase in Collembola diversity, the presence of other arthropod taxa will shift community composition and decrease the relative role of Collembola. In particular, the arrival of ecosystem engineers, such as earthworms, may pose significant challenges to current inhabitants by improving soil habitability and the likelihood of further non-native species establishing (Hughes et al., 2013; Hughes et al., 2020; Wackett et al., 2018; Blume-Werry et al., 2020). The arrival and spread of predators such as invasive carabid beetles on South Georgia and the Kerguelen

Islands pose a direct threat to extant populations, although they are currently unlikely to survive in continental Antarctica (Convey et al., 2011).

Collembola are a major prey item of spiders and mites in the Arctic (Hodkinson and Coulson, 2004; Koltz et al., 2018b) and predatory mites in the continental (Gless, 1967; Fitzsimons, 1971) and maritime Antarctic (Jumeau and Usher, 1987). In the maritime Antarctic, densities of the predatory mite *Gamasellus racovitzai* and predation rates are currently low enough that they are unlikely to have a significant impact on Collembola abundances (Lister et al., 1987). However, many mites are more heat and desiccation tolerant than Collembola and predation by mites is likely to increase under warming conditions (Everatt et al., 2013). Under experimental conditions, increased densities of Arctic wolf spiders led to a decline in Collembola abundances with an accompanying decline in decomposition rates (Koltz et al., 2018b). Under warming conditions, collembolan abundance still declined even with low predator abundance (Franken et al., 2018; Koltz et al., 2018b). Long-term observational data from Greenland showed that Collembola declined from 1996 until 2011, during which time spider abundances increased (Koltz et al., 2018a). These trends were reversed in 2011 with cooler summer temperatures and a resulting decline in spider abundances and an increase in Collembola abundances across three different habitats (Høye et al., 2021). Thus, spiders benefitted while Collembola were negatively affected by higher temperatures (Høye et al., 2021).

Predation pressure will likely exacerbate other stressors particularly for smaller species and juveniles. For example, Thakur et al. (2017) found that *Proisotoma minuta* were driven to extinction under a combination of warming and predation pressure while the larger *Folsomia candida* were less affected. In another experiment involving four species of Collembola, predation had the largest impact on the two smaller species, with the highest impact (75 % decline in abundance) on the smaller, less mobile, species (Aupic-Samain et al., 2021). In this same study, a combination of low moisture, warming, and predation resulted in a >89 % decrease in abundance of all four species relative to low moisture and warming alone (Aupic-Samain et al., 2021).

4.3. Invasive Collembola may have a competitive advantage

The arrival of non-native and/or invasive species will provide further challenges to inhabitants of polar ecosystems. New arrivals have the potential to disrupt existing residents through increased competition for resources, elevated predation pressure and the transformation of soil systems through the arrival of ecosystem engineers. The potential for successful establishment of invasive species varies across polar regions with some locations exposed to considerably higher rates of propagule pressure (Chown et al., 2012; Newman et al., 2018; Vega et al., 2019). Unfortunately, some of the most rapidly warming polar regions are also exposed to the most propagule pressure. The maritime Antarctic and the western Antarctic Peninsula receive the highest number of visitors each year, both researchers and tourists, which increases the risk of species introductions (Chown et al., 2012; Duffy et al., 2017; Hughes et al., 2020). In the Arctic, increased shipping, human occupation, mineral exploration and tourism are also likely to increase the risk of introductions (Ruiz and Hewitt, 2009; Coulson et al., 2013; Hodkinson et al., 2013).

In Antarctica, high endemism and currently low levels of competition and predation suggest an increased vulnerability to non-native and invasive species (Hughes et al., 2015; Enríquez et al., 2018; Chown et al., 2022). The Antarctic Circumpolar Current has restricted all but sporadic natural dispersal events to the continent (Fraser et al., 2018). Increasing habitat availability coupled with increased human activity are likely to reduce dispersal barriers for non-native species. Many sub-Antarctic and maritime Antarctic islands are already climatically suitable for non-native Collembola. *Hypogastrura viatica* was first identified on Deception Island in the 1940s and already appears to be displacing and outcompeting *Cryptopygus antarcticus* in South Georgia (Convey et al., 1999;

Hughes et al., 2015; Enríquez et al., 2018). A total of 36 non-native Collembola species was reported by Baird et al. (2019) in the Antarctic (including the sub-Antarctic). Recent range expansions have also been reported for existing non-native species (Greenslade and Convey 2012; Phillips et al., 2017; Enríquez et al., 2019). Areas of the western Antarctic Peninsula are predicted to become habitable for globally invasive species within the next decades (Duffy et al., 2017). *Protaphorura fimata*, a palearctic species (already found in the sub-Antarctic) is one of 13 species (including plants, freshwater and marine invertebrates) identified as posing a high risk of becoming invasive in the Antarctic Peninsula region (Hughes et al., 2020). Even with increasing climate suitability, the establishment of non-native species in continental areas of the Antarctic (e.g. McMurdo Dry Valleys) remains less likely (Duffy et al., 2017; Duffy and Lee, 2019). Unfortunately, warming may still trigger the loss of diversity if an existing endemic species can, under changing conditions, outcompete other native species. In Svalbard, six non-native Collembola have established accidentally from imported soils although none appear to have spread (two are considered high risk) (Coulson, 2015). Since the last glacial maximum, the Arctic has been susceptible to natural dispersal from lower latitude species, some of which establish, while others are considered vagrant (Coulson et al., 2002b; Alsos et al., 2007). Under warming conditions, non-native and vagrant species could become invasive. With the exception of Svalbard, the identification and monitoring of non-native Collembola in the Arctic is currently limited by a lack of baseline data (Hogg and Hebert, 2004; Porco et al., 2014; Coulson, 2015).

The relative resilience of native and non-native Collembola will depend on local environmental conditions. Native species are particularly adapted to their local environment and many new arrivals may not survive. Accordingly, successful arrivals are likely to exhibit traits such as active dispersal (Enríquez et al., 2018), generalist feeding habits, and wider thermal tolerances (Phillips et al., 2020). Non-native species (regardless of phylogeny or place of origin) consistently have higher upper thermal limits compared to native species (Slabber et al., 2007; Janion-Schepers et al., 2018; Phillips et al., 2020). In a warmer and wetter climate, heightened thermal tolerances coupled with faster reproductive rates may provide non-native species a competitive edge and pose a significant threat to the resilience of existing native taxa.

5. Resilience of polar Collembola in a changing world

The resilience of polar Collembola to climate change is predicated on appropriate resistance capacities and the ability to recover following disturbances. Potential insights can be gained from historical responses to glacial cycles, observational evidence in Antarctica and the Arctic, as well as recovery rates following disturbances in lower latitude environments. However, these lower latitude studies often monitor recovery following short-term, acute disturbances while longer-term climate changes are unlikely to return to pre-disturbance conditions. In this context, successful recovery would be when communities reach a new stable state which would occur through a combination of local adaptation and recolonization processes.

Polar Collembola have persisted through glacial cycles (McGaughan et al., 2019; Collins et al., 2020) with recolonization dependent on migration of individuals from refugial habitats following disturbance. Resilience will depend on whether individuals already inhabit (or are able to migrate to) future refuges from the most damaging environmental changes. Numerous Antarctic glacial refugia have been identified through phylogeographic analyses with geothermal sites also representing possible oases (McGaughan et al., 2011; Fraser et al., 2014; Collins et al., 2020). Past Arctic refugia have included areas of Beringia and much of Siberia in addition to localised cryptic refugia and nearby lower latitude areas (Babenko, 2005; Ávila-Jiménez and Coulson, 2011). Whether similar refugia to escape climate change exist, remains to be seen. The existence of Holarctic species indicates the

potential for widespread dispersal via open sea-ways followed by subsequent localised diversification (Ávila-Jiménez and Coulson, 2011). Glacial retreat provides a useful analogue for likely recolonisation scenarios in Antarctica and areas of the Arctic (Hodkinson et al., 2004; Hågvar, 2010; Hågvar and Pedersen, 2015). Glacial retreat at a High Arctic Svalbard site revealed that after initial colonisation by three to four species (within two years), additional species did not arrive until 100-150 years later. Two low-mobility, deeper-dwelling species only appeared towards the end of the chronosequence – 1900 years later (Hodkinson et al., 2004). This suggests that recovery can be very slow, and if resistance capacities are limited, the overall resilience of polar Collembola is likely to be limited in the face of rapid environmental change.

Antarctic Collembola appear particularly vulnerable to disturbance and are exceedingly slow to recover. Anecdotal evidence from Ross Island in the Ross Sea region suggests that the relatively widespread *Gomphiocephalus hodgsoni* was once common in the vicinity of Hut Point near Scott's 1901 expedition hut (Wise, 1967). Construction activities for McMurdo Station and Scott Base, in the late 1950s, would have resulted in considerable disruption. Despite numerous searches by several different researchers, Collembola have not been recorded on this part of Ross Island for at least 60 years (Stevens and Hogg, 2002; Beet and Lee, 2021). The presence of extant populations of *G. hodgsoni* within ~25 km of the Station suggests that individuals do not effectively disperse and/or recolonise disturbed areas. This is further supported by high levels of genetic differentiation observed within single Dry Valleys indicating limited dispersal and isolation over evolutionary time scales (McGaughan et al., 2010; Collins et al., 2019). Accordingly, recovery within decadal timescales is unlikely for polar Collembola (Convey, 1996). Recovery in areas of human disturbance will be further complicated by the possibility of alien and invading species which may be better at colonising these disturbed sites (Duffy and Lee, 2019; Hughes et al., 2020).

In the Arctic, recovery of taxa following disturbance is likely to be more successful relative to the Antarctic. Higher densities, more widespread distributions, increased inter-population connectivity, and increased niche diversity all increase intrinsic capacities to recolonise disturbed areas. For example, increased vegetative abundances increase niche diversity (and potential refugia) which when coupled with higher abundances reduce the likelihood of complete extirpation of a population or species (Asmus et al., 2018; Myers-Smith et al., 2019). However, recovery would be dependent on the existing inhabitants of the disturbed communities and the proportionate rates of predation. If the surviving community is predominantly composed of smaller individuals, predators could have a more dramatic effect thus limiting any potential recovery (Thakur et al., 2017; Koltz et al., 2018b). Alternatively, recovery could be facilitated if predators were also negatively affected by disturbance (Koltz et al., 2018a; Høye et al., 2021).

Studies on a diverse range of disturbances such as opencast mining (Dunger et al., 2002; Dunger et al., 2004), fire (Huebner et al., 2012; Malmström, 2012), deforestation (Čuchta et al., 2019) and drought (Lindberg and Bengtsson, 2005) have identified common patterns in Collembola recovery following acute disturbances. The first species to recolonise are generally those with a high dispersal capacity, surface-dwelling (epiedaphic) nature, and generalist/opportunistic feeding habits (Malmström, 2012). In Antarctica, most taxa live in the soil profile or beneath rocks and appear to have very limited dispersal, and hence low ability to recolonise habitats (Janetschek, 1967; Collins et al., 2019). In the Arctic, collembolan communities are more diverse and disturbances are likely to have variable effects on different taxa. Deeper-dwelling asexually reproducing species are slower to recolonise and thus are likely to be less resilient to disturbances (Huebner et al., 2012; Malmström, 2012). Ultimately, while some species will recover within decadal timescales, whole communities will not (see Malmström, 2012). Lower latitude studies have demonstrated that whole community recovery is slow, even after 50 years following opencast mining, Collembola

assemblages still failed to resemble neighbouring undisturbed communities (Dunger et al., 2004).

5.1. Conclusions

Polar taxa have adapted over millennia to habitats that are now changing faster than any other on the Earth. Polar Collembola possess a suite of characteristics that enable their survival in extreme conditions and may help them adapt to changing conditions. These include high levels of genetic diversity, wide thermal tolerance ranges, physiological plasticity, generalist-opportunistic feeding habits and considerable capacity for behavioural avoidance. However, the biggest threats to polar Collembola are likely to be increasingly extreme and variable temperature regimes, drought, and changing biotic interactions. More diverse communities are likely to have some member taxa that are able to resist or recover from disturbances (Somero, 2010). Climate change will exacerbate the variance and extremes of environmental conditions which is generally assumed to favour Collembola adapted to variability. Overall, deeper-dwelling species that fail to resist climate change may not recover in ecologically relevant timescales, especially given the current, rapid rates of change (Malmström, 2012). The Arctic, with higher levels of diversity, may have higher levels of taxonomic redundancy which could moderate ecosystem response (Koltz et al., 2018a; Meredith et al., 2019). Unfortunately, areas such as the McMurdo Dry Valleys of Antarctica, with very low levels of taxonomic diversity are potentially more vulnerable and Collembola there will probably see the most profound changes (Collins et al., 2019).

Ongoing understanding of the issues covered in our review will facilitate an integrative approach to study the effects of climate change on polar Collembola. For example, in Antarctica, established baseline genetic data presents opportunities to investigate the interaction between genetic diversity and physiological tolerances at the finer population and individual scale, without the widespread influence of biotic interactions. Profitable areas of research that would benefit from immediate attention include: 1) improved baseline levels of species and genetic diversity for the Arctic fauna; 2) evaluating the behavioural avoidance capacity of polar Collembola to stressors in natural systems; 3) determining physiological tolerances (heat, cold, drought, pollution, and their interactions) for a wider range of Arctic and Antarctic taxa; 4) using genome and transcriptome sequencing to understand the genetic and physiological mechanisms of polar Collembola responses to stressors and their interactions; and 5) employing molecular tools to catalogue the diets a broad array of species and life stages. Collectively, these avenues of research will help to further illuminate the resilience of polar Collembola as well as their role in mediating the resilience of wider polar terrestrial ecosystems to climate change.

Declaration of Competing Interest

The authors declare no financial conflicts associated with this research. Brent J. Sinclair is Editor-in-Chief of Current Research in Insect Science. Given his role, he had no involvement in the evaluation or peer review of this manuscript, and has no access to information regarding its peer review.

CRediT authorship contribution statement

Clare R. Beet: Conceptualization, Writing – original draft, Writing – review & editing. **Ian D. Hogg:** Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing. **S. Craig Cary:** Conceptualization, Funding acquisition, Supervision. **Ian R. McDonald:** Funding acquisition, Supervision, Writing – review & editing. **Brent J. Sinclair:** Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

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References

- A'Bear, A.D., Jones, T.H., Boddy, L., 2014. Potential impacts of climate change on interactions among saprotrophic cord-forming fungal mycelia and grazing soil invertebrates. *Fungal Ecol* 10, 34–43. doi:10.1016/j.funeco.2013.01.009.
- Abnizova, A., Young, K.L., 2010. Sustainability of High Arctic ponds in a polar desert environment. *Arctic* 67–84. doi:10.14430/arctic648.
- Adams, B.J., Bardgett, R.D., Ayres, E., Wall, D.H., Aislabie, J., Bamforth, S., Bargagli, R., Cary, S.C., Cavacini, P., Connell, L., Convey, P., Fell, J.W., Frati, F., Hogg, I.D., Newsham, K.K., O'Donnell, A., Russell, A., Seppelt, R.D., Stevens, M.L., 2006. Diversity and distribution of Victoria Land biota. *Soil Biol. Biochem.* 38, 3003–3018. doi:10.1016/j.soilbio.2006.04.030.
- Aitchison, C.W., 1979. Winter-active subnivean invertebrates in Southern Canada. *I. Collembola*. *Pedobiologia* 19, 113–120.
- Alsos, I.G., Eidesen, P.B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G.H., Landvik, J.Y., Taberlet, P., Brochmann, C., 2007. Frequent long-distance plant colonization in the changing Arctic. *Science* 316, 1606–1609. doi:10.1126/science.1139178.
- Anslan, S., Tedersoo, L., 2015. Performance of cytochrome c oxidase subunit I (COI), ribosomal DNA Large Subunit (LSU) and Internal Transcribed Spacer 2 (ITS2) in DNA barcoding of Collembola. *Eur. J. Soil Biol.* 69, 1–7. doi:10.1016/j.ejsobi.2015.04.001.
- Anthony, S.E., Sinclair, B.J., 2019. Overwintering red velvet mites are freeze tolerant. *Physiol. Biochem. Zool.* 92, 201–205. doi:10.1086/702655.
- Asmus, A.L., Chmura, H.E., Høye, T.T., Krause, J.S., Sweet, S.K., Perez, J.H., Boelman, N.T., Wingfield, J.C., Gough, L., 2018. Shrub shading moderates the effects of weather on arthropod activity in arctic tundra. *Ecol. Entomol.* 43, 647–655. doi:10.1111/een.12644.
- Aupic-Samain, A., Baldy, V., Delcourt, N., Krogh, P.H., Gauquelin, Thierry, Fernandez, C., Santonja, M., 2021. Water availability rather than temperature control soil fauna community structure and prey–predator interactions. *Funct. Ecol.* 35, 1550–1559. doi:10.1111/1365-2435.13745.
- Ávila-Jiménez, M.L., Coulson, S.J., 2011. A Holarctic Biogeographical Analysis of the Collembola (Arthropoda, Hexapoda) Unravels Recent Post-Glacial Colonization Patterns. *Insects* 2, 273–296. doi:10.3390/insects2030273.
- Babenko, A.B., 2005. The structure of springtail fauna (Collembola) of the Arctic. *Entomol. Rev.* 85, 878–890.
- Bahrndorff, S., Petersen, S.O., Loeschcke, V., Overgaard, J., Holmstrup, M., 2007. Differences in cold and drought tolerance of high arctic and sub-arctic populations of *Megaphorura arctica* Tullberg 1876 (Onychiuridae: Collembola). *Cryobiology* 55, 315–323. doi:10.1016/j.cryobiol.2007.09.001.
- Bahrndorff, S., Mariën, J., Loeschcke, V., Ellers, J., 2009. Dynamics of heat-induced thermal stress resistance and hsp70 expression in the springtail. *Orchesella cincta*. *Funct. Ecol.* 23, 233–239. doi:10.1111/j.1365-2435.2009.01541.x.
- Baird, H.P., Moon, K.L., Janion-Scheepers, C., Chown, S.L., 2020. Springtail phylogeography highlights biosecurity risks of repeated invasions and intraregional transfers among remote islands. *Evol. Appl.* 13, 960–973. doi:10.1111/eva.12913.
- Baird, H.P., Janion-Scheepers, C., Stevens, M.L., Leihy, R.L., Chown, S.L., 2019. The ecological biogeography of indigenous and introduced Antarctic springtails. *J. Biogeogr.* 46, 1959–1973. doi:10.1111/jbi.13639.
- Becks, L., Agrawal, A.F., 2010. Higher rates of sex evolve in spatially heterogeneous environments. *Nature* 468, 89–92. doi:10.1038/nature09449.
- Beet, C.R., Hogg, I.D., Collins, G.E., Cowan, D.A., Wall, D.H., Adams, B.J., 2016. Genetic diversity among populations of Antarctic springtails (Collembola) within the Mackay Glacier ecotone. *Genome* 59, 762–770. doi:10.1139/gen-2015-0194.
- Beet, C.R., Lee, C.K., 2021. Baseline terrestrial biology assessment for the Scott Base Redevelopment project. In: Client report prepared for Antarctica New Zealand. Environmental Research Institute, School of Science, The University of Waikato, Hamilton, p. 31.
- Bennett, K.R., Hogg, I.D., Adams, B.J., Hebert, P.D.N., 2016. High levels of intraspecific genetic divergences revealed for Antarctic springtails: evidence for small-scale isolation during Pleistocene glaciation. *Biol. J. Linn. Soc.* 119, 166–178. doi:10.1111/bij.12796.
- Bender, E.A., Case, T.J., Gilpin, M.E., 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65, 1–13. doi:10.2307/1939452.
- Beresford, G.W., Selby, G., Moore, J.C., 2013. Lethal and sub-lethal effects of UV-B radiation exposure on the collembolan *Folsomia candida* (Willem) in the laboratory. *Pedobiologia* 56, 89–95. doi:10.1016/j.pedobi.2012.12.001.
- Birkmoe, T., Leinaas, H.P., 1999. Reproductive biology of the arctic collembolan *Hypogastrura tullbergi*. *Ecography* 22, 31–39.
- Blume-Werry, G., Krab, E.J., Olofsson, J., Sundqvist, M.K., Väisänen, M., Klaminder, J., 2020. Invasive earthworms unlock arctic plant nitrogen limitation. *Nat. Commun.* 11, 1–10. doi:10.1038/s41467-020-15568-3.

- Boitau, L., Salmon, S., Bourlette, C., Ponge, J.F., 2006. Avoidance of low doses of naphthalene by *Collembola*. *Environ. Pollut.* 139, 451–454. doi:10.1016/j.envpol.2005.06.013.
- Boiteau, G., Lynch, D.H., MacKinley, P., 2011. Avoidance tests with *Folsomia candida* for the assessment of copper contamination in agricultural soils. *Environ. Pollut.* 159, 903–906. doi:10.1016/j.envpol.2010.12.023.
- Boiteau, G., MacKinley, P., 2013. Role of avoidance behavior in the response of *Folsomia candida* to above-freezing cooling temperatures. *Entomol. Exp. Appl.* 147, 50–60. doi:10.1111/eea.12048.
- Bokhorst, S., Phoenix, G.K., Bjerke, J.W., Callaghan, T.V., Huyer-Brugman, F., Berg, M.P., 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Glob. Change Biol.* 18, 1152–1162. doi:10.1111/j.1365-2486.2011.02565.x.
- Bokhorst, S., Ronfort, C., Huiskes, A., Convey, P., Aerts, R., 2007. Food choice of Antarctic soil arthropods clarified by stable isotope signatures. *Polar Biol* 30, 983–990. doi:10.1007/s00300-007-0256-4.
- Bokhorst, S., Veen, G.F., Sundqvist, M., De Long, J.R., Kardol, P., Wardle, D.A., 2018. Contrasting responses of springtails and mites to elevation and vegetation type in the sub-Arctic. *Pedobiologia* 67, 57–64. doi:10.1016/j.pedobi.2018.02.004.
- Box, J.E., Colgan, W.T., Christensen, T.R., Schmidt, N.M., Lund, M., Parmentier, F.W., Brown, R., Bhatt, U.S., Euskirchen, E.S., Romanovsky, V.E., 2019. Key indicators of Arctic climate change: 1971–2017. *Environ. Res. Lett.* 14, 045010. doi:10.1088/1748-9326/aafclb.
- Brennan, G., Collins, S., 2015. Growth responses of a green alga to multiple environmental drivers. *Nat. Clim. Change* 5, 892–897. doi:10.1038/nclimate2682.
- Broadly, P.A., 1979. Feeding studies on the collembolan *Cryptopygus antarcticus* Willem at Signy Island, South Orkney Islands. *Br. Antarct. Surv. Bull.* 48, 37–46.
- Buckley, B.A., Somero, G.N., 2008. cDNA microarray analysis reveals the capacity of the cold-adapted Antarctic fish *Trematomus bernacchii* to alter gene expression in response to heat stress. *Polar Biol* 32, 403–415. doi:10.1007/s00300-008-0533-x.
- Callaghan, T.V., Tweedie, C.E., Akerman, J., Andrews, C., Bergstedt, J., Butler, M.G., Christensen, T.R., Cooley, D., Dahlberg, U., Danby, R.K., Daniels, F.J., de Molenaar, J.G., Dick, J., Mortensen, C.E., Ebert-May, D., Emanuelsson, U., Eriksson, H., Hedenas, H., Henry, H.R.G., Hik, D.S., Hobbie, J.E., Jantze, E.J., Jaspers, C., Johansson, C., Johansson, M., Johnson, D.R., Johnstone, J.F., Jonasson, C., Kennedy, C., Kenney, A.J., Keuper, F., Koh, S., Krebs, C.J., Lantuit, H., Lara, M.J., Lin, D., Lougheed, V.L., Madson, J., Matveyeva, N., McEwen, D.C., Myers-Smith, I.H., Narozhnyi, Y.K., Olsson, H., Pohjola, V.A., Price, L.W., Riget, F., Rundqvist, S., Sandstrom, A., Tamstorf, M., Van Bogaert, R., Villarreal, S., Webber, P.J., Zemtsov, V.A., 2011. Multi-decadal changes in tundra environments and ecosystems: synthesis of the International Polar Year-Back to the Future project (IPY-BTF). *Ambio* 40, 705–716. doi:10.1007/s13280-011-0179-8.
- Callahan, S.T., Bidwell, A., Lin, C., DeLuca, T.H., Tobin, P.C., 2019. Effects of copper exposure and increased temperatures on *Collembola* in western Washington, USA. *City and Environment Interactions* 4, 100026. doi:10.1016/j.cacint.2020.100026.
- Cannon, R.J.C., Block, W., 1988. Cold tolerance of microarthropods. *Biol. Rev.* 63, 23–77.
- Carapelli, A., Fanciulli, P.P., Frati, F., Leo, C., 2019. Mitogenomic data to study the taxonomy of Antarctic springtail species (Hexapoda: Collembola) and their adaptation to extreme environments. *Polar Biol* 42, 715–732. doi:10.1007/s00300-019-02466-8.
- Carapelli, A., Greenslade, P., Nardi, F., Leo, C., Convey, P., Frati, F., Fanciulli, P.P., 2020. Evidence for cryptic diversity in the “pan-Antarctic” springtail *Friesia antarctica* and the description of two new species. *Insects* 11, 141. doi:10.3390/insects11030141.
- Caruso, T., Hogg, I.D., Bargagli, R., 2010. Analysing distributional patterns of Antarctic terrestrial arthropods along the Victoria Land latitudinal gradient: identifying appropriate study designs and modelling approaches. *Antarct. Sci.* 22, 742–748. doi:10.1017/S095410201000043X.
- Caruso, T., Hogg, I.D., Nielsen, U.N., Bottos, E.M., Lee, C.K., Hopkins, D.W., Cary, S.C., Barrett, J.E., Green, T.G.A., Storey, B.C., Wall, D.H., Adams, B.J., 2019. Nematodes in a polar desert reveal the relative role of biotic interactions in the coexistence of soil animals. *Commun. Biol.* 2, 63. doi:10.1038/s42003-018-0260-y.
- Case, T.J., Taper, M.L., 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species borders. *Am. Nat.* 155, 583–605. doi:10.1086/303351.
- Chauvat, M., Forey, E., 2021. Temperature modifies the magnitude of a plant response to *Collembola* presence. *Appl. Soil Ecol.* 158, 103814. doi:10.1016/j.apsoil.2020.103814.
- Chernova, N.M., Potapov, M.B., Savenkova, Y.Y., Bokova, A.I., 2010. Ecological significance of parthenogenesis in *Collembola*. *Entomol. Rev.* 90, 23–38. doi:10.1134/S0013873810010033.
- Chown, S.L., Huiskes, A.H., Gremmen, N.J., Lee, J.E., Terauds, A., Crosbie, K., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Raymond, B., Tsujimoto, M., Ware, C., Van de Vijver, B., Bergstrom, D.M., 2012. Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proc. Natl. Acad. Sci. USA* 109, 4938–4943. doi:10.1073/pnas.1119787109.
- Chown, S.L., Nicholson, S.W., 2004. *Insect Physiological Ecology: Mechanisms and Patterns*. Oxford University Press, Oxford, UK.
- Chown, S.L., Bergstrom, D.M., Houghton, M., Kiefer, K., Terauds, A., Leihy, R.I., 2022. Invasive species impacts on sub-Antarctic *Collembola* support the Antarctic climate-diversity-invasion hypothesis. *Soil Biol. Biochem.* 166, 108579. doi:10.1016/j.soilbio.2022.108579.
- Chown, S.L., Sørensen, J.G., Terblanche, J.S., 2011. Water loss in insects: an environmental change perspective. *J. Insect Physiol.* 57, 1070–1084. doi:10.1016/j.jinphys.2011.05.004.
- Chu, W., Dang, N., Kok, Y., Yap, K.I., Phang, S., Convey, P., 2019. Heavy metal pollution in Antarctica and its potential impacts on algae. *Polar Sci* 20, 75–83. doi:10.1016/j.polar.2018.10.004.
- Clem, K.R., Fogt, R.L., Turner, J., Lintner, B.R., Marshall, G.J., Miller, J.R., Renwick, J.A., 2020. Record warming at the South Pole during the past three decades. *Nat. Clim. Change* 10, 762–770. doi:10.5281/zenodo.3712453.
- Colinet, H., Sinclair, B.J., Vernon, P., Renault, D., 2015. Insects in fluctuating thermal environments. *Annu. Rev. Entomol.* 60, 123–140. doi:10.1146/annurev-ento-010814-021017.
- Collins, G.E., Hogg, I.D., 2016. Temperature-related activity of *Gomphiocephalus hodgsoni* (Collembola) mitochondrial DNA (COI) haplotypes in Taylor Valley. *Antarctica. Polar Biol.* 39, 379–389. doi:10.1007/s00300-015-1788-7.
- Collins, G.E., Hogg, I.D., Baxter, J.R., Maggs-Kölling, G., Cowan, D.A., 2019. Ancient landscapes of the Namib Desert harbor high levels of genetic variability and deeply divergent lineages for *Collembola*. *Ecol. Evo.* 9, 4969–4979. doi:10.1002/ece3.5103.
- Collins, G.E., Hogg, I.D., Convey, P., Barnes, A.D., McDonald, I.R., 2019. Spatial and Temporal Scales Matter When Assessing the Species and Genetic Diversity of Springtails (*Collembola*) in Antarctica. *Front. Ecol. Evol.* 7, 76. doi:10.3389/fevo.2019.00076.
- Collins, G.E., Hogg, I.D., Convey, P., Sancho, L.G., Cowan, D.A., Lyons, W.B., Adams, B.J., Wall, D.H., Green, T.G.A., 2020. Genetic diversity of soil invertebrates corroborates timing estimates for past collapses of the West Antarctic Ice Sheet. *Proc. Natl. Acad. Sci. USA* 36, 22293–22302. doi:10.1073/pnas.2007925117.
- Convey, P., Greenslade, P., Arnold, R.J., Block, W., 1999. *Collembola* of sub-Antarctic South Georgia. *Polar Biol* 22, 1–6.
- Convey, P., Abbandonato, H., Bergan, F., Beumer, L.T., Biersma, E.M., Brathen, V.S., DImperio, L., Jensen, C.K., Nilsen, S., Paquin, K., Stenkevit, U., Svoen, M.E., Winkler, J., Muller, E., Coulson, S.J., 2015. Survival of rapidly fluctuating natural low winter temperatures by High Arctic soil invertebrates. *J. Therm. Biol.* 54, 111–117. doi:10.1016/j.jtherbio.2014.07.009.
- Convey, P., Coulson, S.J., Worland, M.R., Sjöblom, A., 2018. The importance of understanding annual and shorter-term temperature patterns and variation in the surface levels of polar soils for terrestrial biota. *Polar Biol* 41, 1587–1605. doi:10.1007/s00300-018-2299-0.
- Convey, P., 1996. The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. *Biol. Rev.* 71, 191–225.
- Convey, P., Key, R.S., Key, R.J.D., Belchier, M., Waller, C.L., 2011. Recent range expansions in non-native predatory beetles on sub-Antarctic South Georgia. *Polar Biol* 34, 597–602. doi:10.1007/s00300-010-0909-6.
- Convey, P., Peck, L.S., 2019. Antarctic environmental change and biological responses. *Sci. Adv.* 5, eaaz0888. doi:10.1126/sciadv.aaz0888.
- Costa, D., Martijn, J.T.N., Timmermans, M.J.T.N., Sousa, J.P., Ribeiro, R., Roelofs, D., Van Straalen, N.M., 2013. Genetic structure of soil invertebrate populations: collembolans, earthworms and isopods. *Appl. Soil Ecol.* 68, 61–66. doi:10.1016/j.apsoil.2013.03.003.
- Coulson, S.J., Hodkinson, I.D., Block, W., Webb, N.R., Worland, M.R., 1995. Low summer temperatures: a potential mortality factor for high arctic soil microarthropods? *J. Insect Physiol.* 41, 783–792.
- Coulson, S.J., Hodkinson, I.D., Strathdee, A.T., Block, W., Webb, N.R., Bale, J.S., Worland, M.R., 1995. Thermal environments of Arctic soil organisms during winter. *Arct. Alp. Res.* 27, 364–370.
- Coulson, S.J., Hodkinson, I.D., Webb, N.R., 2003. Microscale distribution patterns in high Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. *Ecography* 26, 801–809. doi:10.1111/j.0906-7590.2003.03646.
- Coulson, S.J., Hodkinson, I.D., Webb, N.R., Harrison, J.A., 2002a. Survival of Terrestrial Soil-Dwelling Arthropods on and in Seawater: Implications for Trans-Oceanic Dispersal. *Funct. Ecol.* 16, 353–356. <http://www.jstor.org/stable/826589>.
- Coulson, S.J., Hodkinson, I.D., Webb, N.R., Mikkola, K., Harrison, J.A., Pedgley, D.E., 2002b. Aerial colonization of high Arctic islands by invertebrates: the diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) as a potential indicator species. *Divers. Distrib.* 8, 327–334. doi:10.1046/j.1472-4642.2002.00157.
- Coulson, S.J., Leinaas, H.P., Ims, R.A., Søvik, G., 2000. Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community. *Ecography* 23, 299–306. doi:10.1111/j.1600-0587.2000.tb00285.
- Coulson, S.J., 2015. The alien terrestrial invertebrate fauna of the High Arctic archipelago of Svalbard: potential implications for the native flora and fauna. *Polar Res* 34, 27364. doi:10.3402/polar.v34.27364.
- Coulson, S.J., Fjellberg, A., Gwiazdowicz, D.J., Lebedeva, N.V., Melekina, E.N., Solhøy, T., Erseus, C., Maraldo, K., Miko, L., Schatz, H., 2013. The invertebrate fauna of anthropogenic soils in the High-Arctic settlement of Barentsburg, Svalbard. *Polar Res* 32, 19273. doi:10.3402/polar.v32i0.19273.
- Courchamp, F., Berec, J., Gascoigne, J., 2008. *Allee effects in ecology and conservation*. OUP Oxford.
- Čuchta, P., Mikšíšová, D., Kováč, L., 2019. The succession of soil *Collembola* communities in spruce forests of the High Tatras Mountains five years after a windthrow and clear-cut logging. *For. Ecol. Manag.* 433, 504–513. doi:10.1016/j.foreco.2018.11.023.
- Cucini, C., Leo, C., Nardi, F., Greco, S., Manfrin, C., Giulianini, P.G., Carapelli, A., 2021. First de novo transcriptome analysis of the Antarctic springtail *Cryptopygus terranovus* (Collembola: Isotomidae) following mid-term heat exposure. *Antarct. Sci.* 33, 459–468. doi:10.1017/S0954102021000195.
- Dahl, M.B., Priemé, A., Brejnrod, A., Brusvang, P., Lund, M., Nymand, J., Kramshøj, M., Ro-Poulsen, H., Haugwitz, M.S., 2017. Warming, shading and a moth outbreak reduce tundra carbon sink strength dramatically by changing plant cover and soil microbial activity. *Sci. Reports* 7, 1–13. doi:10.1038/s41598-017-16007-y.
- Danks, H.V., 1990. Arctic insects: instructive diversity. In: Harrington, C.R. (Ed.), *Canada's missing dimension: science and history in the Canadian arctic islands*. Canadian Museum of Nature, Ottawa, Canada, pp. 444–470.
- Danks, H.V., 1992. Arctic insects as indicators of environmental change. *Arctic* 45, 159–166.

- Davidson, M.M., Broady, P.A., 1996. Analysis of gut contents of *Gomphiocephalus hodgsoni* Carpenter (Collembola: Hypogastruridae) at Cape Geology, Antarctica. *Polar Biol.* 16, 463–467.
- Detsis, V., 2000. Vertical distribution of Collembola in deciduous forests under Mediterranean climatic conditions. *Belgian J. Zool.* 130, 55–59.
- Dillon, M.E., Arthur Woods, H., Wang, G., Fey, S.B., Vasseur, D.A., Telemeco, R.S., Marshall, K., Pincebourde, S., 2016. Life in the Frequency Domain: the Biological Impacts of Changes in Climate Variability at Multiple Time Scales. *Integr. Comp. Biol.* 56, 14–30. doi:10.1093/icb/icw024.
- Duffy, G.A., Coetzee, B.W.T., Latombe, G., Akerman, A.H., McGeoch, M.A., Chown, S.L., 2017. Barriers to globally invasive species are weakening across the Antarctic. *Divers. Distrib.* 23, 982–996. doi:10.1111/ddi.12593.
- Duffy, G.A., Lee, J.R., 2019. Ice-free area expansion compounds the non-native species threat to Antarctic terrestrial biodiversity. *Biol. Conserv.* 232, 253–257. doi:10.1016/j.biocon.2019.02.014.
- Dunger, W., Schulz, H., Zimdars, B., 2002. Colonization behaviour of Collembola under different conditions of dispersal. *Pedobiologia* 46, 316–327. doi:10.1078/0031-4056-00139.
- Dunger, W., Schulz, H., Zimdars, B., Hohberg, K., 2004. Changes in collembolan species composition in Eastern German mine sites over fifty years of primary succession. *Pedobiologia* 48, 503–517. doi:10.1016/j.pedobi.2004.07.005.
- Elnitsky, M.A., Benoit, J.B., Denlinger, D.L., Lee, R.E., 2008. Desiccation tolerance and drought acclimation in the Antarctic collembolan *Cryptopygus antarcticus*. *J. Insect Physiol.* 54, 1432–1439. doi:10.1016/j.jinsphys.2008.08.004.
- Enríquez, N., Pertierra, L.R., Tejedo, P., Benayas, J., Greenslade, P., Lucíañez, M.J., 2019. The importance of long-term surveys on species introductions in Maritime Antarctica: first detection of *Ceratophylla succinea* (Collembola: Hypogastruridae). *Polar Biol* 42, 1047–1051. doi:10.1007/s00300-019-02490-8.
- Enríquez, N., Tejedo, P., Benayas, J., Albertos, B., Lucíañez, M.J., 2018. Collembola of Barrientos Island, Antarctica: first census and assessment of environmental factors determining springtail distribution. *Polar Biol* 41, 713–725. doi:10.1007/s00300-017-2230-0.
- Errington, I., King, C.K., Wilkins, D., Spedding, T., Hose, G.C., 2018. Ecosystem effects and the management of petroleum-contaminated soils on subantarctic islands. *Chemosphere* 194, 200–210. doi:10.1016/j.chemosphere.2017.11.157.
- Escribano-Álvarez, P., Pertierra, L.R., Martínez, B., Chown, S.L., Olalla-Tárraga, Miguel Á., 2022. Half a century of thermal tolerance studies in springtails (Collembola): A review of metrics, spatial and temporal trends. *Curr. Res. Insect Sci.* 2, 100023. doi:10.1016/j.cris.2021.100023.
- Everatt, M.J., Convey, P., Bale, J.S., Worland, M.R., Hayward, S.A., 2015. Responses of invertebrates to temperature and water stress: A polar perspective. *J. Therm. Biol.* 54, 118–132. doi:10.1016/j.jtherbio.2014.05.004.
- Everatt, M.J., Convey, P., Worland, M.R., Bale, J.S., Hayward, S.A., 2014. Are the Antarctic dipteran, *Eretmoptera murphyi*, and Arctic collembolan, *Megaphorura arctica*, vulnerable to rising temperatures? *Bull. Entomol. Res.* 104, 494–503. doi:10.1017/S0007485314000261.
- Everatt, M.J., Convey, P., Worland, M.R., Bale, J.S., Hayward, S.A., 2013. Heat tolerance and physiological plasticity in the Antarctic collembolan, *Cryptopygus antarcticus*, and mite, *Alaskozetes antarcticus*. *J. Therm. Biol.* 38, 264–271. doi:10.1016/j.jtherbio.2013.02.006.
- Faddeeva-Vakhrusheva, A., Derks, M.F., Anvar, S.Y., Agamennone, V., Suring, W., Smit, S., van Straalen, N.M., Roelofs, D., 2016. Gene family evolution reflects adaptation to soil environmental stressors in the genome of the collembolan *Orchesella cincta*. *Genome Biol. Evol.* 8, 2106–2117. doi:10.1093/gbe/evw134.
- Faddeeva, A., Studer, R.A., Kraaijeveld, K., Sie, D., Ylstra, B., Marien, J., op den Camp, H.J., Datema, E., den Dunnen, J.T., van Straalen, N.M., Roelofs, D., 2015. Collembolan transcriptomes highlight molecular evolution of hexapods and provide clues on the adaptation to terrestrial life. *PLoS One* 10, e0130600. doi:10.1371/journal.pone.0130600.
- Farquharson, L.M., Romanovsky, V.E., Cable, W.L., Walker, D.A., Kokelj, S.V., Nicolsky, D., 2019. Climate change drives widespread and rapid thermokarst development in very cold permafrost in the Canadian High Arctic. *Geophys. Res. Lett.* 46, 6681–6689. doi:10.1029/2019GL082187.
- Ferguson, D.K., Li, C., Jiang, C., Chakraborty, A., Grasby, S.E., Hubert, C.R.J., 2020. Natural attenuation of spilled crude oil by cold-adapted soil bacterial communities at a decommissioned High Arctic oil well site. *Sci. Total Environ.* 722, 137258. doi:10.1016/j.scitotenv.2020.137258.
- Fitzsimons, J.M., 1971. On the food habits of certain Antarctic arthropods from coastal Victoria Land and adjacent islands. *Pac. Insects Monogr.* 25, 121–125.
- Franken, O., Huizinga, M., Ellers, J., Berg, M.P., 2018. Heated communities: large inter- and intraspecific variation in heat tolerance across trophic levels of a soil arthropod community. *Oecologia* 186, 311–322. doi:10.1007/s00442-017-4032-z.
- Franken, O., Ferreira, S.S.D., Jesse, W.A.M., Berg, M.P., Ellers, J., 2018. A common yardstick to measure the effects of different extreme climatic events on soil arthropod community composition using time-series data. *Front. Ecol. Evol.* 6, 195. doi:10.3389/fevo.2018.00195.
- Fraser, C.I., Terauds, A., Smellie, J., Convey, P., Chown, S.L., 2014. Geothermal activity helps life survive glacial cycles. *Proc. Natl. Acad. Sci. USA* 111, 5634–5639. doi:10.1073/pnas.1321437111.
- Fraser, C.I., Morrison, A.K., Hogg, A.M.C., Macaya, E.C., van Sebille, E., Ryan, P.G., Padovan, A., Jack, C., Valdivia, N., Waters, J.M., 2018. Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. *Nat. Clim. Change* 8, 704–708. doi:10.1038/s41558-018-0209-7.
- Fraser, R.H., Kokelj, S.V., Lantz, T.C., McFarlane-Winchester, M., Olthof, I., Laclelle, D., 2018. Climate sensitivity of high Arctic permafrost terrain demonstrated by widespread ice-wedge thermokarst on Banks Island. *Remote Sens.* 10, 954. doi:10.3390/rs10060954.
- Gefen, E., Marlon, A.J., Gibbs, A.G., 2006. Selection for desiccation resistance in adult *Drosophila melanogaster* affects larval development and metabolite accumulation. *J. Exp. Biol.* 209, 3293–3300. doi:10.1242/jeb.02397.
- Gibbs, A.G., Chippindale, A.K., Rose, M.R., 1997. Physiological mechanisms of evolved desiccation resistance in *Drosophila melanogaster*. *J. Exp. Biol.* 200, 1821–1832.
- Gless, E.E., 1967. Notes on the biology of *Coccorhagidia gressitti* Womersley and Strandmann. *Antarct. Res. Ser.* 10, 321–323.
- González-Pleiter, M., Lacerot, G., Edo, C., Pablo Lozoya, J., Leganés, F., Fernández-Piñas, F., Rosal, R., Teixeira-de-Mello, F., 2021. A pilot study about microplastics and mesoplastics in an Antarctic glacier. *Cryosphere* 15, 2531–2539. doi:10.5194/tc-15-2531-2021.
- Gooseff, M.N., Barrett, J.E., Doran, P.T., Fountain, A.G., Lyons, W.B., Parsons, A.N., Porazinska, D.L., Virginia, R.A., Wall, D.H., 2003. Snow-patch influence on soil biogeochemical processes and invertebrate distribution in the McMurdo Dry Valleys. *Arct. Antarct. Alp. Res.* 35, 91–99. doi:10.1657/1523-0430(2003)035[0091:SPIOSB]2.0.CO;2.
- Graham, L.A., Boddington, M.E., Holmstrup, M., Davies, P.L., 2020. Antifreeze protein complements cryoprotective dehydration in the freeze-avoiding springtail *Megaphorura arctica*. *Sci Rep* 10, 3047. doi:10.1038/s41598-020-60060-z.
- Greenslade, P., 2007. The potential of Collembola to act as indicators of landscape stress in Australia. *Aus. J. Exp. Agri.* 47, 424–434. doi:10.1071/EA05264.
- Greenslade, P., Convey, P., 2012. Exotic Collembola on subantarctic islands: pathways, origins and biology. *Biol. Invasions* 14, 405–417. doi:10.1007/s10530-011-0086-8.
- Gutt, J., Isla, E., Xavier, J.C., Adams, B.J., Ahn, I.Y., Cheng, C.H.C., Colesie, C., Cummings, V., di Prisco, G., Griffiths, H., Hawes, I., Hogg, I.D., McIntyre, T., Meiners, K.M., Pearce, D., Peck, L., Piepenburg, D., Reisinger, R., Saba, G., Schloss, I.R., Signori, C.N., Smith, C.R., Vacchi, M., Verde, C., Wall, D.H., 2021. Antarctic ecosystems in transition – life between stresses and opportunities. *Biol. Rev.* 96, 798–821. doi:10.1111/brv.12679.
- Hafer, N., Ebil, S., Uller, T., Pike, N., 2011. Transgenerational effects of food availability on age at maturity and reproductive output in an asexual collembolan species. *Biol. Lett.* 7, 755–758. doi:10.1098/rsbl.2011.0139.
- Hågvar, S., 2010. Primary succession of springtails (Collembola) in a Norwegian glacier foreland. *Arct. Ant. Alp. Res.* 42, 422–429. doi:10.1657/1938-4246-42.4.422.
- Hågvar, S., Pedersen, A., 2015. Food choice of invertebrates during early glacier foreland succession. *Arct. Ant. Alp. Res.* 47, 561–572. doi:10.1657/AAAR0014-046.
- Hawes, T.C., 2011. Rafting in the Antarctic springtail, *Gomphiocephalus hodgsoni*. *Antarct. Sci.* 23, 456–460. doi:10.1017/S0954102011000307.
- Hawes, T.C., Bale, J.S., Worland, M.R., Convey, P., 2007. Plasticity and superplasticity in the acclimation potential of the Antarctic mite *Halozetes belgicae* (Michael). *J. Exp. Biol.* 210, 593–601. doi:10.1242/jeb.02691.
- Hawes, T.C., Bale, J.S., Worland, M.R., Convey, P., 2008. Trade-offs between microhabitat selection and physiological plasticity in the Antarctic springtail, *Cryptopygus antarcticus* (Willem). *Polar Biol* 31, 681–689. doi:10.1007/s00300-008-0406-3.
- Hawes, T.C., Marshall, C.J., Wharton, D.A., 2012. Ultraviolet radiation tolerance of the Antarctic springtail, *Gomphiocephalus hodgsoni*. *Antarct. Sci.* 24, 147–153. doi:10.1017/S0954102011000812.
- Hawes, T.C., Torricelli, G., Stevens, M.I., 2010. Haplotype diversity in the Antarctic springtail *Gressittacantha terranova* at fine spatial scales – a Holocene twist to a Pliocene tale. *Antarct. Sci.* 22, 766–773. doi:10.1017/S0954102010000490.
- Hayward, S.A.L., Worland, M.R., Convey, P., Bale, J.S., 2004. Habitat moisture availability and the local distribution of the Antarctic Collembola *Cryptopygus antarcticus* and *Friesea grisea*. *Soil Biol. Biochem.* 36, 927–934. doi:10.1016/j.soilbio.2004.02.007.
- Hertzberg, K., Leinaas, H.P., 1998. Drought stress as a mortality factor in two pairs of sympatric species of Collembola at Spitsbergen, Svalbard. *Polar Biol* 19, 302–306.
- Hertzberg, K., Leinaas, H.P., Ims, R.A., 1994. Patterns of abundance and demography: Collembola in a habitat patch gradient. *Ecography* 17, 349–359.
- Hilligsoe, H., Holmstrup, M., 2003. Effects of starvation and body mass on drought tolerance in the soil collembolan *Folsomia candida*. *J. Insect Physiol.* 49, 99–104. doi:10.1016/S0022-1910(02)00253-6.
- Hodkinson, I.D., Coulson, S., Webb, N.R., Block, W., Strathdee, A.T., Bale, J.S., 1994. Feeding studies on *Onychiurus arcticus* (Tullberg) (Collembola: Onychiuridae) on West Spitsbergen. *Polar Biol* 14, 17–19.
- Hodkinson, I.D., Coulson, S.J., Webb, N.R., 2004. Invertebrate community assembly along proglacial chronosequences in the high Arctic. *J. Anim. Ecol.* 73, 556–568. www.jstor.org/stable/3505666.
- Hodkinson, I.D., Coulson, S.J., 2004. Are high Arctic terrestrial food chains really that simple?—The Bear Island food web revisited. *Oikos* 106, 427–431. doi:10.1111/j.0030-1299.2004.13091.x.
- Hodkinson, I.D., Babenko, A., Behan-Pelletier, V., et al., 2013. Terrestrial and freshwater invertebrates. In: Meltofte, H. (Ed.), *Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna. Arctic Council. Narayana Press, Denmark*, pp. 246–276.
- Hodkinson, I.D., Coulson, S.J., Webb, N.R., Block, W., 1996. Can high Arctic soil microarthropods survive elevated summer temperatures? *Funct. Ecol.* 10, 314–321.
- Hoffmann, A.A., Hallas, R.J., Dean, J.A., Schiffer, M., 2003. Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science* 301, 100–102. doi:10.1126/science.1084296.
- Hoffmann, A.A., Miller, A.D., Weeks, A.R., 2021. Genetic mixing for population management: From genetic rescue to provenancing. *Evol. Appl.* 14, 634–652. doi:10.1111/eva.13154.
- Hogg, I.D., Wall, D.H., 2011. Global change and Antarctic terrestrial biodiversity. *Polar Biol* 34, 1627. doi:10.1007/s00300-011-1108-9.

- Hogg, I.D., Stevens, M.I., Wall, D.H., 2014. Invertebrates. In: Cowan, D.A. (Ed.), *Antarctic Terrestrial Microbiology*. Springer, Berlin, pp. 55–78.
- Hogg, I.D., Cary, S.C., Convey, P., Newsham, K.K., O'Donnell, A.G., Adams, B.J., Aislabie, J., Frati, F., Stevens, M.I., Wall, D.H., 2006. Biotic interactions in Antarctic terrestrial ecosystems: Are they a factor? *Soil Biol. Biochem.* 38, 3035–3040. doi:10.1016/j.soilbio.2006.04.026.
- Hogg, I.D., Hebert, P.D.N., 2004. Biological identification of springtails (Hexapoda: Collembola) from the Canadian Arctic, using mitochondrial DNA barcodes. *Canadian J. Zool.* 82, 749–754. doi:10.1139/z04-041.
- Hohenlohe, P.A., Funk, W.C., Rajora, O.P., 2021. Population genomics for wildlife conservation and management. *Molec. Ecol.* 30, 62–82. doi:10.1111/mec.15720.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4, 1–23.
- Holmstrup, M., Sømme, L., 1998. Dehydration and cold hardiness in the Arctic collembolan *Onychiurus arcticus* Tullberg 1876. *J. of Comp. Phys. B.* 168, 197–203.
- Holmstrup, M., 2018a. Screening of cold tolerance in fifteen springtail species. *J. Therm. Biol.* 77, 1–6. doi:10.1016/j.jtherbio.2018.07.017.
- Holmstrup, M., 2018b. The springtail *Megaphorura arctica* survives extremely high osmolality of body fluids during drought. *J. Comp. Physiol. B.* 188, 939–945. doi:10.1007/s00360-018-1180-3.
- Holmstrup, M., Aubail, A., Damgaard, C., 2008. Exposure to mercury reduces cold tolerance in the springtail *Folsomia candida*. *Comp. Biochem. Physiol. C* 148, 172–177. doi:10.1016/j.cbpc.2008.05.003.
- Holmstrup, M., Bayley, M., Ramløv, H., 2002. Supercool or dehydrate? An experimental analysis of overwintering strategies in small permeable arctic invertebrates. *Proc. Natl. Acad. Sci. USA* 99, 5716–5720. doi:10.1073/pnas.082580699.
- Holmstrup, M., Sørensen, J.G., Schmidt, I.K., Nielsen, P.L., Mason, S., Tietema, A., Smith, A.R., Bataillon, T., Beier, C., Ehlers, B.K., 2013. Soil microarthropods are only weakly impacted after 13 years of repeated drought treatment in wet and dry heathland soils. *Soil Biol. Biochem.* 66, 110–118. doi:10.1016/j.soilbio.2013.06.023.
- Hopkin, S.P., 1997. *Biology of the Springtails: (Insecta: Collembola)*. OUP Oxford.
- Høye, T.T., Loboda, S., Koltz, A.M., Gillespie, M.A.K., Bowden, J.J., Schmidt, N.M., 2021. Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. *Proc. Natl. Acad. Sci. USA* 118, e2002557117. doi:10.1073/pnas.2002557117.
- Hudson, J., McQuaid, C.D., Rius, M., 2021. Contemporary climate change hinders hybrid performance of ecologically dominant marine invertebrates. *J. Evol. Biol.* 34, 60–72. doi:10.1111/jeb.13609.
- Huebner, K., Lindo, K., Lechowicz, M.J., 2012. Post-fire succession of collembolan communities in a northern hardwood forest. *Eur. J. Soil Biol.* 48, 59–65. doi:10.1016/j.ejsobi.2011.10.004.
- Huey, R.B., Ma, L., Levy, O., Kearney, M.R., 2021. Three questions about the eco-physiology of overwintering underground. *Ecol. Lett.* 24, 170–185. doi:10.1111/ele.13636.
- Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W.P., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70, 931–944.
- Hughes, K.A., Pescott, O.L., Peyton, J., Adriaens, T., Cottier-Cook, E.J., Key, G., Rabitsch, W., Tricarico, E., Barnes, D.K.A., Baxter, N., 2020. Invasive non-native species likely to threaten biodiversity and ecosystems in the Antarctic Peninsula region. *Glob. Change Biol.* 26, 2702–2716. doi:10.1111/gcb.14938.
- Hughes, K.A., Worland, M.R., Thorne, M.A.S., Convey, P., 2013. The non-native chironomid *Eretmoptera murphyi* in Antarctica: erosion of the barriers to invasion. *Biol. Invasions* 15, 269–281. doi:10.1007/s10530-012-0282-1.
- Hughes, K.A., Pertierra, L.R., Molina-Montenegro, M.A., Convey, P., 2015. Biological invasions in terrestrial Antarctica: what is the current status and can we respond? *Biodivers. Conserv.* 24, 1031–1055. doi:10.1007/s10531-015-0896-6.
- Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Chase, T.J., Dietzel, A., Hill, T., Hoey, A.S., Hoogenboom, M.O., Jacobson, M., Kerswell, A., Madin, J.S., Mieg, A., Paley, A.S., Pratchett, M.S., Torda, G., Woods, R.M., 2019. Global warming impairs stock-recruitment dynamics of corals. *Nature* 568, 387–390. doi:10.1038/s41586-019-1081-y.
- Ingrisch, J., Bahn, M., 2018. Towards a comparable quantification of resilience. *Trends Ecol. Evol.* 33, 251–259. doi:10.1016/j.tree.2018.01.013.
- Janetschek, H., 1967. Arthropod ecology of south Victoria Land. *Antarct. Res. Ser.* 10, 205–293.
- Jangjoo, M., Matter, S.F., Roland, J., Keyghobadi, N., 2016. Connectivity rescues genetic diversity after a demographic bottleneck in a butterfly population network. *Proc. Natl. Acad. Sci. USA* 113, 10914–10919. doi:10.1073/pnas.1600865113.
- Janion-Scheepers, C., Phillips, L., Sgro, C.M., Duffy, G.A., Hallas, R., Chown, S.L., 2018. Basal resistance enhances warming tolerance of alien over indigenous species across latitude. *Proc. Natl. Acad. Sci. USA* 115, 145–150. doi:10.1073/pnas.1715598115.
- Ju, H., Zhu, D., Qiao, M., 2019. Effects of polyethylene microplastics on the gut microbial community, reproduction and avoidance behaviors of the soil springtail, *Folsomia candida*. *Environ. Pollut.* 247, 890–897. doi:10.1016/j.envpol.2019.01.097.
- Jumeau, P.J.A.M., Usher, M.B., 1987. The Antarctic predatory mite *Gamasellus racovitzai* (Trouessart) (Mesostigmata)—A morphometric study of two subspecies. *Acarologia* 28, 15–26. doi:10.1016/j.cois.2016.07.001.
- Kærsgaard, C.W., Holmstrup, M., Malte, H., Bayley, M., 2004. The importance of cuticular permeability, osmolyte production and body size for the desiccation resistance of nine species of Collembola. *J. Insect Physiol.* 50, 5–15. doi:10.1016/j.jinsphys.2003.09.003.
- Kaunisto, S., Ferguson, L.V., Sinclair, B.J., 2016. Can we predict the effects of multiple stressors on insects in a changing climate? *Curr. Opin. Insect Sci.* 17, 55–61. doi:10.1016/j.cois.2016.07.001.
- Klepsatel, P., Gálíková, M., Xu, Y., Kühnlein, R.P., 2016. Thermal stress depletes energy reserves in *Drosophila*. *Sci. Rep.* 6, 1–12. doi:10.1038/srep33667.
- Koltz, A.M., Schmidt, N.M., Høye, T.T., 2018a. Differential arthropod responses to warming are altering the structure of Arctic communities. *Royal Soc. Open Sci.* 5, 171503. doi:10.1098/rsos.171503.
- Koltz, A.M., Classen, A.T., Wright, J.P., 2018b. Warming reverses top-down effects of predators on belowground ecosystem function in Arctic tundra. *Proc. Natl. Acad. Sci. USA* 115, E7541–E7549. doi:10.1073/pnas.1808754115.
- Koltz, A.M., Asmus, A., Gough, L., Pressler, Y., Moore, J.C., 2018c. The detritus-based microbial-invertebrate food web contributes disproportionately to carbon and nitrogen cycling in the Arctic. *Polar Biol* 41, 1531–1545. doi:10.1007/s00300-017-2201-5.
- Kovacevic, A., 2019. The effect of temperature on the physiological and behavioural responses of Collembola. Monash University, Australia PhD thesis doi:10.26180/5da5390eda13a.
- Krab, E.J., Lantman, I.M.V.S., Cornelissen, J.H.C., Berg, M.P., 2013. How extreme is an extreme climatic event to a subarctic peatland springtail community? *Soil Biol. Biochem.* 59, 16–24. doi:10.1016/j.soilbio.2012.12.012.
- Kumar, N., Shah, V., Walker, V.K., 2012. Influence of a nanoparticle mixture on an arctic soil community. *Environ. Toxicol. Chem.* 31, 131–135. doi:10.1002/etc.721.
- Kutcherov, D., Slotsbo, S., Sigurdsson, B.D., Leblans, N.I.W., Berg, M.P., Ellers, J., Mariën, J., Holmstrup, M., 2020. Temperature responses in a subarctic springtail from two geothermally warmed habitats. *Pedobiologia* 78, 150606. doi:10.1016/j.pedobi.2019.150606.
- Lee, C.K., Laughlin, D.C., Bottos, E.M., Caruso, T., Joy, K., Barrett, J.E., Brabyn, L., Nielsen, U.N., Adams, B.J., Wall, D.H., Hopkins, D.W., Pointing, S.B., McDonald, I.R., Cowan, D.A., Banks, J.C., Stichbury, G.A., Jones, I., Zawar-Reza, P., Katurji, M., Hogg, I.D., Sparrow, A.D., Storey, B.C., Green, T.G.A., Cary, S.C., 2019. Biotic interactions are an unexpected yet critical control on the complexity of an abiotically driven polar ecosystem. *Commun. Biol.* 2, 62. doi:10.1038/s42003-018-0274-5.
- J. D. Lee, J.R., Raymond, B., Bracegirdle, T.J., Chades, I., Fuller, R.A., Shaw, J.D., Terauds, A., 2017. Climate change drives expansion of Antarctic ice-free habitat. *Nature* 547, 49–54. doi:10.1038/nature22996.
- Lindberg, N., Bengtsson, J., 2005. Population responses of oribatid mites and collembolans after drought. *Appl. Soil Ecol.* 28, 163–174. doi:10.1016/j.apsoil.2004.07.003.
- Lister, A., Usher, M.B., Block, W., 1987. Description and quantification of field attack rates by predatory mites: an example using an electrophoresis method with a species of Antarctic mite. *Oecologia* 72, 185–191.
- Liu, A.W.P., Phillips, L.M., Terblanche, J.S., Janion-Scheepers, C., Chown, S.L., 2020. Strangers in a strange land: globally unusual thermal tolerance in Collembola from the Cape Floristic Region. *Funct. Ecol.* 34, 1601–1612. doi:10.1111/1365-2435.13584.
- Lynch, M., Ackerman, M.S., Gout, J., Long, H., Sung, W., Thomas, W.K., Foster, P.L., 2016. Genetic drift, selection and the evolution of the mutation rate. *Nat. Rev. Genetics* 17, 704. doi:10.1038/nrg.2016.104.
- Ma, J., Hung, H., Tian, C., Kallenborn, R., 2011. Revolatilization of persistent organic pollutants in the Arctic induced by climate change. *Nat. Clim. Change* 1, 255–260. doi:10.1038/nclimate1167.
- Makkonen, M., Berg, M.P., van Hal, J.R., Callaghan, T.V., Press, M.C., Aerts, R., 2011. Traits explain the responses of a sub-arctic Collembola community to climate manipulation. *Soil Biol. Biochem.* 43, 377–384. doi:10.1016/j.soilbio.2010.11.004.
- Malmström, A., 2012. Life-history traits predict recovery patterns in Collembola species after fire: A 10 year study. *Appl. Soil Ecol.* 56, 35–42. doi:10.1016/j.apsoil.2012.02.007.
- Marshall, K.E., Sinclair, B.J., 2012. The impacts of repeated cold exposure on insects. *J. Exp. Biol.* 215, 1607–1613. doi:10.1242/jeb.059956.
- Marshall, K.E., Gotthard, K., Williams, C.M., 2020. Evolutionary impacts of winter climate change on insects. *Curr. Opin. Insect Sci.* 41, 54–62. doi:10.1016/j.cois.2020.06.003.
- McGaughan, A., Hogg, I.D., Convey, P., 2011. Extended ecophysiological analysis of *Gomphiocephalus hodgsoni* (Collembola): flexibility in life history strategy and population response. *Polar Biol* 34, 1713–1725. doi:10.1007/s00300-011-1001-6.
- McGaughan, A., Hogg, I.D., Stevens, M.I., 2008. Patterns of population genetic structure for springtails and mites in southern Victoria Land. *Antarctica. Mol. Phylogenet. Evol.* 46, 606–618. doi:10.1016/j.ympev.2007.10.003.
- McGaughan, A., Stevens, M.I., Hogg, I.D., Carapelli, A., 2011. Extreme glacial legacies: a synthesis of the Antarctic springtail phylogeographic record. *Insects* 2, 62–82. doi:10.3390/insects2020062.
- McGaughan, A., Stevens, M.I., Holland, B.R., 2010. Biogeography of circum-Antarctic springtails. *Mol. Phylogenet. Evol.* 57, 48–58. doi:10.1016/j.ympev.2010.06.003.
- McGaughan, A., Terauds, A., Convey, P., Fraser, C.I., 2019. Genome-wide SNP data reveal improved evidence for Antarctic glacial refugia and dispersal of terrestrial invertebrates. *Mol. Ecol.* 28, 4941–4957. doi:10.1111/mec.15269.
- McGaughan, A., Torricelli, G., Carapelli, A., Frati, F., Stevens, M.I., Convey, P., Hogg, I.D., 2010. Contrasting phylogeographical patterns for springtails reflect different evolutionary histories between the Antarctic Peninsula and continental Antarctica. *J. Biogeogr.* 37, 103–119. doi:10.1111/j.1365-2699.2009.02178.x.
- McGeoch, M.A., Le Roux, P.C., Hugo, E.A., Chown, S.L., 2006. Species and community responses to short-term climate manipulation: microarthropods in the sub-Antarctic. *Austral Ecol* 31, 719–731. doi:10.1111/j.1442-9993.2006.01614.x.
- Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, A., Kofinas, G., Mackintosh, A., Melbourne-Thomas, J., Muelbert, M.M.C., Ottersen, G., 2019. Polar Regions. In: Pörtner, H.-O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegria, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N.M. (Eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. IPCC.
- Michaud, M.R., Benoit, J.B., Lopez-Martinez, G., Elnitsky, M.A., Lee Jr., R.E., Denlinger, D.L., 2008. Metabolomics reveals unique and shared metabolic changes in response to heat shock, freezing and desiccation in the Antarctic mite, *Belgica antarctica*. *J. Insect Physiol.* 54, 645–655. doi:10.1016/j.jinsphys.2008.01.003.

- Mikkelsen, N., Mikkelsen, G.H., Holmstrup, M., Jensen, J., 2019. Recovery period of *Folsomia candida* influence the impact of nonylphenol and phenanthrene on the tolerance of drought and heat shock. *Environ. Pollut.* 4, 113105. doi:10.1016/j.envpol.2019.113105.
- Monsanto, D.M., van Vuuren, B.J., Jagatap, H., Jooste, C.M., Janion-Scheepers, C., Teske, P.R., Emami-Khoyi, A., 2019. The complete mitogenome of the springtail *Cryptopygus antarcticus* travei provides evidence for speciation in the Sub-Antarctic region. *Mitochondrial DNA B* 4, 1195–1197. doi:10.1080/23802359.2019.1591219.
- Mooney, T.J., Wasley, J., Raymond, B., Andrew, N.R., King, C.K., 2019. Response of the Native Springtail *Parisetoma insularis* to Diesel Fuel-Contaminated Soils Under Field-Realistic Exposure Conditions at Subantarctic Macquarie Island. *Integr. Environ. Assess. Manag.* 15, 565–574. doi:10.1002/ieam.4148.
- Morrison, A.L., Kay, J.E., Chepfer, H., Guzman, R., Yettella, V., 2018. Isolating the liquid cloud response to recent Arctic sea ice variability using spaceborne lidar observations. *J. Geophys. Res. Atmos.* 123, 473–490. doi:10.1002/2017JD027248.
- Myers-Smith, I.H., Kerby, J.T., Phoenix, G.K., Bjerke, J.W., Epstein, H.E., Assmann, J.J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P.S.A., 2020. Complexity revealed in the greening of the Arctic. *Nat. Clim. Change* 10, 106–117. doi:10.1038/s41558-019-0688-1.
- Myers-Smith, I.H., Grabowski, M.M., Thomas, H.J.D., Angers-Blondin, S., Daskalova, G.N., Bjorkman, A.D., Cunliffe, A.M., Assmann, J.J., Boyle, J.S., McLeod, E., 2019. Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change. *Ecol. Monogr.* 89, e01351. doi:10.1002/ecm.1351.
- Nakamori, T., Fujimori, A., Kinoshita, K., Ban-nai, T., Kubota, Y., Yoshida, S., 2010. mRNA expression of a cadmium-responsive gene is a sensitive biomarker of cadmium exposure in the soil collembolan *Folsomia candida*. *Environ. Pollut.* 158, 1689–1695. doi:10.1016/j.envpol.2009.11.022.
- Newman, J., Poirot, C., Roper-Gee, R., Leihy, R.I., Chown, S.L., 2018. A decade of invertebrate colonization pressure on Scott Base in the Ross Sea region. *Biol. Invas.* 20, 2623–2633. doi:10.1007/s10530-018-1722-3.
- Nielsen, U.N., Wall, D.H., 2013. The future of soil invertebrate communities in polar regions: different climate change responses in the Arctic and Antarctic? *Ecol. Lett.* 16, 409–419. doi:10.1111/ele.12058.
- Nimmo, D.G., MacNally, R., Cunningham, S.C., Haslem, A., Bennett, A.F., 2015. Vive la resistance: reviving resistance for 21st century conservation. *Trends Ecol. Evol.* 30, 516–523. doi:10.1016/j.tree.2015.07.008.
- Nolan, L., Hogg, I.D., Stevens, M.I., Haase, M., 2006. Fine scale distribution of mtDNA haplotypes for the springtail *Gomphiocephalus hodgsoni* (Collembola) corresponds to an ancient shoreline in Taylor Valley, continental Antarctica. *Polar Biol* 29, 813–819. doi:10.1007/s00300-006-0119-4.
- Obbard, R.W., 2018. Microplastics in polar regions: the role of long range transport. *Curr. Opin. Environ. Sci. Health* 1, 24–29. doi:10.1016/j.coesh.2017.10.004.
- Obrist, D., Agnan, Y., Jiskra, M., Olson, C.L., Colegrove, D.P., Hueber, J., Moore, C.W., Sonke, J.E., Helmig, D., 2017. Tundra uptake of atmospheric elemental mercury drives Arctic mercury pollution. *Nature* 547, 201–204. doi:10.1038/nature22997.
- Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., Proenca, V., Raffaelli, D., Suttle, K.B., Mace, G.M., Martin-Lopez, B., Woodcock, B.A., Bullock, J.M., 2015. Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.* 30, 673–684. doi:10.1016/j.tree.2015.08.009.
- Parnikoza, I., Convey, P., Dykyy, I., Trokhymets, V., Milinevsky, G., Tyschenko, O., Inozemtseva, D., Kozaretska, I., 2009. Current status of the Antarctic herb tundra formation in the Central Argentine Islands. *Glob. Chang. Biol.* 15, 1685–1693.
- Pauli, J.N., Zunkerberg, B., Whiteman, J.P., Porter, W., 2013. The subnivium: a deteriorating seasonal refugium. *Front. Ecol. Environ.* 11, 260–267. doi:10.1890/12022.
- Peng, X., Zhang, T., Frauenfeld, O.W., Wang, S., Qiao, L., Du, R., Mu, C., 2020. Northern Hemisphere greening in association with warming permafrost. *J. Geophys. Res.: Biogeosci.* 125, e2019JG005086. doi:10.1029/2019JG005086.
- Pentinsaari, M., Blagoev, G.A., Hogg, I.D., Levesque-Beaudin, V., Perez, K., Sobel, C.N., Vandenbrink, B., Borisenko, A., 2020. A DNA barcoding survey of an Arctic arthropod community: implications for future monitoring. *Insects* 11, 46. doi:10.3390/insects11010046.
- Peterson, A.J., 1971. Population studies on the Antarctic collembolan *Gomphiocephalus hodgsoni* Carpenter. *Pac. Insects Monogr.* 25, 75–98.
- Phillips, L., Janion-Scheepers, C., Houghton, M., Terauds, A., Potapov, M., Chown, S.L., 2017. Range expansion of two invasive springtails on sub-Antarctic Macquarie Island. *Polar Biol* 40, 2137–2142. doi:10.1007/s00300-017-2129-9.
- Phillips, L.M., Aitkenhead, I., Janion-Scheepers, C., King, C.K., McGeoch, M.A., Nielsen, U.N., Terauds, A., Liu, W.P.A., Chown, S.L., 2020. Basal tolerance but not plasticity gives invasive springtails the advantage in an assemblage setting. *Conserv. Physiol.* 8, coaa049. doi:10.1093/conphys/coaa049.
- Ponge, J.F., 2000. Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. *Biol. Fert. Soils* 32, 508–522. doi:10.1007/s003740000285.
- Ponge, J.F., Gillet, S., Dubs, F., Fédoroff, E., Haese, L., Sousa, J.P., Lavelle, P., 2003. Collembolan communities as bioindicators of land use intensification. *Soil Biol. Biochem.* 35. doi:10.1016/S0038-0717(03)00108-1.
- Porco, D., Skarzynski, D., Decaens, T., Hebert, P.D.N., Deharveng, L., 2014. Barcoding the Collembola of Churchill: a molecular taxonomic reassessment of species diversity in a sub-Arctic area. *Mol. Ecol. Resour.* 14, 249–261. doi:10.1111/1755-0998.12172.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., Aastrup, P., 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325, 1355–1358. doi:10.1126/science.1173113.
- Pugh, P.J.A., Convey, P., 2008. Surviving out in the cold: Antarctic endemic invertebrates and their refugia. *J. Biogeogr.* 35, 2176–2186. doi:10.1111/j.1365-2699.2008.01953.x.
- Rudnicka-Kępa, P., Zaborska, A., 2021. Sources, fate and distribution of inorganic contaminants in the Svalbard area, representative of a typical Arctic critical environment—a review. *Environ. Monit. Assess.* 193, 1–25. doi:10.1007/s10661-021-09305-6.
- Ruiz, G.M., Hewitt, C., 2009. Latitudinal patterns of biological invasions in marine ecosystems: a polar perspective. In: Krupnik, I., Lang, M.A., Miller, S.E. (Eds.), *Smithsonian at the poles: contributions to International Polar Year science*. Smithsonian Institution Scholarly Press, Washington, DC, pp. 347–358.
- Rusek, J., 1998. Biodiversity of Collembola and their functional role in the ecosystem. *Biodiv. Conserv.* 7, 1207–1219. doi:10.1023/A:1008887817883.
- Schacht, J., Heinold, B., Quaas, J., Backman, J., Cherian, R., Ehrlich, A., Herber, A., Huang, W.T.K., Kondo, Y., Massling, A., 2019. The importance of the representation of air pollution emissions for the modeled distribution and radiative effects of black carbon in the Arctic. *Atmos. Chem. Phys.* 19, 11159–11183. doi:10.5194/acp-19-11159-2019.
- Schmidt, N.M., Rieneckens, J., Christensen, J.H., Olesen, M., Roslin, T., 2019. An ecosystem-wide reproductive failure with more snow in the Arctic. *PLoS Biol* 17, e3000392. doi:10.1371/journal.pbio.3000392.
- Scott, M.B., Dickinson, K.J.M., Barratt, B.I.P., Sinclair, B.J., 2008. Temperature and moisture trends in non-sorted earth hummocks and stripes on the Old Man Range, New Zealand: implications for mechanisms of maintenance. *Permafrost. Periglac. Proc.* 19, 305–314. doi:10.1002/ppp.627.
- Sengupta, S., Ergon, T., Leinaas, H.P., 2017. Thermal plasticity in postembryonic life history traits of a widely distributed Collembola: Effects of macroclimate and microhabitat on genotypic differences. *Ecol. Evol.* 7, 8100–8112. doi:10.1002/ece3.3333.
- Sengupta, S., Ergon, T., Leinaas, H.P., 2016. Genotypic differences in embryonic life history traits of *Folsomia quadrioculata* (Collembola: Isotomidae) across a wide geographical range. *Ecol. Entomol.* 41, 72–84. doi:10.1111/een.12270.
- Siebert, M.J., Rumble, J., Atkinson, A., Rogelj, J., Edwards, T., Davies, B.J., Banwell, A., Hubbard, B., Brandon, M., Stroeve, J., 2019. The Antarctic Peninsula under a 1.5°C global warming scenario. *Front. Environ. Sci.* 7, 102. doi:10.3389/fenvs.2019.00102.
- Sinclair, B.J., Coello Alvarado, L.E., Ferguson, L.V., 2015. An invitation to measure insect cold tolerance: Methods, approaches, and workflow. *J. Therm. Biol.* 53, 180–197. doi:10.1016/j.jtherbio.2015.11.003.
- Sinclair, B.J., Klok, C.J., Scott, M.B., Terblanche, J.S., Chown, S.L., 2003. Diurnal variation in supercooling points of three species of Collembola from Cape Hallett. *Antarctica. J. Insect Physiol.* 49, 1049–1061. doi:10.1016/j.jinsphys.2003.08.002.
- Sinclair, B.J., Terblanche, J.S., Scott, M.B., Blatch, G.L., Klok, C.J., Chown, S.L., 2006b. Environmental physiology of three species of Collembola at Cape Hallett, North Victoria Land. *Antarctica. J. Insect Physiol.* 52, 29–50. doi:10.1016/j.jinsphys.2005.09.002.
- Sinclair, B.J., Ferguson, L.V., Salehipour-shirazi, G., MacMillan, H.A., 2013. Cross-tolerance and cross-talk in the cold: relating low temperatures to desiccation and immune stress in insects. *Integr. Comp. Biol.* 53, 545–556. doi:10.1093/icb/ict004.
- Sinclair, B.J., Scott, M.B., Klok, C.J., Terblanche, J.S., Marshall, D.J., Reyers, B., Chown, S.L., 2006a. Determinants of terrestrial arthropod community composition at Cape Hallett. *Antarctica. Antarct. Sci.* 18, 303–312. doi:10.1017/S0954102006000356.
- Sinclair, B.J., Sjursen, H., 2001a. Cold tolerance of the Antarctic springtail *Gomphiocephalus hodgsoni* (Collembola, Hypogastruridae). *Antarct. Sci.* 13, 271–279. doi:10.1017/S0954102001000384.
- Sinclair, B.J., Sjursen, H., 2001b. Terrestrial invertebrate abundance across a habitat transect in Keble Valley, Ross Island, Antarctica. *Pedobiologia* 45, 134–145. doi:10.1078/0031-4056-00075.
- Sinclair, B.J., Stevens, M.L., 2006. Terrestrial microarthropods of Victoria Land and Queen Maud Mountains, Antarctica: Implications of climate change. *Soil Biol. Biochem.* 38, 3158–3170. doi:10.1016/j.soilbio.2005.11.035.
- Sjursen, H., Sverdrup, L.E., Krogh, P.H., 2001. Effects of polycyclic aromatic compounds on the drought tolerance of *Folsomia fimetaria* (Collembola, Isotomidae). *Environ. Toxicol. Chem.* 20, 2899–2902. doi:10.1002/etc.56202012133.
- Slabber, S., Worland, M.R., Leinaas, H.P., Chown, S.L., 2007. Acclimation effects on thermal tolerances of springtails from sub-Antarctic Marion Island: indigenous and invasive species. *J. Insect Physiol.* 53, 113–125. doi:10.1016/j.jinsphys.2006.10.010.
- Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine winners and losers. *J. Exp. Biol.* 213, 912–920. doi:10.1242/jeb.037473.
- Sømme, L., 1999. Cold adaptations in terrestrial invertebrates. In: Margesin, R., Schinner, F. (Eds.), *Cold-Adapted Organisms*. Springer, Berlin, pp. 137–164.
- Sømme, L., 1986. Ecology of *Cryptopygus sverdrupi* (Insecta: Collembola) from Dronning Maud Land. *Antarctica. Polar Biol.* 6, 179–184.
- Sørensen, J.G., Holmstrup, M., 2011. Cryoprotective dehydration is widespread in Arctic springtails. *J. Insect Physiol.* 57, 1147–1153. doi:10.1016/j.jinsphys.2011.03.001.
- Sørensen, J.G., Holmstrup, M., 2013. Candidate gene expression associated with geographical variation in cryoprotective dehydration of *Megaphorura arctica*. *J. Insect Physiol.* 59, 804–811. doi:10.1016/j.jinsphys.2013.05.007.
- Sørensen, T.S., Holmstrup, M., 2005. A comparative analysis of the toxicity of eight common soil contaminants and their effects on drought tolerance in the collembolan *Folsomia candida*. *Ecotoxicol. Environ. Saf.* 60, 132–139. doi:10.1016/j.ecoenv.2004.02.001.
- Stevens, M.I., Hogg, I.D., 2003. Long-term isolation and recent range expansion from glacial refugia revealed for the endemic springtail *Gomphiocephalus hodgsoni* from Victoria Land. *Antarctica. Mol. Ecol.* 12, 2357–2369. doi:10.1046/j.1365-294X.2003.01907.x.

- Stevens, M.I., DHaese, C.A.D., 2014. Islands in ice: isolated populations of *Cryptopygus sverdrupi* (Collembola) among nunataks in the Sør Rondane Mountains, Dronning Maud Land, Antarctica. *Biodiversity* 15, 169–177. doi:10.1080/14888386.2014.928791.
- Stevens, M.I., Frati, F., McGaughran, A., Spinsanti, G., Hogg, I.D., 2007. Phylogeographic structure suggests multiple glacial refugia in northern Victoria Land for the endemic Antarctic springtail *Desoria klovetadi* (Collembola, Isotomidae). *Zool. Scr.* 36, 201–212. doi:10.1111/j.1463-6409.2006.00271.x.
- Stevens, M.I., Hogg, I.D., 2002. Expanded distributional records of Collembola and Acari in southern Victoria Land, Antarctica. *Pedobiologia* 46, 485–495. doi:10.1078/0031-4056-00154.
- Stewart, K.J., Grogan, P., Coxson, D.S., Siciliano, S.D., 2014. Topography as a key factor driving atmospheric nitrogen exchanges in arctic terrestrial ecosystems. *Soil Biol. Biochem.* 70, 96–112. doi:10.1016/j.soilbio.2013.12.005.
- Strandtmann, R.W., 1967. Terrestrial Prostigmata (trombidiform mites). *Antarct. Res. Ser.* 10, 51–80.
- Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey, R.B., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl. Acad. Sci. USA* 111, 5610–5615. doi:10.1073/pnas.1316145111.
- Sung, W., Ackerman, M.S., Miller, S.F., Doak, T.G., Lynch, M., 2012. Drift-barrier hypothesis and mutation-rate evolution. *Proc. Natl. Acad. Sci. USA* 109, 18488–18492. doi:10.1073/pnas.1216223109.
- Sweeney, B.W., Vannote, R.L., 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* 200, 444–446.
- Swindell, W.R., Bouzat, J.L., 2006. Gene flow and adaptive potential in *Drosophila melanogaster*. *Conserv. Genet.* 7, 79–89. doi:10.1007/s10592-005-8223-5.
- Szabó, B., Lang, Z., Bakonyi, G., Mariën, J., Roelofs, D., van Gestel, C.A.M., Seres, A., 2019. Transgenerational and multigenerational stress gene responses to the insecticide etofenprox in *Folsomia candida* (Collembola). *Ecotoxicol. Environ. Saf.* 175, 181–191. doi:10.1016/j.ecoenv.2019.03.052.
- Teets, N.M., Denlinger, D.L., 2013. Physiological mechanisms of seasonal and rapid cold-hardening in insects. *Physiol. Entomol.* 38, 105–116. doi:10.1111/phen.12019.
- Thakur, M.P., Künne, T., Griffin, J.N., Eisenhauer, N., 2017. Warming magnifies predation and reduces prey coexistence in a model litter arthropod system. *Proc. R. Soc. B* 284, 20162570. doi:10.1098/rspb.2016.2570.
- Thomas, J.A., Welch, J.J., Lanfear, R., Bromham, L., 2010. A generation time effect on the rate of molecular evolution in invertebrates. *Mol. Biol. Evol.* 27, 1173–1180. doi:10.1093/molbev/msq009.
- Tiusanen, M., Huotari, T., Hebert, P.D.N., Andersson, T., Asmus, A., Bêty, J., Davis, E., Gale, J., Hardwick, B., Hik, D., 2019. Flower-visitor communities of an arcto-alpine plant - Global patterns in species richness, phylogenetic diversity and ecological functioning. *Mol. Ecol.* 28, 318–335. doi:10.1111/mec.14932.
- Todgham, A.E., Stillman, J.H., 2013. Physiological responses to shifts in multiple environmental stressors: relevance in a changing world. *Integr. Comp. Biol.* 53, 539–544. doi:10.1093/icb/ict086.
- Torricelli, G., Frati, F., Convey, P., Telford, M., Carapelli, A., 2010. Population structure of *Friesea grisea* (Collembola, Neanuridae) in the Antarctic Peninsula and Victoria Land: evidence for local genetic differentiation of pre-Pleistocene origin. *Antarct. Sci.* 22, 757–765. doi:10.1017/S0954102010000775.
- Urbanowicz, C., Virginia, R.A., Irwin, R.E., 2018. Pollen limitation and reproduction of three plant species across a temperature gradient in western Greenland. *Arct. Antarct. Alp. Res.* 50, S100022. doi:10.1080/15230430.2017.1414485.
- Vega, G.C., Convey, P., Hughes, K.A., Olalla-Tárraga, M.A., 2020. Humans and wind, shaping Antarctic soil arthropod biodiversity. *Insect Conserv. Div.* 13, 63–76. doi:10.1111/icad.12375.
- Velasco-Castrillón, A., Gibson, J.A.E., Stevens, M.I., 2014. A review of current Antarctic limno-terrestrial microfauna. *Polar Biol* 37, 1517–1531. doi:10.1007/s00300-014-1544-4.
- Verberk, W.C.E.P., Atkinson, D., Hoefnagel, K.N., Hirst, A.G., Horne, C.R., Siepel, H., 2021. Shrinking body sizes in response to warming: explanations for the temperature-size rule with special emphasis on the role of oxygen. *Biol. Rev.* 96, 247–268. doi:10.1111/brv.12653.
- Wackett, A.A., Yoo, K., Olofsson, J., Klaminder, J., 2018. Human-mediated introduction of geoengineering earthworms in the Fennoscandian arctic. *Biol. Invas.* 20, 1377–1386. doi:10.1007/s10530-017-1642-7.
- Wardle, D.A., Bardgett, R.D., John N 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. doi:10.1126/science.1094875.
- Widenfalk, L.A., Leinaas, H.P., Bengtsson, J., Birkemoe, T., 2018. Age and level of self-organization affect the small-scale distribution of springtails (Collembola). *Ecosphere* 9, e02058. doi:10.1002/ecs2.2058.
- Williams, C.M., Henry, H.A.L., Sinclair, B.J., 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biol. Rev.* 90, 214–235. doi:10.1111/brv.12105.
- Wirta, H.K., Vesterinen, E.J., Hambäck, P.A., Weingartner, E., Rasmussen, C., Reineken, J., Schmidt, N.M., Gilg, O., Roslin, T., 2015. Exposing the structure of an Arctic food web. *Ecol. Evol.* 5, 3842–3856. doi:10.1002/ece3.1647.
- Wise, K.A.J., 1967. Collembola (Springtails). *Antarct. Res. Ser.* 10, 123–148.
- Wise, K.A.J., 1971. The Collembola of Antarctica. *Pac. Insects Monogr.* 25, 57–74.
- Worland, M.R., 2005. Factors that influence freezing in the sub-Antarctic springtail *Tullbergia antarctica*. *J. Insect Physiol.* 51, 881–894. doi:10.1016/j.jinsphys.2005.04.004.
- Worland, M.R., Block, W., 2003. Desiccation stress at sub-zero temperatures in polar terrestrial arthropods. *J. Insect Physiol.* 49, 193–203. doi:10.1016/S0022-1910(02)00264-0.
- Worland, M.R., 1996. The relationship between water content and cold tolerance in the Arctic collembolan *Onychiurus arcticus* (Collembola: Onychiuridae). *Eur. J. Entomol.* 93, 341–348.
- Worland, M.R., Convey, P., 2001. Rapid cold hardening in Antarctic microarthropods. *Funct. Ecol.* 15, 515–524. www.jstor.org/stable/826673.
- Worland, M.R., Grubor-Lajsic, G., Montiel, P.O., 1998. Partial desiccation induced by sub-zero temperatures as a component of the survival strategy of the Arctic collembolan *Onychiurus arcticus* (Tullberg) *J. Insect Physiol.* 44, 211–219.
- Worland, M.R., Leinaas, H.P., Chown, S.L., 2006. Supercooling point frequency distributions in Collembola are affected by moulting. *Funct. Ecol.* 20, 323–329. www.jstor.org/stable/3806567.
- Yang, Z., Fang, W., Lu, X., Sheng, G.P., Graham, D.E., Liang, L., Stan D Wullschlegler, S.D., Gu, B., 2016. Warming increases methylmercury production in an Arctic soil. *Environ. Pollut.* 214, 504–509. doi:10.1016/j.envpol.2016.04.069.
- Zizzari, Z.V., Eilers, J., 2011. Effects of exposure to short-term heat stress on male reproductive fitness in a soil arthropod. *J. Insect Physiol.* 57, 421–426. doi:10.1016/j.jinsphys.2011.01.002.
- Zizzari, Z.V., Eilers, J., 2014. Rapid shift in thermal resistance between generations through maternal heat exposure. *Oikos* 123, 1365–1370. doi:10.1111/oik.01496.
- Zortéa, T., Baretta, D., Maccari, A.P., Segat, J.C., Boiago, E.S., Sousa, J.P., Da Silva, A.S., 2015. Influence of cypermethrin on avoidance behavior, survival and reproduction of *Folsomia candida* in soil. *Chemosphere* 122, 94–98. doi:10.1016/j.chemosphere.2014.11.018.