The Resilience of Polar Collembola to Climate Change

A thesis

Submitted in partial fulfilment

of the requirements for the degree

of

Doctor of Philosophy

at

The University of Waikato

by

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THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2023

“The more I learn, the more I realize how much I don't know.”

-Albert Einstein

Thesis Abstract

Polar Collembola have adapted over millions of years to an environment that is changing faster than any other on earth. Globally, Collembola (springtails) are among the most abundant and widely-distributed arthropods and are key components of species-poor polar ecosystems. Understanding the resilience of polar collembola to climate change is therefore an urgent research priority. Here we explore the links between genetic diversity and physiology in shaping the resilience of polar Collembola to climate change.

I have reviewed the resilience of polar Collembola considering genetic diversity, behavioural avoidance and physiological tolerances along with an examination of the potential impacts of biotic interactions. I also explored potential recovery dynamics with reference to temperate taxa and colonisation patterns of new habitat exposed by glacial retreat. This review illustrated that polar Collembola exhibit a suite of traits that have enabled their survival in extreme conditions and may serve as pre-adaptations to changing conditions. However, if resistance capacities are insufficient, complete community level recovery following disturbances is exceedingly slow, especially among Collembola that inhabit deeper microhabitats within the soil column (deeper-dwelling). Overall, it appears that deeper-dwelling species that fail to resist climate changes may not recover in ecologically realistic timescales, especially given the projected pace of climate changes.

The largest spatial scale study and analysis of the genetic diversity of Collembola from the central Canadian High Arctic location of Cambridge Bay (Ikaluktuktiak) was undertaken to refine species identifications, examine levels of population diversity, and explore the role of geological processes and glacial dynamics in shaping the current Arctic collembolan fauna. I identified 68 Barcode Index Numbers (BINs, as a proxy for species diversity) representing an estimated 43 morphological species, with 29 BINs unique to Cambridge Bay. The geographic linkages between populations across the High Arctic supported hypothesised east to west dispersal patterns in accordance with prevailing ocean currents.

The physiology of five of the most abundant surface-active species from the Canadian High Arctic was explored to determine how resistant local species are likely to be to rising temperatures and increasing drought pressure. Some individuals were found to exhibit remarkably high heat tolerances (>40 °C) with only limited cold tolerance capacities (64 %

had supercooling points higher than -10 °C). Survival rates in response to a desiccation stress were also variable among individuals (range: 1.0-13.5 hrs). This indicated that Arctic Collembola may be pre-adapted to a level of climate warming.

I also explored the specific relationship between two populations of the Antarctic collembolan *Gomphiocephalus hodgsoni* found in the largest ice-free area in continental Antarctica, McMurdo Dry Valleys. I tested whether the genetic variation found between coastal and inland individuals of *G. hodgsoni* corresponded with differences in physiological tolerances of hot and cold temperatures was tested. Individuals from the population nearest the warmer coastal site had higher upper thermal limits (mean CT_{max} 31.3 °C) compared to individuals from the more inland population (mean CT_{max} 27.2 °C). However, these differences in heat tolerance weren't significant until accounting for microhabitat temperature at time of collection (site + microhabitat at time of collection, $p=0.0029$). Coastal individuals also had higher mean supercooling points (coastal: -14.3 °C; inland: -22.6 °C, $p=0.011$). Under climate change associated warming warm-adapted populations may have a selective advantage relative to more cold adapted individuals, leading to changes in population genetic structure, a decline in genetic diversity, and associated decline in resilience.

Collectively my thesis chapters have identified that the biggest threats to the ongoing survival of polar Collembola are sustained heat stress, desiccation stress, changing biotic interactions, and the arrival and spread of invasive species. Despite this, polar Collembola exhibit considerable levels of genetic diversity and physiological tolerances that may make them pre-adapted to climate change induced environmental changes.

Acknowledgements

Few have been as lucky as I to visit both poles within a single year. I cannot thank my supervisors enough for the incredible opportunities I have been afforded – including camping next to a penguin colony, and flying over the Arctic tundra in a sea-plane. I would like to thank Craig Cary for offering me the opportunity to undertake this PhD, Ian McDonald for always responding quickly to emails and providing useful feedback. I'd like to thank Brent Sinclair for letting me borrow his field physiology device, teaching me a whole new way to study Collembola and for always providing constructive (if sometimes brutal feedback) that helped improve my writing immensely. Finally, thank you to Ian Hogg who started me on this journey years ago with a late-night email asking if I wanted to go to Antarctica. You have helped guide me along the way for the better part of the past 10 years, I wouldn't have finished this PhD without you. Thank you to the two PhD reviewers whose comments helped improve this thesis substantially.

I would not have been able to do this research without the financial assistance from the Waikato Doctoral Scholarship. Financial support for the Antarctic portion of this PhD was provided through funding from the New Zealand Antarctic Research Institute to IDH; New Zealand Ministry of Business Industry and Employment Contract UOWX1401 to SCC, IDH, IRM. Antarctic fieldwork would not have been possible without logistic support from Antarctica New Zealand. Thank you to my Antarctic field team Charlie Lee, Andrew Barnes and Claudia Colesie. The Arctic portion of this PhD was supported by a Polar Knowledge Canada Contract 3Y004-210046 to BJS with logistic support through the Canadian High Arctic Research Station (CHARS) campus. I had an amazing time in Ikaluktuktiak meeting fellow researchers and getting amongst the community. A particular thank you to Danielle Nowosad for helping with fieldwork.

I'd like to thank my friends who supported and inspired along the way, including all my fellow TRU students. There's nothing like having friends along for the same ride. I'd really like to thank everyone in the TRU lab, especially Roanna for always keeping the ships running on time. Throughout this process I have learnt so much, not only about polar Collembola, but myself. Most of all, I'd like to thank my family for always providing a peaceful safe haven I could escape to. Lastly, I could not have done this thesis without the unwavering support of my partner Brady who carried our little family financially, I know this PhD took a toll on you as well, I love you.

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CHAPTER I

Thesis Introduction

Climate change is likely to transform soil ecosystems, particularly across polar regions, parts of which are warming faster than anywhere else on earth (Meredith et al. 2019, Clem et al. 2020, Masson-Delmotte et al. 2021). Climate change is already starting to have visible impacts on polar ecosystems (Hodkinson et al. 2013, Koltz et al. 2018, Høye et al. 2021). Indigenous peoples have observed the arrival of winged beetles in Unalakleet (Alaska) and changing emergence patterns with black flies appearing before mosquitoes on the Kola Peninsula (Hodkinson et al. 2013). In the Antarctic, ice-free areas are expanding and the likelihood of invasive species establishing is increasing (Lee et al. 2017, Duffy and Lee 2019, Hughes et al. 2020). It is therefore an urgent research priority to predict how resilient different populations, species and ecosystems will be to climate change (Kellermann and van Heerwaarden 2019). However, predicting levels of resilience requires extensive underlying knowledge about intrinsic resistance traits such as genetic diversity, physiological tolerances and behavioural avoidance along with the capacity for recovery which is generally influenced by life-history traits (Somero 2010, Beet et al. 2022, Chapter II). Although there are some examples where we have both genetic and physiological information across a species' geographic range (Kitano et al. 2012, Sengupta et al. 2017, Harada et al. 2019, Pruisscher et al. 2022), we are a long way from making robust predictions, or even general pronouncements, about the structure of resilience in natural populations.

Collembola are among the most abundant and widely distributed soil arthropods, found in an array of extreme habitats from the seashore (Imms 1906) to the upper reaches of the Himalayas (Yossi 1966) and the deserts of Namibia (Collins et al. 2019a) with densities in some cases exceeding 10^5 per m^2 (Reddy and Alfred 1989). Collembola are found in both polar regions and every continent in between (Hopkin 1997). However, they play a larger relative role in polar ecosystems that are otherwise species-poor (Hogg et al. 2014). Polar Collembola play critical roles in soil food-webs and decomposition processes in addition to serving as prey for mites and spiders (Danks 1990, Krab et al. 2013, Hogg et al. 2014). Collembola have long been considered indicators of environmental change (Danks 1992, Hopkin 1997, Ponge et al. 2003), and are recognised bioindicators of overall soil health

(Greenslade 2007, Nakamori et al. 2010). It is therefore critical that we address gaps in baseline knowledge of intrinsic resistance traits and overall resilience of extant polar Collembola before they are irrevocably transformed. Understanding the resilience of this globally important fauna in dynamic and rapidly changing environments could provide early indications of the likely impacts of climate change on polar ecosystems.

Antarctica is a desert continent that has been isolated for the past 28 million years by the circum-polar current which has prevented all but sporadic dispersal events (Sinclair and Stevens 2006, Pugh and Convey 2008). Consequently, the terrestrial Antarctic fauna is highly endemic and species-poor with Collembola representing the largest permanent terrestrial animals on the continent (Strandtmann 1967, Wise 1967, Wise 1971). By comparison, the Arctic is a tundra landscape that 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 and Coulson 2004, Hodkinson et al. 2013). Accordingly, the Antarctic presents opportunities to investigate the fine-scale genetic diversity of old endemic species that are highly adapted to local conditions; while the Arctic presents ecosystems with much higher levels of diversity, low levels of endemism, frequent Holarctic distributional patterns and the complicating effects of widespread biotic interactions.

Globally there are over 8,000 described species of Collembola, although true diversity is estimated to be over 65,000 species (Hammond 1994, Deharveng 2004, Porco et al. 2012). A large portion of the disparity between described and estimated species is the lack of taxonomic specialists. DNA barcoding presents a valuable tool to help overcome this taxonomic impediment (Porco et al. 2012). DNA barcoding employs a standardised 658 base-pair sequence fragment of the highly variable mitochondrial cytochrome c oxidase subunit I (*COI*) gene (Hebert et al. 2003). DNA barcoding allows for insights into not only current levels of diversity and the spatial distribution of that diversity but the history of a species or population and the geological processes that have shaped it (McGaughran et al. 2010b, Ávila-Jiménez and Coulson 2011, Collins et al. 2020). Several studies have also demonstrated that diversity within the *COI* gene is indicative of diversity across the wider genome (Stevens and Hogg 2003, McGaughran et al. 2019, Monsanto et al. 2019). Improving our understanding of genetic diversity and the geographic structure of that diversity enables better predictions of resistance capacities and the intrinsic potential for rapid adaptation (Somero 2010). However, much of the Arctic Collembola fauna has not been sampled, with levels of genetic diversity largely unknown. By comparison, the Antarctic fauna has been better sampled although the relationships between populations remain less understood in addition to the interactions between genetic diversity and physiological tolerances (Collins et al. 2019b).

Collembola are ectotherms with body temperatures that largely track that of their environment, making them particularly vulnerable to temperature changes (Sinclair et al. 2015). Understanding how physiologically adapted individuals are to changing environmental conditions is thus a direct measure of their resistance capacity and a critical contributor to their overall resilience (Somero 2010, Nimmo et al. 2015). The success of Collembola in hostile polar environments is an outcome of evolutionary processes and physiological plasticity over a range of timescales (Sinclair et al. 2003, Sinclair et al. 2006b, Everatt et al. 2013b). Determining how resistant polar Collembola will be to climate change requires an assessment of their capacity to avoid stressors, how close their physiological limits are to current environmental conditions and extremes (e.g. thermal safety margins) along with consideration of how environmental stressors may be altered by climate change (Somero 2010, Sunday et al. 2014). Physiological studies on polar Collembola have been restricted to a few species, with a focus on cold tolerance, limiting our ability to predict the tolerances of a broader range of species and populations to increasing heat and drought stress (Worland and Convey 2008, Sørensen and Holmstrup 2011, Holmstrup 2018). Improving our understanding of heat tolerances and drought resistance across a broader range of species and populations is critical to better understanding the resistance potential of polar Collembola to climate change.

Here I explore the links between genetic diversity and physiology in shaping the potential resilience of polar Collembola to climate change. In the first research chapter (Chapter II), I review current knowledge of resilience for polar Collembola, including: genetic diversity, behavioural avoidance and physiological tolerances along with an examination of the potential for biotic interactions to modulate response. I also cover potential recovery dynamics with reference to temperate examples and colonisation patterns of new habitat exposed by glacial retreat. In the second research chapter (Chapter III), I examine the genetic diversity of Collembola from the Canadian Arctic to refine species identifications, analyse levels of genetic diversity within populations and explore the geographic links between habitats and the role of geological processes in shaping the current fauna. In the third research chapter (Chapter IV), I examined the physiology (heat, cold, desiccation tolerance) of five species from the Canadian Arctic to determine how resistant local species are likely to be to increasingly variable and extreme temperatures along with increasing drought stress. In the fourth chapter (Chapter V), I examined the specific relationship between genetics and physiology for two populations of the Antarctic collembolan *Gomphiocephalus hodgsoni* found in the largest ice-free area in continental Antarctica, the McMurdo Dry Valleys. The two populations were isolated to opposite ends of a single valley by a large paleo-glacial lake which shaped both the genetic diversity and thermal physiology of the two closely related yet genetically distinct populations. In the final chapter (Chapter VI), I provide a synthesis of the findings of the aforementioned chapters and highlight several important avenues for future research.

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CHAPTER II

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

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* Published as: Beet, C. R., I. D. Hogg, S. C. Cary, I. R. McDonald, and B. J. Sinclair. 2022. The Resilience of Polar Collembola (Springtails) in a Changing Climate. Current Research in Insect Science:100046. https://doi.org/10.1016/j.cris.2022.100046

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.

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

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.

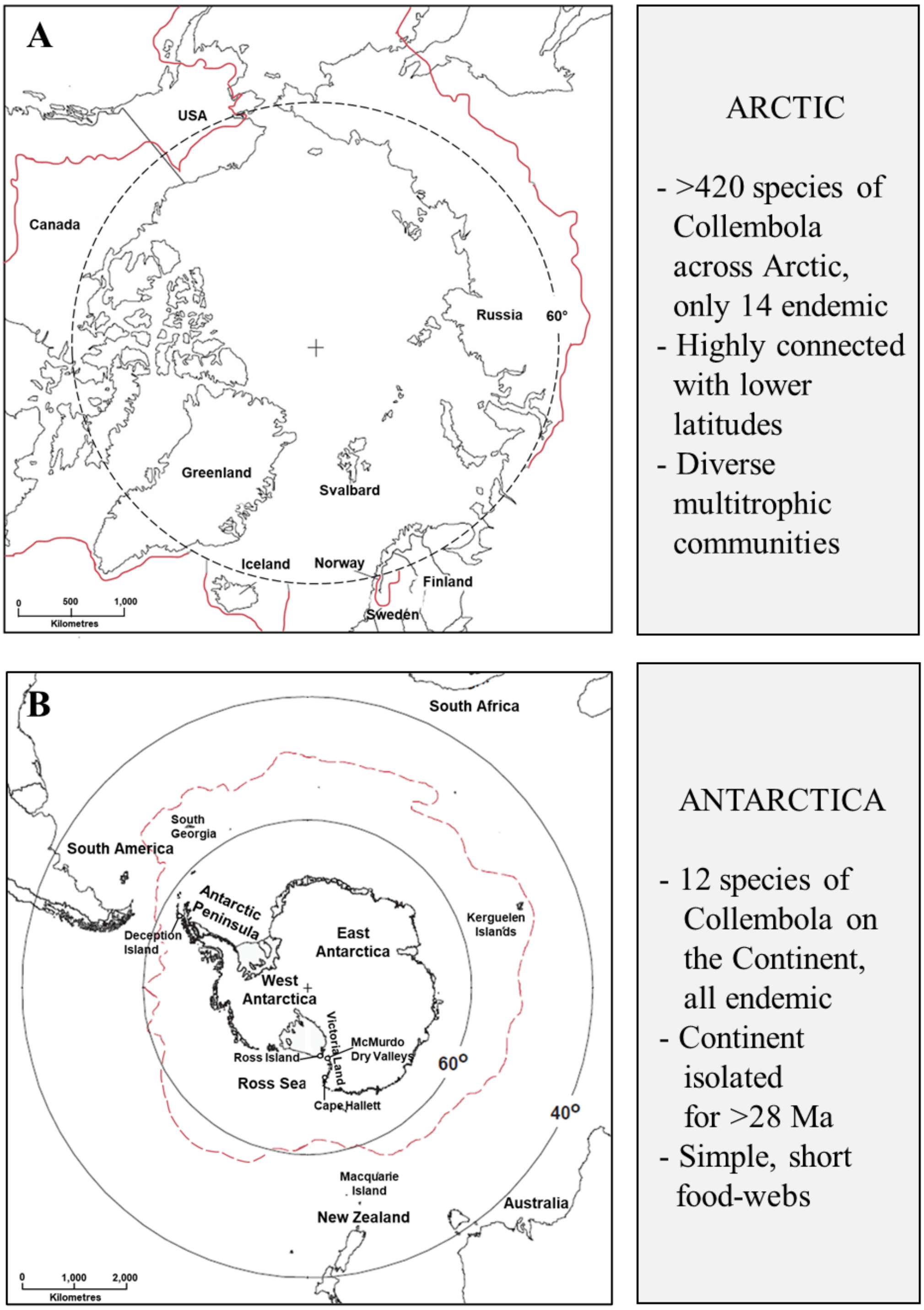
Climate change is primarily a press perturbation (sensu Bender et al., 1984) and will result in a suite of potentially interacting stressors (Fig. 3). ‘Resilience’ is narrowly defined as the product of a species’ ability to survive (its resistance) and its ability to recover from perturbation (see Box 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).

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



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**).

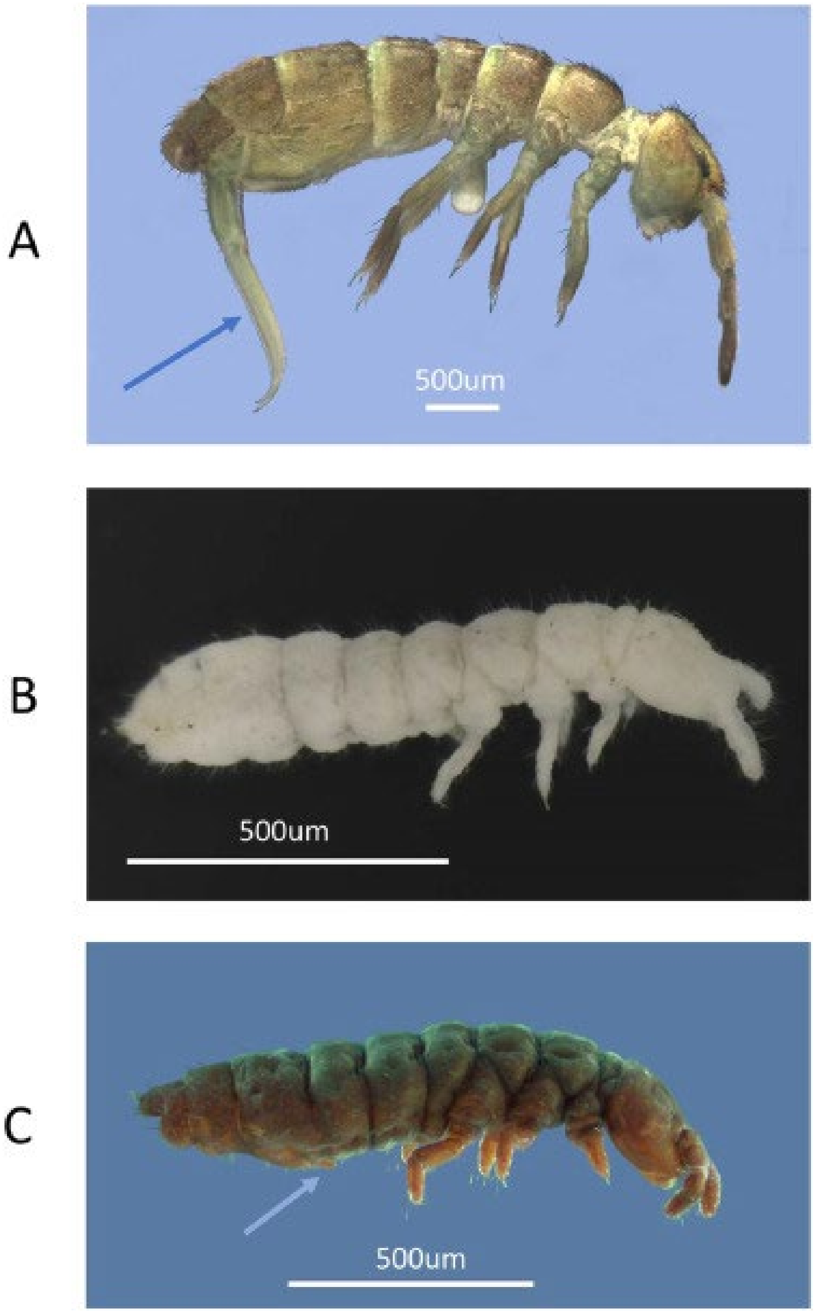


Fig. 2. Examples of: A) an epiedaphic (surface-dwelling) Collembola (*Isotomurus* sp. from the Canadian Arctic) showing elongated appendages including legs, antennae, furcula (indicated by blue arrow), and 'ventral tube' (collophore, visible between the second and third pairs of legs); B) an eudaphic 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 (500 μm) are shown for each taxon. All images copyright University of Waikato.

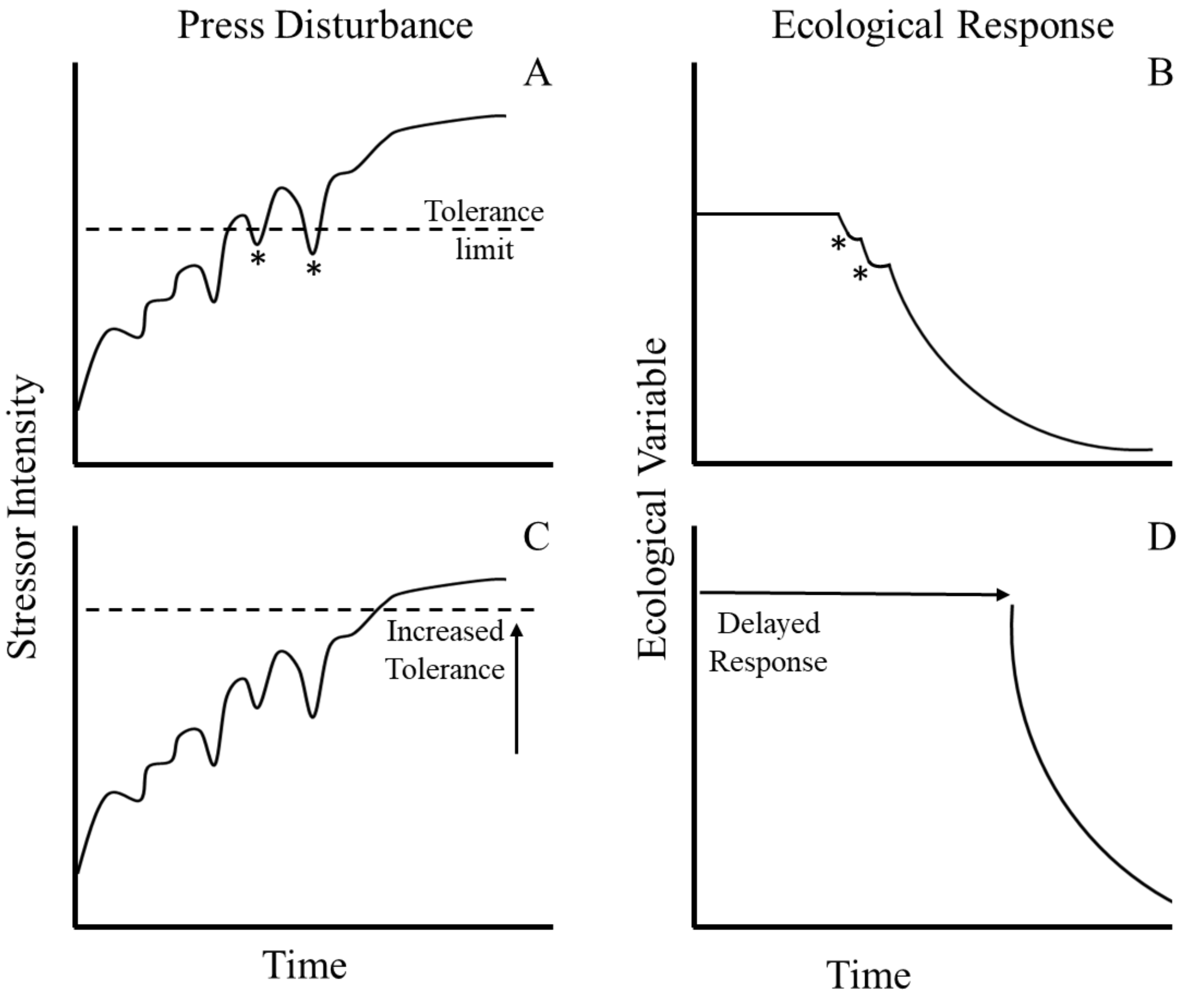


Fig. 3. Conceptual diagram showing a hypothetical and fluctuating press disturbance (A) and corresponding ecological response (B) resulting from climate change. Once maximal tolerance limits (maximum resistance capacity) are exceeded, steep declines in associated ecological responses such as fecundity 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 ongoing resistance capacities.

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 redescribed 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 infilled 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 °C (Coulson et al., 1995; Velasco-Castrillón et al., 2014), daily temperature fluctuations of 30 °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 (Boitaud 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°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 °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 Sjursen 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°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 springtails.

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 Sjursen 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 Sjursen, 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, Antarctica, 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 (Bahrndorff et al., 2009). This improved thermotolerance can persist for two days, thereby improving resistance to future thermal extremes and stochasticity (Bahrndorff 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 underlying 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 Sjursen, 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 desiccation and high temperature tolerance (Sjursen 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 Sjursen 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-Scheepers 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 (McGaughran 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 (McGaughran 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 (McGaughran 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 recolonize 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 recolonize 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).

6. 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.

Acknowledgements

Financial support provided through funding from the New Zealand Antarctic Research Institute to IDH; New Zealand Ministry of Business Industry and Employment Contract UOWX1401 to SCC, IDH, IRM, and Polar Knowledge Canada Contract 3Y004-210046 to BJS. We thank Barry O’Brien and Gemma Collins for images taken at the University of Waikato Imaging Facility and used in Fig. 2. This manuscript is a partial contribution to the PhD thesis of CRB.

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CHAPTER III

Population genetic diversity of Canadian Arctic Collembola and patterns of shared genetic diversity across the Arctic*

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CHAPTER III

Abstract

Collembola are abundant in Arctic terrestrial and aquatic ecosystems, yet their diversity and distribution remain largely unknown, particularly in the central and western Canadian Arctic. Here, we collected Collembola from Victoria Island in the vicinity of Cambridge Bay, Nunavut over three boreal summers (2019-2021) and assessed levels of diversity using sequence fragments of the mitochondrial DNA cytochrome c oxidase subunit I (*COI*) gene region. Sequences were then compared with available records on Barcode of Life Data Systems (BOLD) database to determine species identifications as well as patterns of shared genetic diversity among geographic locations. Sequencing of 512 individuals revealed 204 unique haplotypes and 68 Barcode Index Numbers (BINs; as a surrogate for species diversity) including representatives from eight taxonomic families. Eight morphologically based species were represented by multiple BINs with sequence divergences ranging from 1.28 – 18.39 %. Molecular clock calibrations of 2.3-3.54 % My^{-1} suggested that the majority of these multi-BIN taxa diverged 2.6-0.43 Ma during the Pleistocene. Comparison with available BOLD records, showed that 29 BINs (42 %) were currently unique to our study area on Victoria Island, 20 (29 %) clustered together with individuals collected from lower latitude mainland Canada sites, 21 (31 %) were shared with other locations on the Canadian Arctic Archipelago, seven (10 %) were shared with Greenland and Svalbard and a single BIN contained individuals collected from Herschel Island near the border between the Yukon and Alaska. The current Victoria Island Collembola fauna potentially comprises taxa that have survived in situ throughout glaciations coupled with more recent colonists. The fact that there are shared BINs with locations primarily to the east (but not the west), could potentially support an east to west rafting dispersal route with additional mixing among the archipelago as well as northward migrations from lower latitude populations.

1. Introduction

The Arctic is warming rapidly, disrupting both above- and below-ground soil ecosystems (Meredith et al. 2019, Høye et al. 2021). However, limited knowledge of the distribution and diversity of Arctic terrestrial invertebrates, particularly soil invertebrates, has limited the monitoring of environmental changes (Bardgett and Van Der Putten 2014). Collembola are key components of Arctic food-webs, and are prey for spiders, mites, and migratory birds (Hodkinson and Coulson 2004, Wirta et al. 2015, Koltz et al. 2018a). They also play major roles in decomposition, soil nutrient cycling, and facilitating plant-microbe interactions (Birkemoe and Liengen 2000, Wardle et al. 2004, Potapov et al. 2020). Collembola are particularly critical in polar ecosystems where overall arthropod species diversity is low, but Collembola are abundant (e.g. 590,000/m^2 in Svalbard; (Coulson 2000). Any loss of Arctic collembolan diversity due to changing environmental conditions could, therefore, have wider consequences for broader ecosystem functioning (Koltz et al. 2018b, Høye et al. 2021).

The >425 species of Arctic Collembola include representatives from >60 % of described families and 20 % of known genera (Babenko 2005, Hodkinson et al. 2013). However, Collembola have not been surveyed for much of the the Arctic because of the large geographic scale coupled with jurisdictional and logistical challenges (Nielsen and Wall 2013). The main exceptions to this are surveys undertaken in Svalbard (Hertzberg and Leinaas 1998, Coulson 2000, Coulson et al. 2003, Coulson et al. 2013, Convey et al. 2015, Coulson et al. 2015, Ávila-Jiménez et al. 2019) and Greenland (Wirta et al. 2016, Høye and Culler 2018, Høye 2020, Høye et al. 2021). Forty-nine Collembola species from 29 genera have been reported from the central and western Canadian Arctic and Alaskan islands by Danks (1981, 1990), Fjellberg (1986) and Hogg and Hebert (2004). The 49 species previously reported across the Canadian Arctic Archipelago (Danks 1990) most resemble that of Svalbard with an absence of Palearctic species (Babenko 2005). However, the Canadian Arctic includes 36,563 islands across more than 1.4 million km^2, so the low sampling effort almost certainly underestimates species counts. By contrast, 68 species of Collembola have been recorded in Svalbard, which covers only 62,045 km^2 (Coulson et al. 2014).

There are even fewer population-level studies of Arctic Collembola, which limits our understanding of population structure for species distributed across this very large region.

Understanding levels of genetic diversity within and among populations is especially relevant, as this will influence the longer-term evolutionary responses of Collembola to climate change (Somero 2010, Beet et al. 2022, Chapter II). Ongoing morphological and taxonomic work (Babenko 2017, 2018, Babenko et al. 2019) coupled with genetic studies using cytochrome c oxidase subunit 1 (COI) gene sequences (Hogg and Hebert 2004, Porco et al. 2014, Wirta et al. 2016, Pentinsaari et al. 2020) have started to address this issue. Genetic studies have highlighted that there are high levels of intraspecific and cryptic diversity over broad geographic scales.

In nature, Collembola generally disperse poorly (Hawes et al. 2007, Hawes 2011), but human-assisted dispersal has been well-documented, particularly in the sub-Antarctic (Frenot et al. 2005, Hughes et al. 2015). Collembola are highly desiccation intolerant (due to their hydrophobic cuticles), so rafting (floating individually or in groups) on the surface of open marine- and fresh-waters is likely a key means of dispersal (Hawes 2011, McGaughran et al. 2011). In polar regions, liquid water for rafting is available only seasonally, and the possibility of rafting likely waxes and wanes on geological timescales as glaciation cycles create and remove dispersal barriers and contiguous water bodies (McGaughran et al. 2009, Ávila-Jiménez and Coulson 2011, Collins et al. 2020). The Arctic has been repeatedly glaciated over the past 2.6 Ma most recently by the Wisconsin glaciation (150,000 – 50,000 years B.P.) which covered much of North America until the last glacial maximum (LGM, 20,000 years B.P.) and included multiple large ice sheets which would have limited dispersal and habit suitability for many areas. The Wisconsin Glaciation included the Greenland ice sheet, the Innuitian ice sheet which covered the Canadian Arctic Archipelago, the Laurentide Ice Sheet which covered the majority of modern-day Canada and the Cordilleran Ice Sheet which extended west of the Laurentide ice sheet into Alaska (Lacelle et al. 2018). Ice-sheet retreat following the LGM and the opening of sea-ways would have enabled dispersal via rafting. At present, Arctic Ocean currents largely move in an east to west direction with the Beaufort Gyre and local currents around islands providing further complexity (Figure 1).

Most present-day Canadian Arctic terrestrial invertebrates have recolonized since the last glacial maximum (20,000 years B.P.) (Már Gíslason 2005, Clark et al. 2009). Of the 49 Collembola species recorded by Danks (1990), 34 had Holarctic or cosmopolitan distributions, seven were Beringian, six were Nearctic in origin, and two were from the North-Atlantic. A study by Ávila-Jiménez and Coulson (2011) employed phylogeographic analyses on species distribution patterns to determine possible dispersal routes and likely glacial refugia for Arctic Collembola. This study suggested that while most Arctic Collembola are post-glacial colonists some may have survived in situ in refugia (Ávila-Jiménez and Coulson, 2011). Ávila-Jiménez and Coulson (2011) also suggested that Arctic dispersal routes proceeded in an east to west direction consistent with the prevailing ocean currents, although any directionality of dispersal in the Canadian High Arctic was unknown owing to limited genetic data. Antarctic Collembola appear to have persisted in localised ice-free refugia through numerous glaciations over the past 5 Ma (Stevens et al. 2006, Stevens et al. 2007, Collins et al. 2020). The primary Arctic refugia are thought to be large unglaciated regions in the South, Beringia and possibly areas of Ellesmere and Baffin Islands (Hultén 1937, England and Bradley 1978, Stewart and England 1986, Mangerud et al. 2002). Phylogeography of plant records from the Canadian Arctic imply that the current flora is comprised entirely of post-glacial colonists (Brochmann et al. 2003). However, lemming phylogeography (Fedorov and Stenseth 2002), beetle fossils (Elias and Matthews Jr 2002), and mosquito fossil records (Thomas et al. 2008) all suggest the presence of at least some local glacial refugia (England and Bradley 1978, Stewart and England 1986). Thus, the post-glacial history of Collembola in the Canadian Arctic is unclear. Understanding the evolutionary history of the current inhabitants is important as it could help inform their future resilience. Recent arrivals from lower latitudes may be more heat tolerant relative to existing species, which could increase their resilience to climate change (Beet et al. 2022; Chapter II).

Victoria Island is one of the largest Canadian Arctic Islands and lies between the mainland continent and an array of islands that make up the Canadian Arctic Archipelago. Victoria Island is also near predicted ice-free areas on Banks Island and Beringia, one of the largest known refugium during the last glacial maximum (Mangerud et al. 2002, Lacelle et al. 2018). This island presents a good opportunity to not only improve knowledge of local population and species diversity but explore potential patterns of shared genetic diversity across the Arctic to close the knowledge gap identified by Ávila-Jiménez and Coulson (2011). We assessed intra- and inter-species level genetic diversity of Victoria Island Collembola using COI sequences. We identified 68 Barcode Index Numbers (BINs, molecular operational taxonomic units) exceeding previously known levels of diversity and found high levels of intraspecific diversity. We examined what locations also contained individuals that clustered together in Cambridge Bay BINs and found high levels of shared genetic diversity with Mainland Canada, Arctic Archipelago Islands, along with Greenland and Svalbard. We then explored potential dispersal routes and patterns of colonisation.

2. Methods

2.1 Study area and sample collection

Fieldwork was conducted in the vicinity of Cambridge Bay/Ikaluktuktiak (also spelled Iqaluktuuttiaq, Ekaluktutiak and ᐃᖃᓗᒃᑑᑦᑎᐊᖅ; 69.1141-105.0472) located on southern Victoria Island (Kilinoyak) in the Kitikmeot Region of Nunavut, Canada (Fig. 1). Cambridge Bay is situated amongst a largely flat thermokarst landscape with numerous small ponds and lakes (Fig. 2A). The vegetation is dominated by non-tussock-sedges (Fig. 2B), dwarf-shrubs (Fig. 2C), herbaceous wildflowers, lichens, and moss (Fig. 2D). Further details of the study area are provided in Pentinsaari et al. (2020).

We collected a total of 512 individual Collembola within 50 km of Cambridge Bay (Supp. Fig. 1) over two boreal summers in 2018 and 2019 as part of a broad-scale assessment of invertebrate diversity in the Canadian Arctic (Arctic BIOSCAN https://arcticbioscan.ca/). Collection methods included malaise traps, pan traps, pitfall traps, and sweep-netting, along with soil and litter sifting which covered both terrestrial and semi-aquatic habitats (Pentinsaari et al. 2020). Collembola were hand-picked from samples and individual specimens photographed and placed in 100% ethanol in single wells of a 96 well plate (95 individuals plus a control) for further processing at the Canadian Centre for DNA barcoding (CCDB), University of Guelph (Guelph, Ontario, Canada) as per Pentinsaari et al. (2020).

2.2 DNA sequencing

We assessed genetic diversity using sequence fragments of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene (Hebert et al. 2003). Genomic DNA was extracted and COI sequence fragments amplified and sequenced according to standard CCDB protocols (see Ivanova et al. 2006 http://ccdb.ca/resources/), using the LepFol primer set (Hernández-Triana et al. 2014). All photographs, specimen and sequence data are available from the Barcode of Life DataSystems (BOLD) database (www. boldsystems.org; Ratnasingham and Hebert 2013) under dataset DS-AFCHAR. We excluded any individuals flagged by BOLD as contaminated or from which useable sequences could not be obtained.

2.3 Data analyses

Sequences were aligned using MUSCLE and trimmed in Geneious v.11.1.5 (https://www.geneious.com). A final alignment of 627 base pairs included 512 sequences which were reduced to 204 unique haplotypes using the “find unique sequences” function in Genious to simplify downstream analyses with the number of individuals for each haplotype retained. We used the Barcode Index Numbers (BINs; n=68 unique BINs) provided by BOLD to serve as a proxy for species diversity (Ratnasingham and Hebert 2013), and refined our species-level identifications with reference to publicly available, and morphologically-identified, reference sequences on BOLD (19 species) (e.g. Hogg and Hebert 2004, Porco et al. 2014). We then further refined potential taxonomic species identifications by visually examining BIN and phylogenetic tree relationships to suggest identification of a further 26 taxonomic species.

We constructed phylogenetic trees using neighbour joining (Saitou and Nei 1987), maximum likelihood (Felsenstein 1981), and Bayesian approaches (Ronquist and Huelsenbeck 2003) to refine our species identifications. Neighbour joining and maximum likelihood trees were constructed in MEGA version X 10.0.5 (Kumar et al. 2018). For the neighbour-joining tree the default Kimura 2- parameter model (Kimura 1980) of evolution was selected with all other default settings maintained and 1000 bootstrap replications selected. For the maximum likelihood and Bayesian trees, the most appropriate model of evolution was determined as GTR+I+G using bModelTest. The maximum likelihood tree was constructed using the GTR+I+G model of evolution, 1,000 bootstrap replicates and all other default settings maintained, and the Bayesian tree was generated using BEAST2 software v2.5.2 (Drummond and Rambaut 2007). A strict clock model and speciation yule process as the tree prior were employed in BEAUTI v2.5.2, with the Markov chain Monte Carlo (MCMC) set at 10,000,000 generations, sampling trees every 1,000 generations. The quality of the Bayesian analysis was evaluated using TRACER v1.7.1. A burn in of 500 trees was entered into Tree Annotator v2.5.2. All phylogenetic trees were visually compared. As the Bayesian tree best resolved the deeper phylogenetic relationships, it formed the basis of our results, with the neighbour joining and maximum likelihood trees provided in the supplementary materials.

We used accumulation curves (calculated using the in-built sequence analysis platform on BOLD) to estimate levels of sampling bias and to determine which taxa may benefit from further sampling coverage. Briefly, we generated total diversity and Family-level accumulation curves of cumulative number of BINs versus the number of individuals sequenced from 100 iterations of randomised sampling order randomised. Family-level accumulation curves are provided in the supplementary materials.

We manually examined the collection location of all individuals clustered together in the 68 BINs identified here, to determine whether any BINs contained individuals that had been collected outside of Cambridge Bay. The number of BINs containing individuals collected outside of Cambridge Bay (shared BINs) and where non-Cambridge Bay individuals were collected from was then noted. To explore which areas had the highest rates of shared genetic diversity we then mapped out which locations had shared BINs and which locations had the highest incidence of shared BINs.

Levels of intra- and interspecific divergence for taxonomically recognised species possessing multiple BINs (i.e. containing potential species-level differences) were calculated using MEGA version X 10.0.5. Pairwise distances were calculated using uncorrected pairwise distances, Kimura-2-parameter (K2P), and Tamura-Nei 93 (Tamura and Nei 1993) models of evolution. We estimated potential divergence times among BINs within a nominal species using a standardised clock-like rate of divergence for arthropod mitochondrial DNA (see (Brower 1994)), assuming mutation rates of 2.3% My^{-1} (cf. Myburgh et al. 2007, Bennett et al. 2016, Carapelli et al. 2017) and 3.54 % My^{-1} (as proposed for American cave Collembola (Katz et al. 2018)). We acknowledge that universal molecular clock approaches have limitations in their ability to accurately determine divergence times and use them here to provide broad estimates of divergence times.

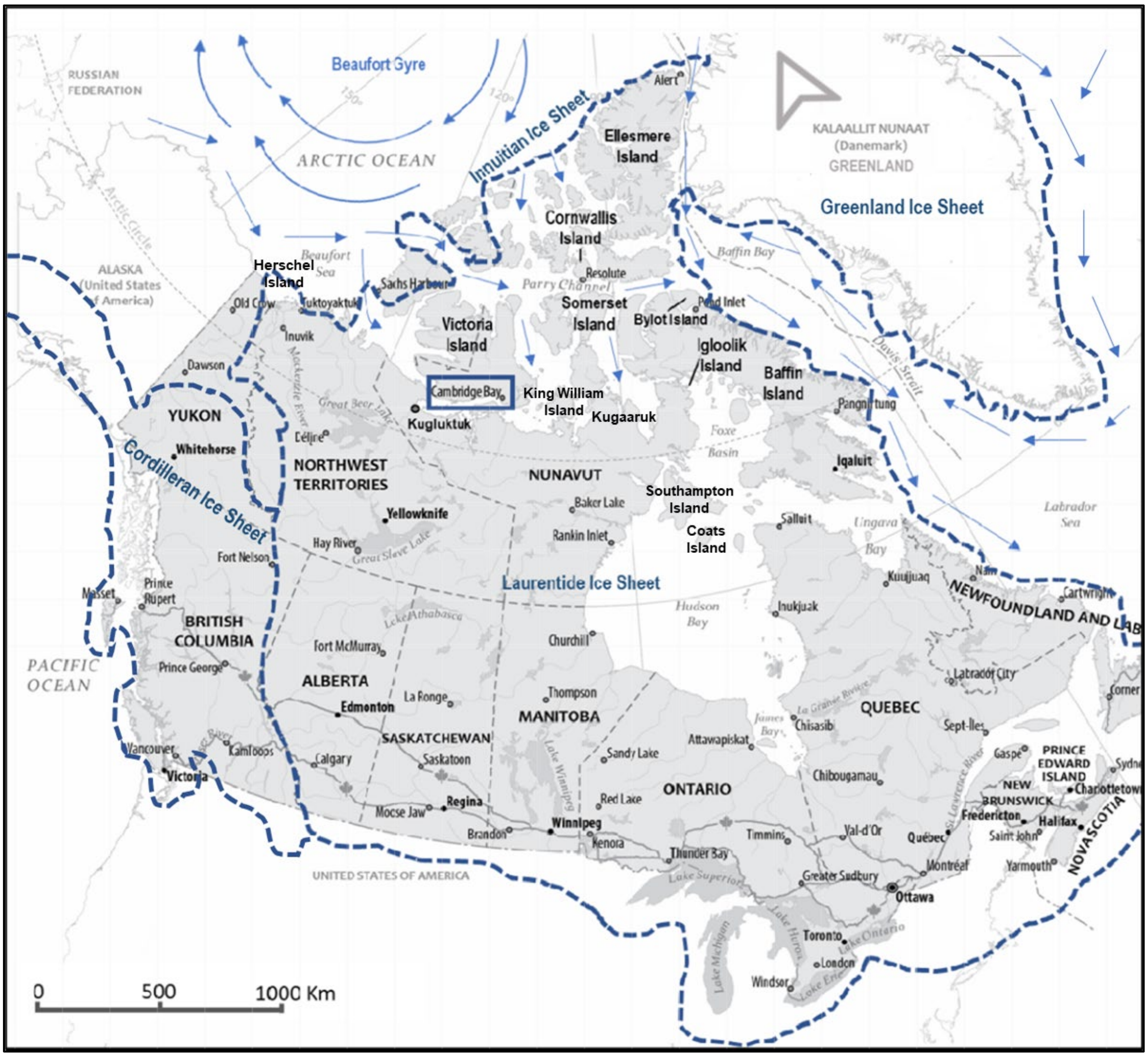

Figure 1. Map of Canada indicating the location of Cambridge Bay (noted by the blue box) on Victoria Island within Nunavut. Locations referenced in the text are also indicated on the map. Approximate ice sheet extent denoted by blue dashed lines, taken from Lacelle et al. (2018). Blue arrows indicate ocean current direction, taken from http://library.arcticportal.org/id/eprint/1494. Base map adapted from: Atlas of Canada, https://www.nrcan.gc.ca/earth-sciences/geography/atlas-canada/explore-our-maps/reference-maps/16846

Figure 2: Examples of sampling sites where Collembola were collected: A = Flat thermokarst tundra landscape with numerous ponds; B = Non-tussock sedge vegetation, particularly near ponds; C = Dwarf willow (*Salix arctica*) surrounded by moss and lichen covered rocks. Surface-dwelling Collembola including *Entomobrya* spp. and *Isotomurus* spp. were commonly found beneath the flat rocks; D = Dwarf willow and moss meadows with lichen covered rocks. Photo credit*s:* Clare Beet

3. Results

Here we found 204 haplotypes (unique sequences) and 68 BINs (putative species), 28 of which were represented by single individuals (Table 1). Nineteen of the 68 BINS were genetically matched to taxonomic species using morphologically identified reference sequences on BOLD, a further 23 to genus, and the remaining 26 BINs could not be matched beyond the family level (Fig. 3, Table 1). A Bayesian phylogenetic tree confirmed that taxonomic assignments to Order were monophyletic, and that all family designations except the Sminthuridae were monophyletic (Fig. 3). We estimate that our sequences represent a total of 45 putative species including the 19 species matched to reference specimens and a further 26 species estimated using a combination of BIN designation and phylogenetic relationships (marked with an asterisk in Figure 3).

Seventy two percent of individuals and 78 % of BINs fell into three families: Isotomidae (n=194, 87 haplotypes and 38 BINs), Sminthuridae (n=108 individuals, 21 haplotypes, 7 BINs) and Hypogastruridae (n = 67 individuals, 29 haplotypes, 8 BINs) (Table 1). Most Symphypleona sequences were identifiable only to the family level with two (of 11) BINs attributable to species levels based on available BOLD reference sequences (Table 1). The overall taxon accumulation curve based on BINs (Fig 4) had not approached asymptote, suggesting that further Collembola BINs are likely to be found in the vicinity of Cambridge Bay and Victoria Island. Accumulation curves for BINs within taxonomic families had approached or were approaching asymptote for four families (Poduridae, Onychiuridae, Sminthuridae, Entomobryidae; Supplementary Fig 4). By contrast, accumulation curves for Bourletiellidae, Neanuridae, Isotomidae, and Hypogastruridae had not approached an asymptote (Supplementary Fig 5).

Of all 68 BINs, 42 % (n=29) were found exclusively in the Cambridge Bay area. Twenty BINs (29 %) had individuals collected from lower latitude mainland Canada sites (Kugluktuk, Nunavut; Kugaaruk, Nunavut; Churchill, Manitoba; and multiple locations in Alberta, Saskatchewan and British Columbia), 21 BINs (31 %) were shared with other Canadian Arctic Islands, seven BINs (10 %) contained individuals collected from Greenland and Svalbard, and a single BIN contained individuals collected from Herschel Island near the border between the Yukon and Alaska (Table 2, supplementary Table 1, Fig. 5). Of the 19 taxa matched at the species-level to morphologically identified reference sequences, eight species were represented by two or more BINs (Table 2). Four of the eight species had two

BINs each, three species had three BINs each, while *Isotoma anglicana* had five BINs. Of the eight species represented by multiple BINS, five had at least one BIN found exclusively within the Cambridge Bay study area (total n = 29 BINs, Table 2).

Average levels of intraspecific divergence for our eight species represented by multiple BINS were 5.2 % and ranged from 1.28 % between *Entomobrya comparata* BINs to 14.35 % between *Folsomia quadrioculata* BINs (Table 3). Assuming divergent populations of Collembola accumulated mutations in a clock-like manner at a rate of 3.54 % per million years - divergence times for BINs within the eight nominal species ranged from 0.36-5.19 Mya with an average divergence time of 1.58 Mya (Table 3). Divergence times based on a clock rate of 2.3 % per Mya ranged from 0.56-7.99 Mya with an average of 2.4 Mya (Table 3). Based on the 3.54 % rate, all species except for *F. quadrioculata* diverged in the Pleistocene (2.58-0.0117 Mya). *Ceratophysella denticulata*, *Isotoma anglicana* and *Sminthurides malmgreni* had divergence times (2.6-2.66 My) in the Pliocene (5.33-2.58 Mya). By contrast, *Folsomia quadrioculata* potentially diverged (4 - 7.99 Mya) within the Pliocene or Miocene, (Table 3).

Table 1: Summary of sequencing data of Cambridge Bay Collembola. The number of Barcode Index Numbers (BINs), species, haplotypes identified, and number of individuals sequenced are broken down by Collembola Family.

Family	**Poduridae**	**Hypogastruridae**	**Onychiuridae**	**Neanuridae**	**Entomobryidae**	**Isotomidae**	**Bourletiellidae**	**Sminthuridae**	**TOTALS**
BINS	1	8	3	4	7	34	4	7	68
Species	1	4	1	1	1	10	0	1	19
Haplotypes	3	29	17	9	13	106	6	21	204
No. Individuals	10	67	44	13	65	194	11	108	512

Table 2: Intraspecific pairwise distances and estimated divergence times of Cambridge Bay Collembola species represented by more than one BIN. Taxa are identified by order, family then species. Intraspecific distances were calculated using three different methods; P-distance refers to uncorrected pairwise distances; K2P refers to p-distances calculated using the Kimura 2 Parameter, TN93+G refers to pairwise distances between BINs calculated using the Tamura-Nei method. All pairwise distances and subsequent divergence rates were calculated relative to the first BIN displayed. Divergence times between intraspecific BINs were calculated using a rate of 3.54 % divergence My^{-1} first proposed by (Papadopoulou et al. 2010) and 2.3% My^{-1} first proposed by (Brower 1994). Displayed divergence times are an average (mean) of the time calculated from all three pairwise distance methods with the range of divergence times (from all methods) displayed in brackets. BIN distribution notes refers to the collection location of other individuals on BOLD clustered together in the same BIN. Collection location codes are as follows CB= Cambridge Bay only, MC= Mainland Canada, BI= Baffin Is., CH=Churchill, KU=Kugluktuk, GL=Greenland, CI=Cornwallis Is., BY=Bylot Is., EI=Ellesmere Is., II=Igloolik Is., SI=Somerset Is., SV=Svalbard, KW=King Williams Is. The range distance shows the minimum and maximum distance between two locations that individuals of the same BIN were collected from.

Taxon	**BIN**	**Bin Distribution Notes**	**Range Distance within BIN**	**Available References**	**P-distance (%)**	**K2P (%)**	**TN93+G (%)**	**Divergence Time (3.54% My^{-1})**	**Divergence Time (2.3% My^{-1})**
Poduromorpha **Hypogastruridae**									
Ceratophysella denticulata	AAI3740	MC, BI, CH	430-2,850 km	Porco et al. 2014					
	AAA4808	MC, KU, CH, GL	430-4,000 km	Porco et al. 2014	5.58	6.17	6.21	1.69 (1.75-1.58)	2.6 (2.7-2.43)
Hypogastrura concolor	AAF4674	CI, SI, BY, EI	700-1,800 km	Hogg and Hebert 2004					
	AAZ3245	CB	0		4.94	5.35	5.38	1.48 (1.52-1.40)	2.27 (2.34-2.15)
Entomobryomorpha **Entomobryidae**									

Entomobrya comparata	ADR2480	KU	0-430 km						
	AAF7753	II, BY	450-1,000 km	Hogg and Hebert 2004	4.31	4.63	4.68	1.28 (1.32-1.22)	1.97 (2.03-1.87)
	ADT5266	KU	0-430 km		1.28	1.31	1.99	0.43 (0.56-0.36)	0.66 (0.87-0.56)
Entomobryomorpha									
Isotomidae									
Isotoma anglicana	AEC7009	CB	0						
	ACC1604	MC	0-2,000 km		2.87	3.03	3.14	0.85 (0.89-0.81)	1.31 (1.37-1.25)
	ADU7515	CB	0	Porco et al. 2014	2.55	2.68	2.72	0.76 (0.77-0.74)	1.15 (1.18-1.11)
	AAI2075	KW	0-420 km		5.58	6.16	6.2	1.69 (1.75-1.58)	2.60 (2.70-2.43)
	AAI8142	BI, BY, CI, EI, KW	420-1800 km	Porco et al. 2014	3.83	4.09	4.12	1.13 (1.16-1.08)	1.74 (1.79-1.67)
Folsomia quadrioculata	ADV2839	CB	0	Porco et al. 2014					
	AAC6483	SI, KW	420-570 km	Hogg and Hebert 2004	14.35	18.00	18.39	4.77 (5.19-4.05)	7.35 (8.00-6.24)
	AAI5662	MC, CH, GL	1,200-2,250 km		11.96	14.62	14.86	3.90 (4.20-3.38)	6.01 (6.46-5.20)
Folsomia fimetaria	AEC7431	CB	0						
	AEC8159	CH	0-1200 km		4.31	4.66	4.69	1.29 (1.32-1.22)	1.98 (2.04-1.87)
	AAI2061	CH, GL	1,200-2,250 km	Hogg and Hebert 2004	1.59	1.65	1.66	0.46 (0.47-0.45)	0.71 (0.72-0.69)
Folsomia bisetosa	AAF6760	CI, GL	700-2,250 km						
	ACS8135	SV	0-3,500 km		3.83	4.09	4.1	1.13 (1.16-1.08)	1.74 (1.78-1.67)

Symphypleona									
Sminthuridae									
Sminthurides malmgreni	AAF4771	II, EI, SI		Hogg and Hebert 2004					
	ADV3522	CB	0		5.74	6.29	6.31	1.73 (1.78-1.62)	2.66 (2.74-2.50)


Oligaphorura groenlandica AAE5068
Onychiuridae * ADW4932
Onychiuridae * ADW4933
Ceratophysella denticulata AAI3740
Ceratophysella denticulata AAA4808
Hypogastruridae * ADT8756
Ceratophysella longispina ACS8679
Hypogastrura concolor AAF4674
Hypogastrura concolor AAZ3245
Hypogastrura sp.|AEC9904 *
Hypogastrura sensilis AAC9746
Neanuridae * AEC0860
Neanuridae * ADT4856
Morulina mackenziana|AAK6575
Morulina thulensis AEC7112
Podura aquatica AAB2100
Entomobrya comparata ADT5266
Entomobrya comparata AAF7753
Entomobrya comparata ADR2480
Desoria sp.|ADW1777|ADW2666 *
Isotomurus sp. * AAI5790
Isotomidae * AEB9708
Isotomidae|AEC8859 *
Isotomidae * AEC7603
Isotomidae|AEC0734 *
Desoria tshernovi AAL1339
Isotoma anglicana ADU7515
Isotoma anglicana AEC7009
Isotoma anglicana|ACC1604
Isotoma anglicana AAI2075
Isotoma anglicana AAI8142
Isotomidae * ADS8791
Isotomurus sp. AEC9230
Isotomurus sp. * AAI2046
Isotomurus sp. ADS4400
Isotomurus sp. ADS8788
Pseudisotoma sp.1 AAG0697
Isotomidae|ADT9652 *
Stachanorema tolerans AAF2586
Parisotoma ekmani AEC8684
Isotomidae|ADW3436 *
Isotomidae * ADS9160
Folsomia quadrioculata AAC6483
Folsomia quadrioculata AAI5662
Folsomia quadrioculata ADV2839
Isotomidae * ADW4336
Folsomia fimetaria|AEC7431
Folsomia fimetaria AAI2061
Folsomia fimetaria|AEC8159
Folsomia bisetosa AAF6760
Folsomia bisetosa ACS8135
Uzelia hansoni|AAB3534
Isotomidae|ADW2503 *
Isotomidae AEC0555
Isotomidae * AEC0925
Isotomidae * ADZ9063
Bourletiellidae * AEC7525
Bourletiellidae|AEC7611
Bourletiellidae * AEC7380
Sminthuridae ACU4299
Sminthuridae * ADS2746
Sminthuridae * ADS9388
Sminthurides malmgreni|ADV3522
Sminthurides malmgreni AAF4771
Sminthuridae ADU2654
Sminthuridae * AEB7283
Sminthuridae * ADU4449
Onychiuridae
Hypogastruridae
N.
P.
E.
Isotomidae
B.
Sminthuridae
Poduromorpha
Entomobryomorpha
Symphypleona
0.06

Figure 3. Unrooted Bayesian phylogenetic tree Cambridge Bay Collembola. Tree is of 204 unique haplotypes which were reduced from a total of 512 individual sequences (numbers in brackets on the tree refer to the number of individuals with that haplotype). Bootstrap values above 0.9 are displayed. Branch length indicates pairwise distance between haplotypes; the scale refers to 6 % pairwise distance. Seven-digit alphanumeric codes indicate Barcode Index Number or BIN, as registered in boldsystems.org. The bars on the furthest right indicate Order and the bars to the right of those indicate Family. Family abbreviations: N.= Neanuridae, P.= Poduridae, E.= Entomobryidae, B.= Bourletiellidae. The * refers to BINs that were unable to be identified beyond family level but likely represent a putative species.

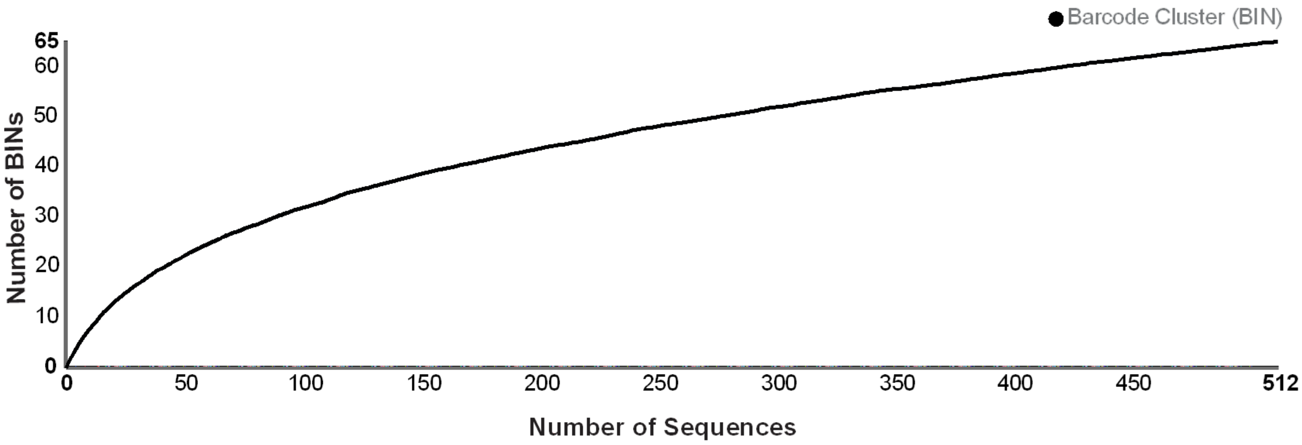

Figure 4: Species accumulation curve of the 68 Barcode Index Number (BINs) identified from 512 individual Collembola collected from Cambridge Bay, Nunavut. The species accumulation curve was calculated using inbuilt software on the boldsystems.org database.

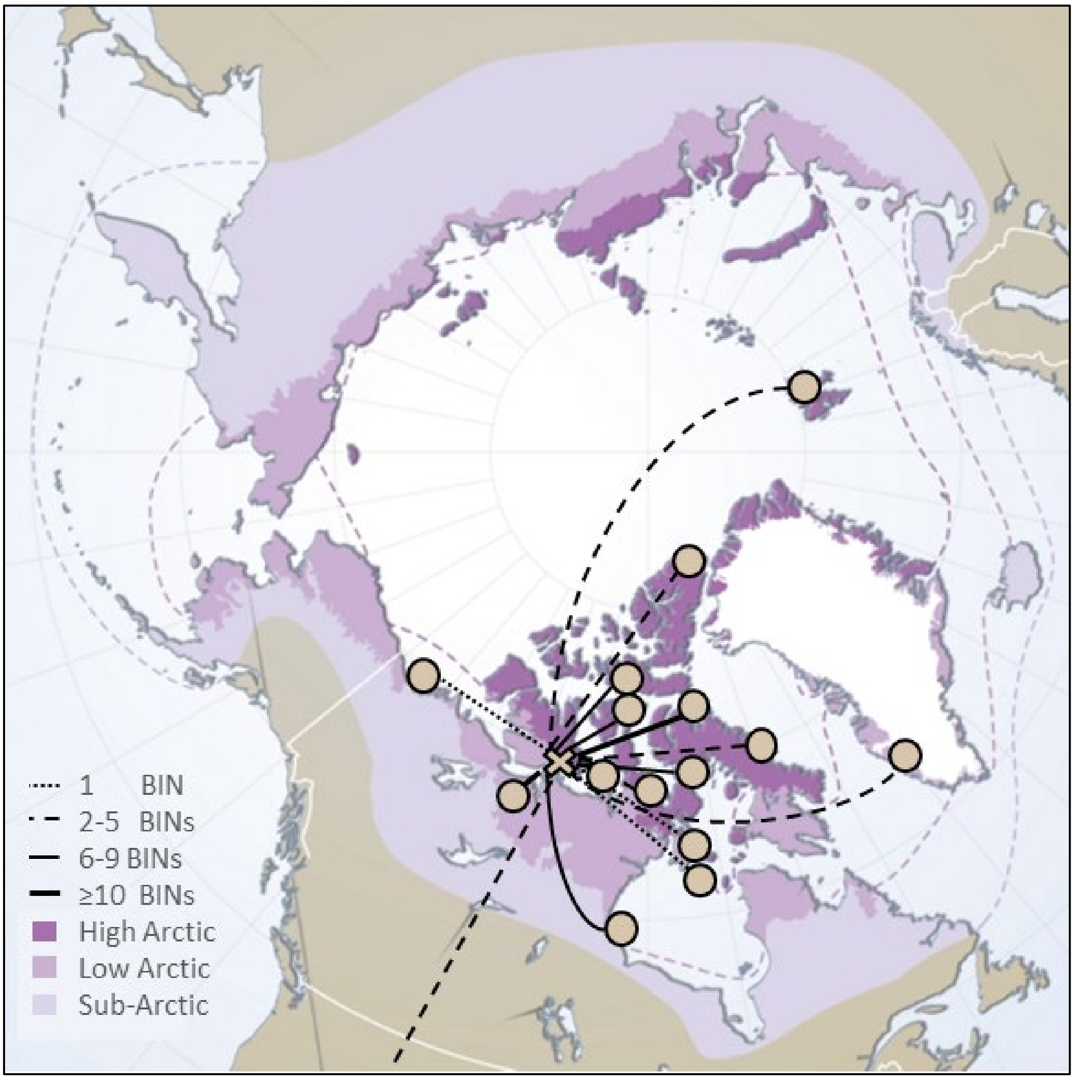

Figure 5: Map of the Arctic showing the genetic linkages between populations of Collembola. Cambridge Bay is marked with an "X" for reference. Each circle represents a site containing shared BINs with individuals from Cambridge Bay based on available COI sequences on boldsystems.org. The High, Low and Sub-Arctic regions as defined by CAFF (the Conservation of Arctic Flora and Fauna; https://www.caff.is/) are indicated with different shades of purple. Base image sourced from: https://www.grida.no/resources/6264.

5. Discussion

The Collembola from Cambridge Bay and Victoria Island included 68 putative species based on DNA sequences. This expands coverage of Hogg and Hebert (2004) which sampled the nearby Igloolik, Cornwallis, and Somerset Islands and found a total of 19 species from 13 genera. Earlier morphologically based estimates by Danks (1990) suggested 49 species from across the entire Canadian High Arctic. Accordingly, the estimated 68 putative species (BINs) recorded from southern Victoria Island represents a relatively comprehensive coverage of the local fauna. While the diversity of Collembola was higher in the sub-Arctic area of Churchill where Porco et al. 2014 recorded 97 putative species (based on morphology and BINs), this was comparable to the 68 found near Cambridge Bay.

There were high levels of sequence divergence recorded within eight of the 19 nominate species. These high levels of intraspecific diversity were consistent with findings from Hogg and Hebert (2004) and Porco et al. (2014) who also found high levels of intraspecific divergence within multiple species. For example, *Folsomia quadrioculata* is a widespread Holarctic species which had individuals up to 13 % divergent from each other in Hogg and Hebert (2004) and up to ~18 % divergent in our present study. Porco et al. (2014) also found high levels of intraspecific divergence (20-30 %) within *F. quadrioculata*, *Ceratophysella denticulata*, *Podura aquatica*, *Sminthurides aquaticus*, *S. malmgreni* and *Entomobrya comparata.* We found a total of five BINs for *Isotoma anglicana*, two of which were currently unique to our study area. This level of intraspecific divergence could indicate that *I. anglicana* represents a species complex of multiple distinct species, or alternatively is the result of potential misidentifications for reference specimens on the BOLD database (e.g. see Pentinsaari et al. 2020b).

Of the individuals that were sequenced, the majority (84.8 %) belonged to four families; Isotomidae (n = 194, 37.9 %), Sminthuridae (n = 108, 21.1 %), Hypogastruridae (n = 67, 13.1 %) and Entomobryidae (n = 65, 12.7 %). The prevalence of Sminthuridae and Entomobryidae contrasts with Babenko (2005) who reported that nearly 90 % of all Arctic Collembola species belong to three families - Isotomidae, Onychiuridae and Hypogastruridae. This discrepancy could, in part, be due to sampling of the extensive aquatic habitats found near Cambridge Bay and resulting in increased incidence of the semi-aquatic Symphypleona. The abundance of Entomobryidae was solely due to the presence of the soil-surface species *Entomobrya comparata,* which was the most abundant and commonly observed species in our study area (Chapter IV). Species from nine taxonomic families known from other Arctic and sub-Arctic areas, were absent from our study. These included Tomoceridae, Neelidae, Odontellidae and Tullbergiidae in addition to several Symphypleona genera. Only one Symphypleona BIN was attributable to a species level indicating the absence of available reference sequences on BOLD. Our remaining sequences for individuals of Symphypleona could only be identified to family level indicating that this group would benefit from further morphological work and the addition of associated reference material on BOLD. Based on our family level species accumulation curves, we suggest that the Neanuridae, and Bourletiellidae families would also benefit from further sampling and reference material on BOLD. The Bourletiellidae sequences are likely to be *Heterosminthurus* which is a common Arctic genus, although further reference sequences are required (Babenko 2005). The semi-aquatic Symphypleona and Poduridae collectively made up 25 % (n = 129) of the individuals we collected and indicate the prevalence of the limnetic habitats for abundances of Collembola, particularly in this region of the Arctic (Hodkinson et al. 2013). We collected 26 taxa (putative species) that could not be matched to morphological identifications beyond the family level and further taxonomic assessments are required to provide accurate reference specimens and their associated COI sequences.

The taxa we collected from Victoria Island shared genetic diversity (BINs) with individuals collected from other nearby Arctic Islands, Greenland and Svalbard as well as lower latitude mainland sites. Of the BINs recorded in our study, only one was shared with specimens collected from Herschel Island near the border of the Yukon and Alaska. There was no shared genetic diversity with Collembola (including *E. comparata* individuals) collected from the Northwest Territories where sampling has been undertaken around Inuvik, Norman Wells and Yellowknife (Supplementary Fig. 6). There were no other BINs shared with individuals from Alaska, eastern Russia or the remaining Palearctic, although this could be due to a lack of available data. The BOLD database contained few records from Alaska or Boreal Russia and as of June 2023, there were only 28 Collembola COI sequences from Alaska representing seven species and 17 BINs (Supplementary Fig. 6). A Holarctic study of Collembola biogeography (Ávila-Jiménez and Coulson, 2011), demonstrated that Arctic Collembola generally dispersed in an east to west direction with populations dispersing from Siberia to Greenland. However, Ávila-Jiménez and Coulson (2011) could not resolve any directionality between Greenland and the Canadian Arctic Archipelago, owing to a lack of available data. The fact that there are shared BINs with locations primarilyto the east (but not the west), could potentially support an east to west rafting dispersal route with additional mixing among the archipelago as well as northward migrations from lower latitude populations. However, further phylogeographic analyses are needed to test this.

Estimated divergence times of BINs within eight of our nominate species pre-date the retreat of the last glacial maximum and could suggest the *in-situ* survival of Collembola in the Arctic during the Wisconsin Glaciation. All of these species contained BINs that were estimated to have diverged in the Pleistocene. The exception was *F. quadrioculata* which contained BINs that had potentially diverged in the Pliocene or Miocene. This corresponds with fossil records of beetles (Coleoptera) from across the Arctic which demonstrated that 97 % of the late tertiary beetle fauna survived a series of glaciations throughout the Pleistocene and up to the present time, with only five fossil species noted as extinct (Elias and Matthews Jr 2002). By contrast, the species composition of Chironomidae (Diptera) appears to have changed dramatically, despite representatives having persisted on Victoria Island throughout the past few thousand years (Thomas et al. 2008, Porinchu et al. 2009). These changes were likely a consequence of climate warming following the little ice age (1550 to 1850 CE), when cold adapted species were replaced by those that were adapted to the warmer conditions (Grove 2001, Ogilvie and Jónsson 2001, Porinchu et al. 2009). Collectively, the facts that many taxa here likely diverged long before the LGM, that several Antarctic Collembola survived through glaciations (Pugh and Convey 2008, Fraser et al. 2014, Collins et al. 2020), that other fauna likely persisted in-situ (Elias and Matthews Jr 2002, Fedorov and Stenseth 2002, Thomas et al. 2008), and the identification of potential refugia on Ellesmere and Baffin Islands (Hultén 1937, England and Bradley 1978, Stewart and England 1986) support the notion that some Collembola may survived in Arctic refugia throughout glacial periods

Our study extends previous efforts to document the diversity of Arctic Collembola (Hogg and Hebert 2004, Porco et al. 2014). Contributions to the BOLD database will aid in the ongoing monitoring of Arctic habitats particularly for studies using environmental DNA and/or metabarcoding approaches (Braukmann et al. 2019; Young and Hebert 2022). Enhancing sampling and taxonomic coverage for the Canadian Arctic Archipelago, northern Yukon, Alaska and Russia would help fill sampling gaps and further assess levels of shared genetic diversity among populations. The high levels of genetic diversity we observed within some taxa could indicate the potential to respond to changing environmental conditions

(Somero 2010, Beet et al. 2022; Chapter II). Further, evidence of shared genetic diversity with neighbouring Canadian Arctic Islands and mainland Canada suggest that dispersal (and colonization) of Collembola in response to climate change is possible. Finally, monitoring of temporal variability in distribution and diversity of Collembola (sensu Høye et al. 2021), would enable the detection of interannual changes relative to any directional changes in species diversity and corresponding changes in ecosystem functioning as a result of climate change.

Table 3: Table of Collembola species reported from Cambridge Bay, Victoria Island and five other locations. Displayed numbers refer to the number of morphologically identified species in each family while the number in brackets indicate the number of BINs reported for each family. Values for Coulson (2007), Ávila-Jiménez and Coulson (2011), and Babenko and Fjellberg (2006) are based exclusively on morphological identifications. A total of 68 Collembola species were reported for Svalbard in Coulson et al. (2014), however species lists for only 41 were found from the references listed below.

Order	**Family**	**This study**	**Hogg & Hebert 2004**	**Porco et al. 2014**	**Wirta et al. 2016**	**Coulson 2007 & Avila Jimenez and Coulson 2011**	**Babenko & Fjellberg 2006**
		Cambridge Bay, Canadian Arctic	Canadian Arctic	Churchill, Canadian Sub-Arctic	Greenland	Svalbard	Holarctic
Entomobryomorpha	Entomobryidae	1 (3)	1 (1)	6(7)	0	1	23
	Isotomidae	10 (36)	10 (11)	19(31)	5 (7)	12	132
	Tomoceridae	0 (0)	0	1(1)	0	0	5
Neelipleona	Neelidae	0 (0)	0	0(2)	1 (3)	1	1
Poduromorpha	Hypogastruridae	4 (7)	3 (3)	10(11)	3 (4)	9	67
	Neanuridae	1 (3)	1 (1)	4(11)	0	2	53
	Odontellidae	0 (0)	0	1(1)	0	1	4
	Onychiuridae	1 (3)	1 (1)	1(6)	0	4	62
	Poduridae	1 (1)	1 (1)	1(1)	0	0	1
	Tullbergiidae	0 (0)	0	0(3)	0	5	23
Symphypleona	Arrhopalitidae	0 (0)	0	2(4)	0	1	5
	Bourletiellidae	0 (4)	0	0(5)	0	0	11
	Katiannidae	0 (0)	0	0(2)	0	2	8
	Sminthurididae	1 (8)	2 (3)	2(12)	2 (3)	3	11
	Mackenziellidae	0 (0)	0	0	0	0	1
	Dicyrtomidae	0 (0)	0	0	0	0	5
Total		**19 (68)**	**19 (21)**	**47(97)**	**11 (17)**	**41**	**420**

Acknowledgements

We thank Polar Knowledge Canada for financial support to BJS and to JRD via the ARCBIO program. The University of Waikato provided PhD scholarship support to CRB.

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CHAPTER III

Wirta, H. K., E. J. Vesterinen, P. A. Hambäck, E. Weingartner, C. Rasmussen, J. Reneerkens, N. M. Schmidt, O. Gilg, and T. Roslin. 2015. Exposing the structure of an Arctic food web. Ecology and evolution **5**:3842-3856.

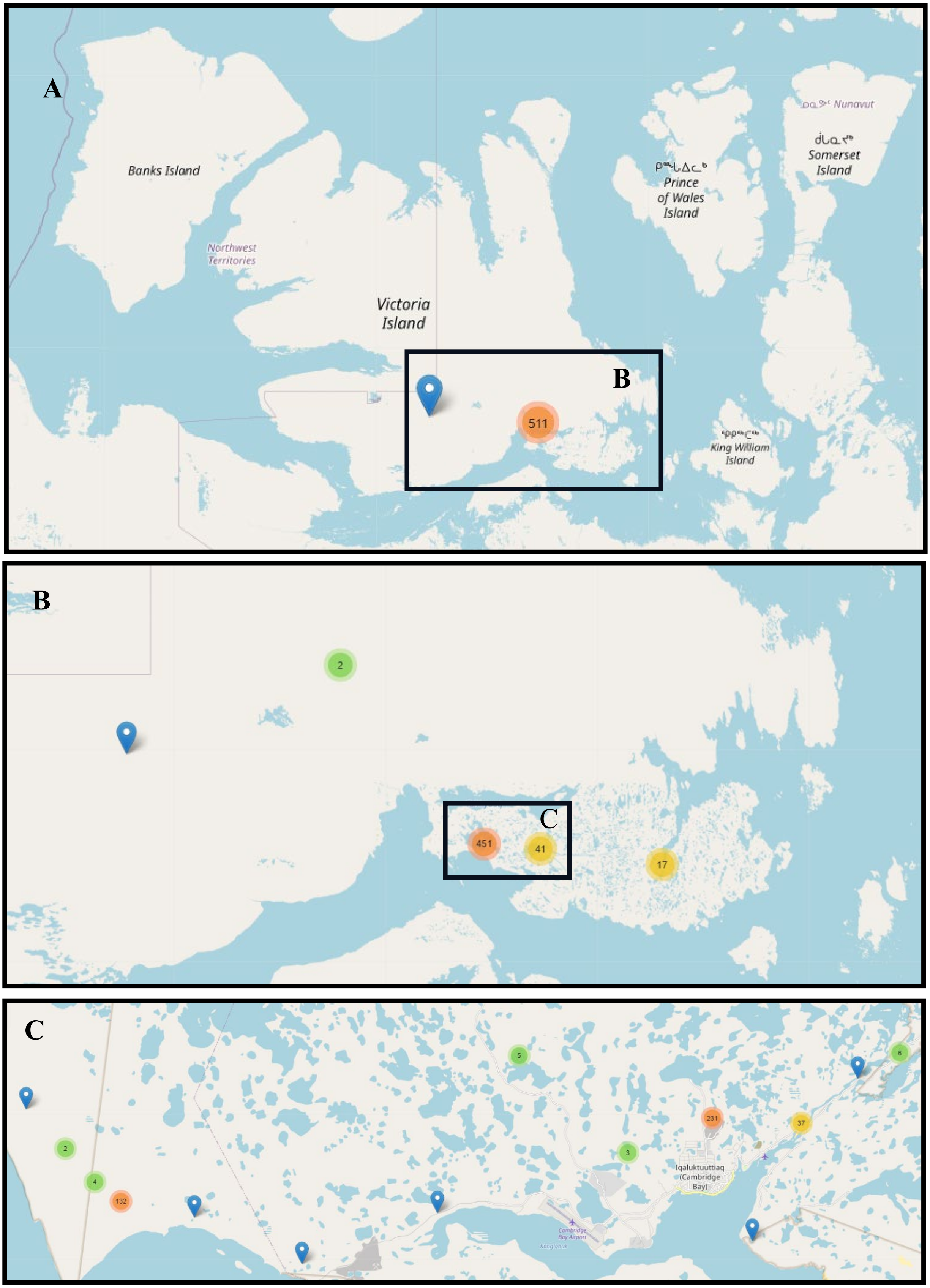
Supplementary Materials

Table S1: Geographic information for each unique BIN including notes on instances where sequences correspond with previous studies. Collection location codes are as follows CB= Cambridge Bay only, MC= Mainland Canada, BI= Baffin Is., CH=Churchill, KU=Kugluktuk, GL=Greenland, CI=Cornwallis Is., BY=Bylot Is., EI=Ellesmere Is., II=Igloolik Is., SI=Somerset Is., SV=Svalbard, KW=King Williams Is, CO=Coats Is., SH=Southampton Is., HI=Herschel Is., KG=Kugaark.

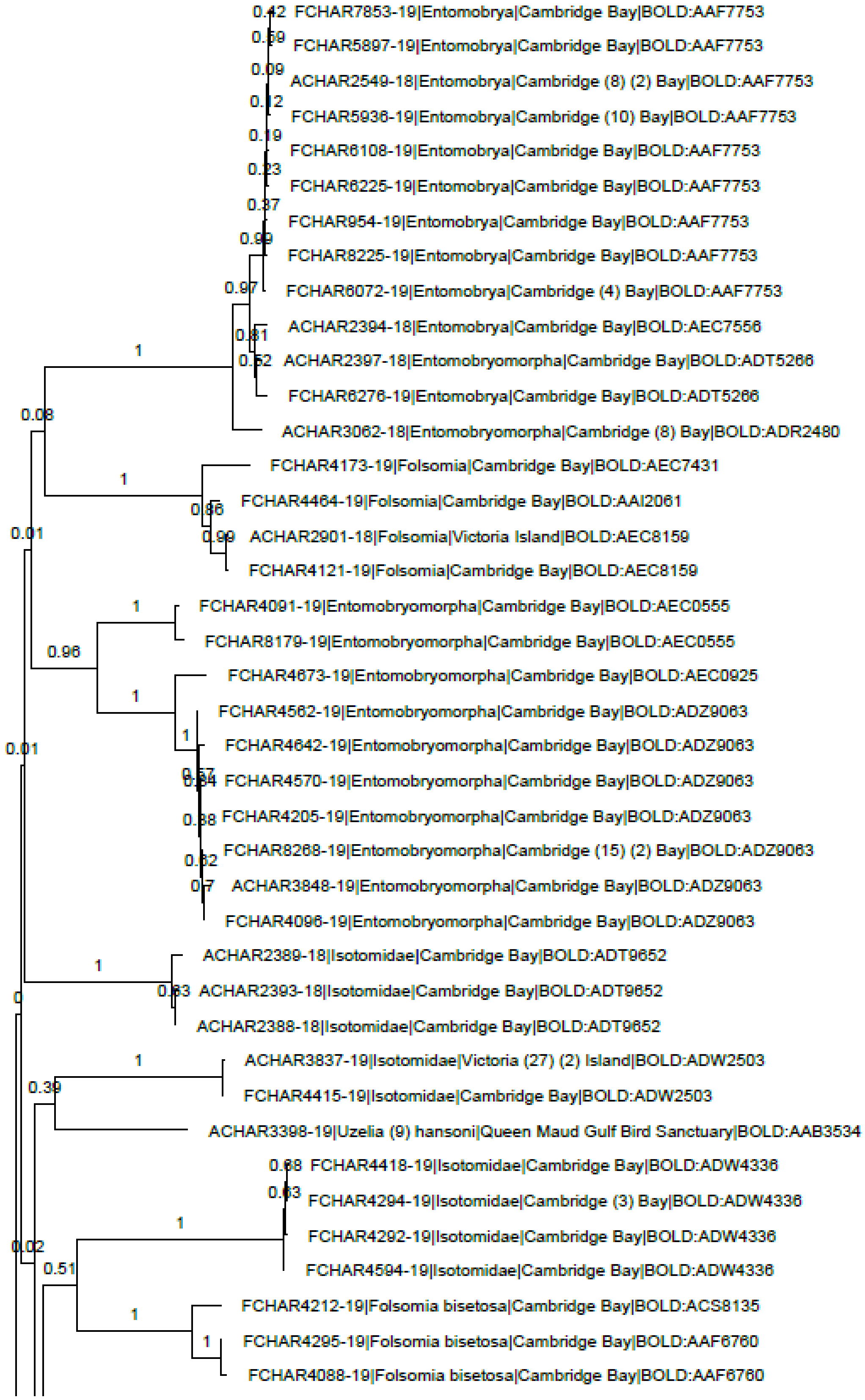
Species	BIN	Distribution notes	Reference
Poduromorpha			
Hypogastruridae			
Ceratophysella denticulata	AAA4808	MC, KU, CH, GL	Porco et al. 2014
	AAI3740	MC, BI, CH	Porco et al. 2014
Ceratophysella longispina	ACS8679	KU, SV	
Hypogastrura concolor	AAF4674	CI, SI, BY, EI	Hogg and Hebert 2004
	AAZ3245	CB	
Hypogastrura sensilis	AAC9746	CI, II	Hogg and Hebert 2004
Hypogastrura sp.	AEC9904	CB	
Hypogastruridae	ADT8756	KU	
Neanuridae			
Morulina mackenziana	AAK6575	KW, KG, II, BY	Hogg and Hebert 2004
Morulina thulensis	AEC7112	CB	
Neanuridae	ADT4856	KW	
	AEC0860	KU, KW	
Poduridae			
Podura aquatica	AAB2100	II, CI, BY	Hogg and Hebert 2004
Onychiuridae			
Oligaphorurua groenlandica	AAE5068	CI, CH, GL, SV	Hogg and Hebert 2004, Porco et al. 2014, Wirta et al. 2016
Onychiuridae	ADW4932	KU	
	ADW4933	CB	
Entomobryomorpha			
Entomobryidae			
Entomobrya comparata	AAF7753	II, BY	Hogg and Hebert 2004
	ADR2480	KU	
	ADT5266	KU	
Isotomidae			

Desoria sp.	ADW1777	CB	
	ADW2666	SI	
Desoria tschernovi	AAL1339	SI, BY	Hogg and Hebert 2004
Folsomia bisetosa	AAF6760	CI, GL	
	ACS8135	SV	
Folsomia fimetaria	AAI2061	CH, GL	Porco et al. 2014
	AEC7431	CB	
	AEC8159	CH	Porco et al. 2014
Folsomia quadrioculata	AAC6483	SI, KW	Hogg and Hebert 2004
	AAI5662	MC, CH, GL	Porco et al. 2014, Wirta et al. 2016
	ADV2839	CB	
Isotoma anglicana	AAI2075	KW	
	AAI8142	BI, BY, CI, EI, KW	Hogg and Hebert 2004
	ACC1604	MC	
	ADU7515	CB	
	AEC7009	CB	
Isotomidae	ADS8791	CB	
	ADS9160	CB	
	ADT9652	CB	
	ADW2503	KU	
	ADW3436	KU	
	ADW4336	CB	
	ADZ9063	KU, KW	
	AEB9708	CB	
	AEC0555	CB	
	AEC0734	CB	
	AEC0925	CB	
	AEC7603	CB	
	AEC8859	BY	
Isotomurus sp.	AAI2046	II, BY	Hogg and Hebert 2004
	AAI5790	BY, HI.	
	ADS4400	CB	
	ADS8788	CB	
	AEC9230	CB	
Parisotoma ekmani	AEC8684	CB	
Pseudoistoma sp. 1	AAG0697	KU, CH, KG	Porco et al. 2014
Stanchorema tolerans	AAF2586	SI, KW	Hogg and Hebert 2004
Uzelia hansoni	AAB3534	CH	Porco et al. 2014

Symphypleona			
Sminthuridae			
Sminthurides malmgreni	AAF4771	II, EI, SI	Hogg and Hebert 2004
	ADV3522	CB	
Sminthuridae	ACU4299	CO, SH	
	ADS2746	CB	
	ADS9388	KU	
	ADU2654	CB	
	ADU4449	CB	
	AEB7283	CB	
Bourletiellidae	AEC7380	CB	
	AEC7525	KU, BY, KG	
	AEC7611	CB	



Supplementary Figure 1: Map of sampling locations of all 512 individuals generated from boldsystems.org. The majority of individuals were collected from the south west of Victoria Island in the surrounds of Cambridge Bay.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0.19 FCHAR6108-19|Entomobrya|Cambridge Bay|BOLD:AAF7753
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0.99 FCHAR8225-19|Entomobrya|Cambridge Bay|BOLD:AAF7753
0.97 FCHAR6072-19|Entomobrya|Cambridge (4) Bay|BOLD:AAF7753
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FCHAR6276-19|Entomobrya|Cambridge Bay|BOLD:ADT5266
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ACHAR3062-18|Entomobryomorpha|Cambridge (8) Bay|BOLD:ADR2480
FCHAR4173-19|Folsomia|Cambridge Bay|BOLD:AEC7431
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FCHAR4121-19|Folsomia|Cambridge Bay|BOLD:AEC8159
1 FCHAR4091-19|Entomobryomorpha|Cambridge Bay|BOLD:AEC0555
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FCHAR8179-19|Entomobryomorpha|Cambridge Bay|BOLD:AEC0555
FCHAR4673-19|Entomobryomorpha|Cambridge Bay|BOLD:AEC0925
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FCHAR4562-19|Entomobryomorpha|Cambridge Bay|BOLD:ADZ9063
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FCHAR4642-19|Entomobryomorpha|Cambridge Bay|BOLD:ADZ9063
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FCHAR8268-19|Entomobryomorpha|Cambridge (15) (2) Bay|BOLD:ADZ9063
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0.51
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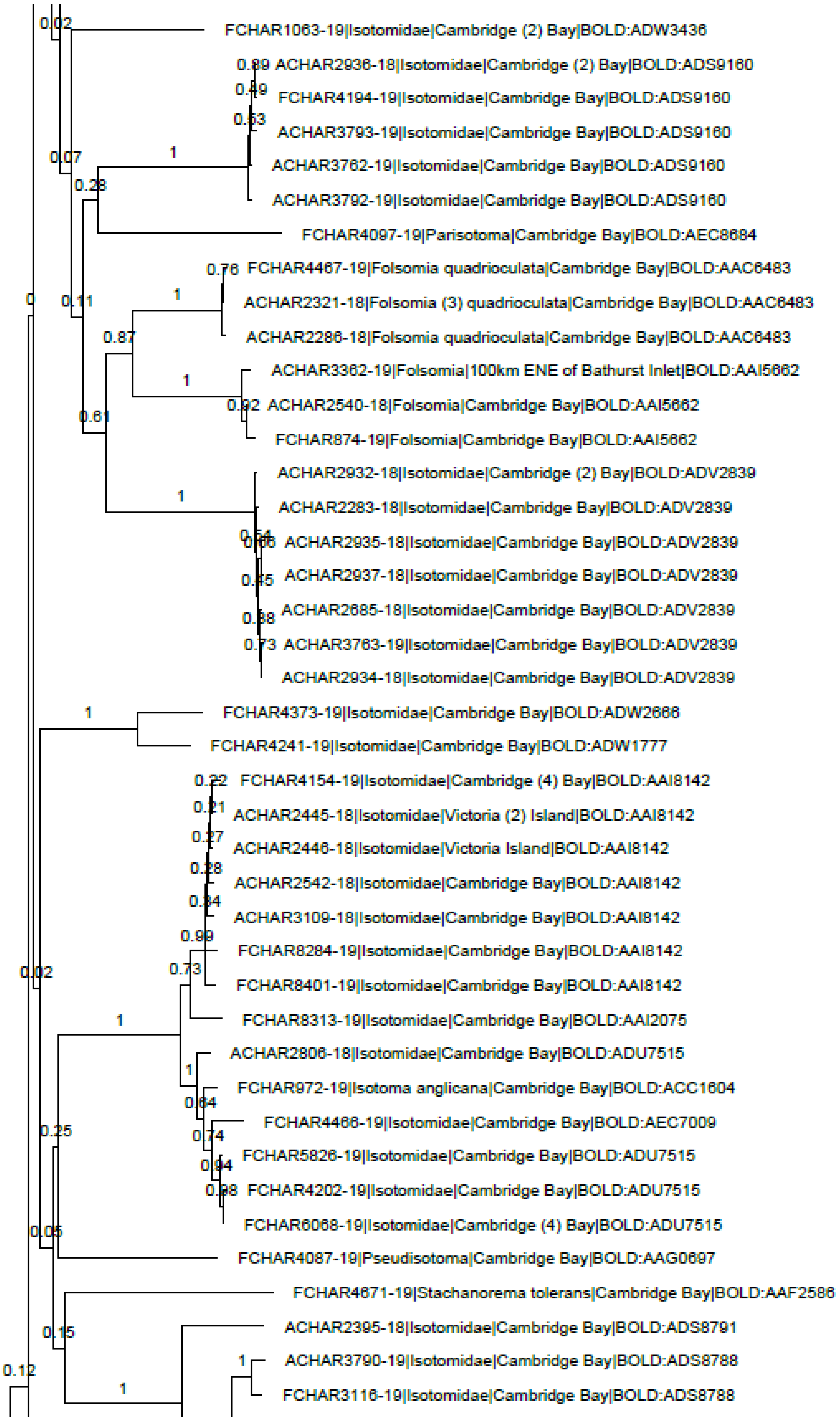
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0.11
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ACHAR2286-18|Folsomia quadrioculata|Cambridge Bay|BOLD:AAC6483
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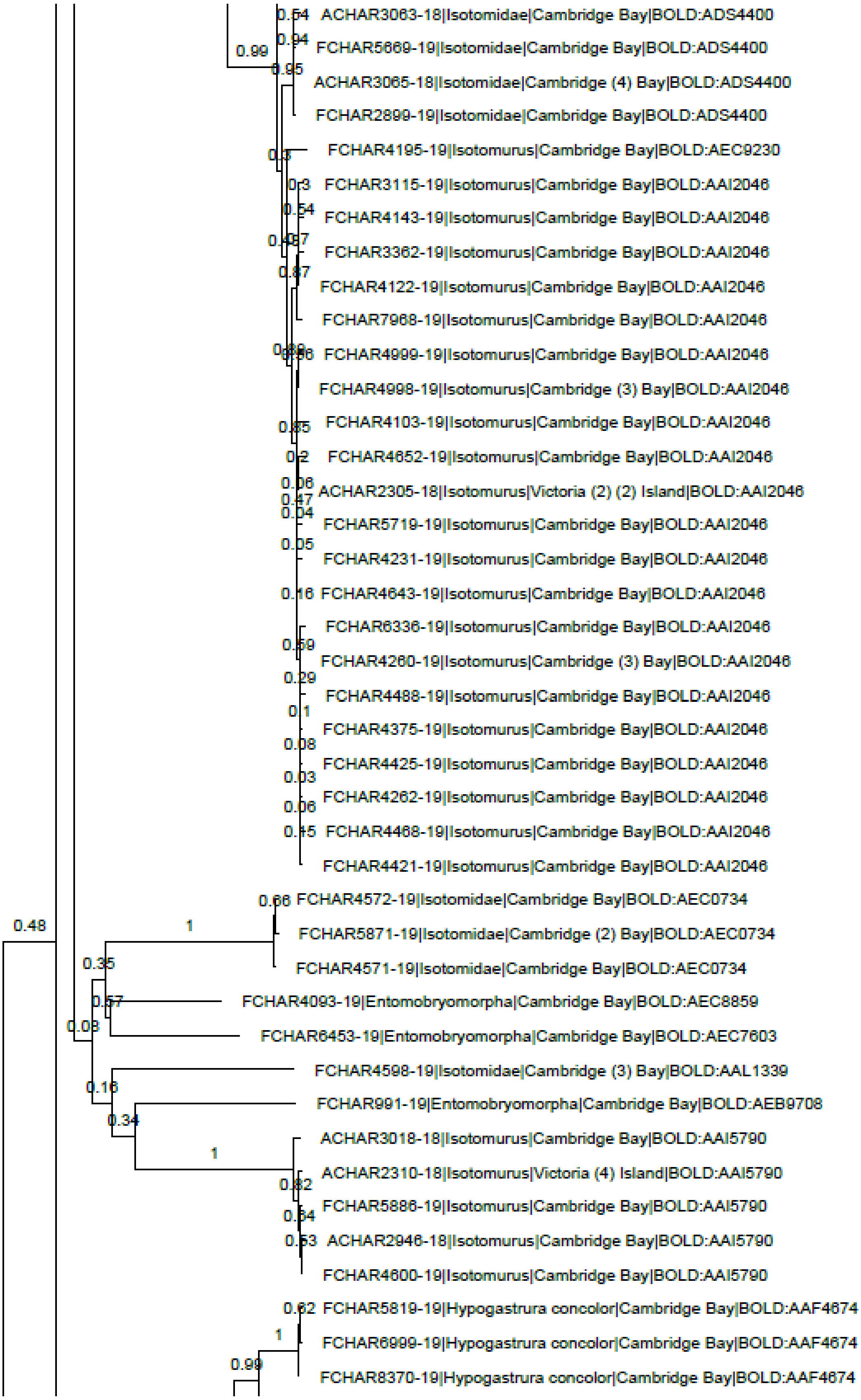
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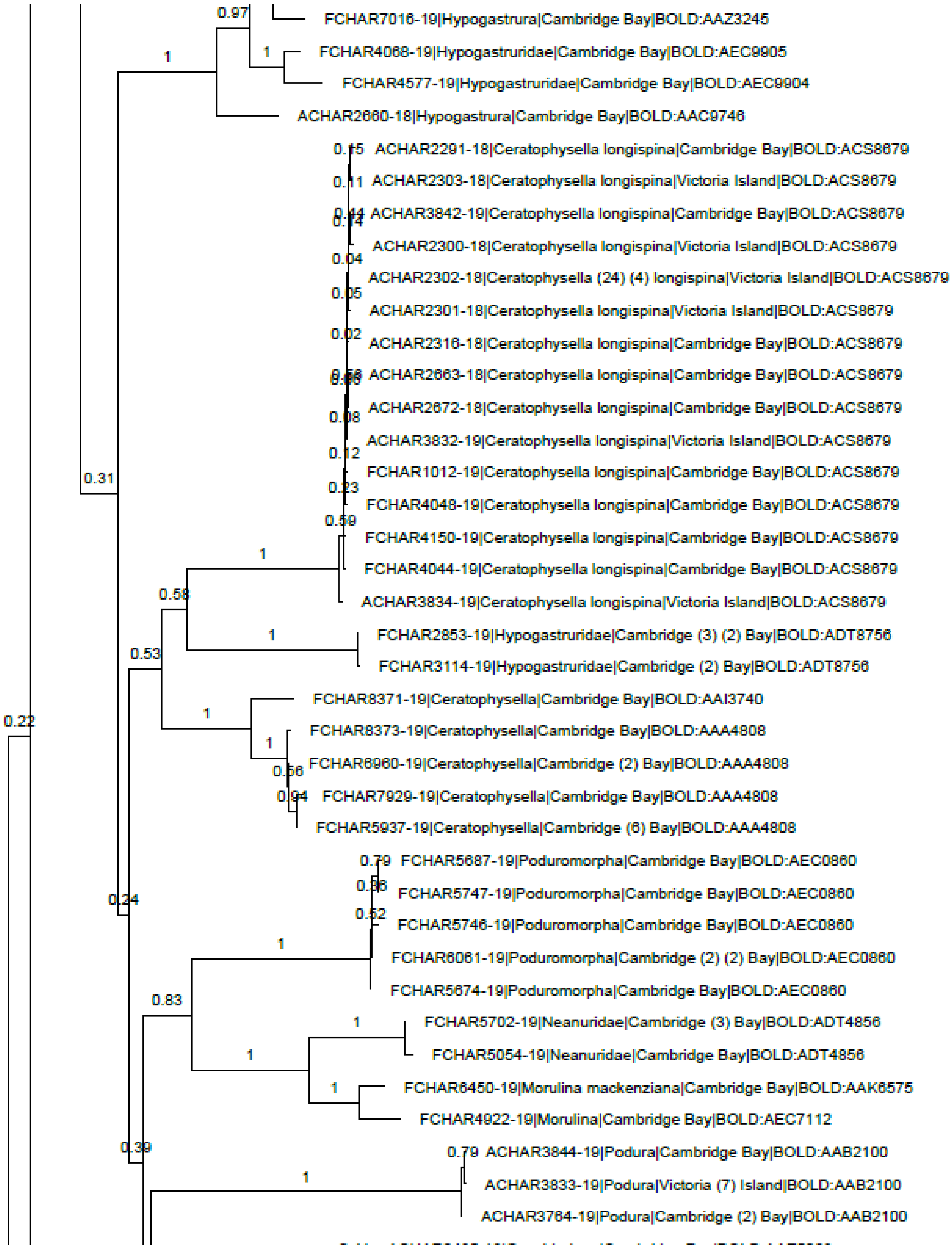
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ACHAR2302-18|Ceratophysella (24) (4) longispina|Victoria Island|BOLD:ACS8679
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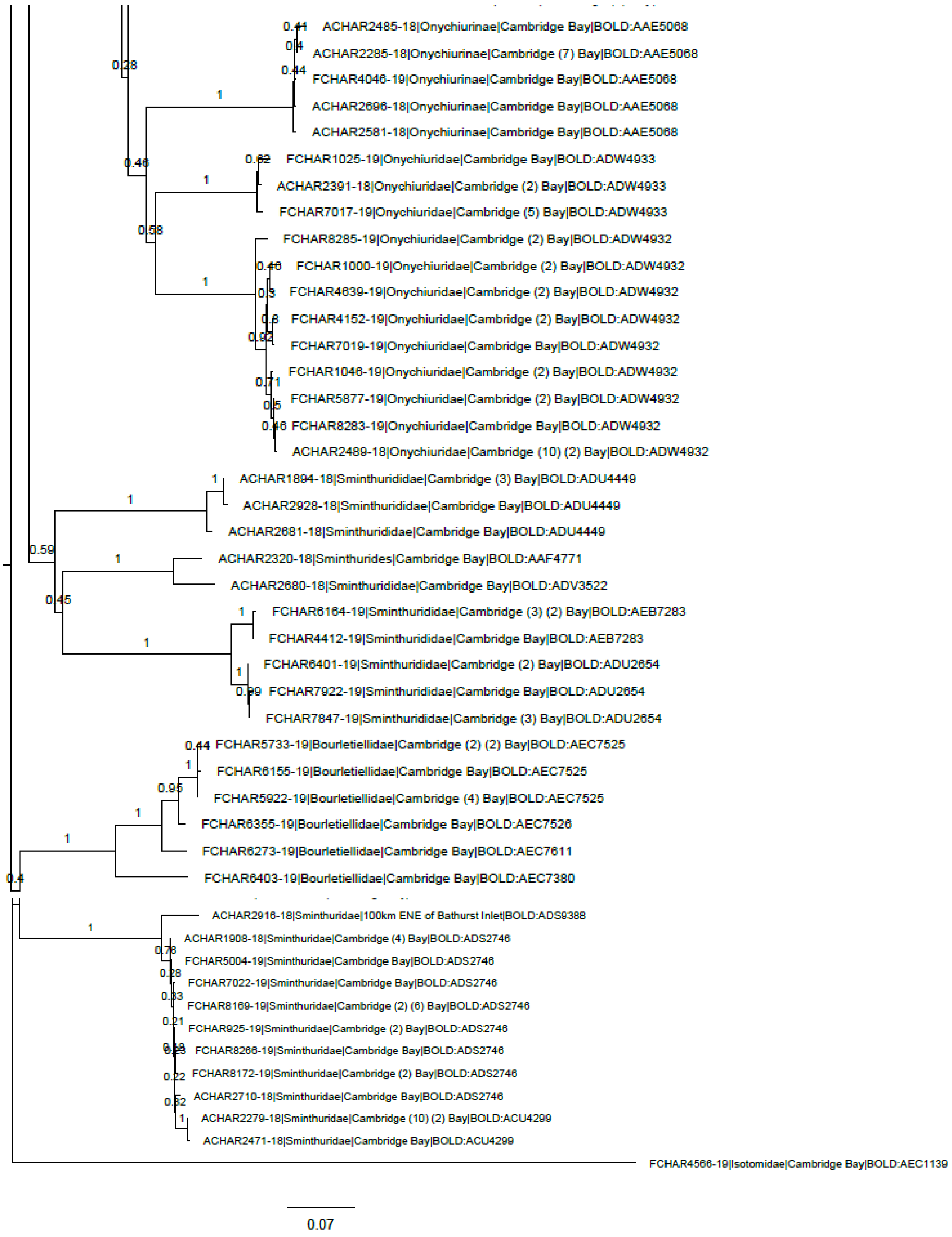
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ACHAR2391-18|Onychiuridae|Cambridge (2) Bay|BOLD:ADW4933
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FCHAR4639-19|Onychiuridae|Cambridge (2) Bay|BOLD:ADW4932
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FCHAR4152-19|Onychiuridae|Cambridge (2) Bay|BOLD:ADW4932
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FCHAR7019-19|Onychiuridae|Cambridge Bay|BOLD:ADW4932
FCHAR1046-19|Onychiuridae|Cambridge (2) Bay|BOLD:ADW4932
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FCHAR5877-19|Onychiuridae|Cambridge (2) Bay|BOLD:ADW4932
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FCHAR8283-19|Onychiuridae|Cambridge Bay|BOLD:ADW4932
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ACHAR1894-18|Sminthurididae|Cambridge (3) Bay|BOLD:ADU4449
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ACHAR2681-18|Sminthurididae|Cambridge Bay|BOLD:ADU4449
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FCHAR6401-19|Sminthurididae|Cambridge (2) Bay|BOLD:ADU2654
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0.99
FCHAR7922-19|Sminthurididae|Cambridge Bay|BOLD:ADU2654
FCHAR7847-19|Sminthurididae|Cambridge (3) Bay|BOLD:ADU2654
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FCHAR5733-19|Bourletiellidae|Cambridge (2) (2) Bay|BOLD:AEC7525
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FCHAR6155-19|Bourletiellidae|Cambridge Bay|BOLD:AEC7525
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FCHAR5922-19|Bourletiellidae|Cambridge (4) Bay|BOLD:AEC7525
1
FCHAR6355-19|Bourletiellidae|Cambridge Bay|BOLD:AEC7526
1
FCHAR6273-19|Bourletiellidae|Cambridge Bay|BOLD:AEC7611
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FCHAR6403-19|Bourletiellidae|Cambridge Bay|BOLD:AEC7380
ACHAR2916-18|Sminthuridae|100km ENE of Bathurst Inlet|BOLD:ADS9388
1
ACHAR1908-18|Sminthuridae|Cambridge (4) Bay|BOLD:ADS2746
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FCHAR5004-19|Sminthuridae|Cambridge Bay|BOLD:ADS2746
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FCHAR7022-19|Sminthuridae|Cambridge Bay|BOLD:ADS2746
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FCHAR8169-19|Sminthuridae|Cambridge (2) (6) Bay|BOLD:ADS2746
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FCHAR925-19|Sminthuridae|Cambridge (2) Bay|BOLD:ADS2746
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0.23
FCHAR8266-19|Sminthuridae|Cambridge Bay|BOLD:ADS2746
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FCHAR8172-19|Sminthuridae|Cambridge (2) Bay|BOLD:ADS2746
ACHAR2710-18|Sminthuridae|Cambridge Bay|BOLD:ADS2746
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ACHAR2279-18|Sminthuridae|Cambridge (10) (2) Bay|BOLD:ACU4299
ACHAR2471-18|Sminthuridae|Cambridge Bay|BOLD:ACU4299
FCHAR4566-19|Isotomidae|Cambridge Bay|BOLD:AEC1139
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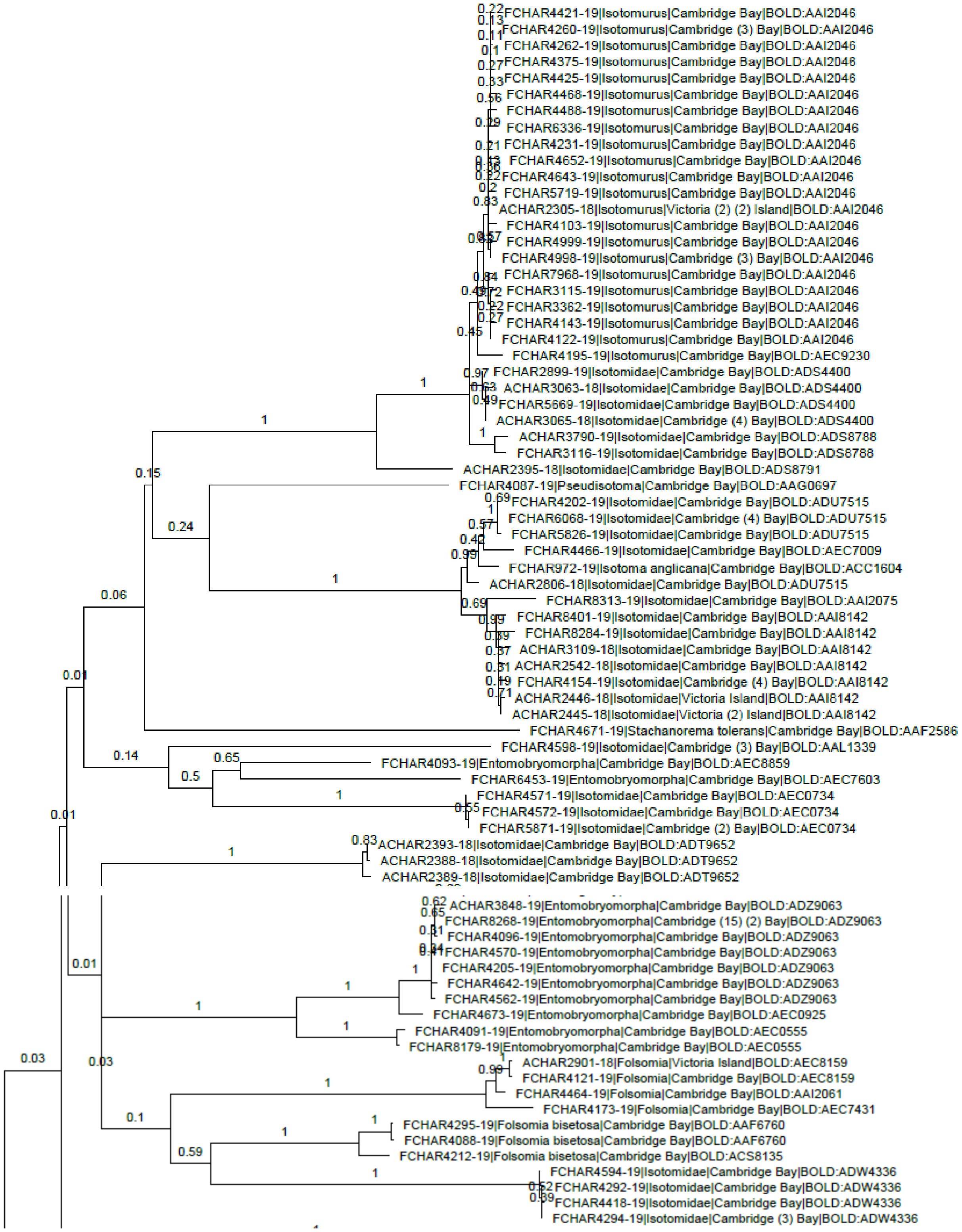
Supplementary Figure 2: Neighbour-Joining tree of 204 unique sequences. All bootstrap values are displayed. Sequence labels follow the following convention: BOLD process identification number| Taxonomic identification| Collection location and number of individuals representing each unique sequence in parentheses| BIN number.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FCHAR4488-19|Isotomurus|Cambridge Bay|BOLD:AAI2046
FCHAR6336-19|Isotomurus|Cambridge Bay|BOLD:AAI2046
FCHAR4231-19|Isotomurus|Cambridge Bay|BOLD:AAI2046
FCHAR4652-19|Isotomurus|Cambridge Bay|BOLD:AAI2046
FCHAR4643-19|Isotomurus|Cambridge Bay|BOLD:AAI2046
FCHAR5719-19|Isotomurus|Cambridge Bay|BOLD:AAI2046
ACHAR2305-18|Isotomurus|Victoria (2) (2) Island|BOLD:AAI2046
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FCHAR4195-19|Isotomurus|Cambridge Bay|BOLD:AEC9230
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FCHAR5669-19|Isotomidae|Cambridge Bay|BOLD:ADS4400
ACHAR3065-18|Isotomidae|Cambridge (4) Bay|BOLD:ADS4400
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FCHAR3116-19|Isotomidae|Cambridge Bay|BOLD:ADS8788
ACHAR2395-18|Isotomidae|Cambridge Bay|BOLD:ADS8791
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FCHAR6068-19|Isotomidae|Cambridge (4) Bay|BOLD:ADU7515
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ACHAR2542-18|Isotomidae|Cambridge Bay|BOLD:AAI8142
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FCHAR6453-19|Entomobryomorpha|Cambridge Bay|BOLD:AEC7603
FCHAR4571-19|Isotomidae|Cambridge Bay|BOLD:AEC0734
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ACHAR2388-18|Isotomidae|Cambridge Bay|BOLD:ADT9652
ACHAR2389-18|Isotomidae|Cambridge Bay|BOLD:ADT9652
ACHAR3848-19|Entomobryomorpha|Cambridge Bay|BOLD:ADZ9063
FCHAR8268-19|Entomobryomorpha|Cambridge (15) (2) Bay|BOLD:ADZ9063
FCHAR4096-19|Entomobryomorpha|Cambridge Bay|BOLD:ADZ9063
FCHAR4570-19|Entomobryomorpha|Cambridge Bay|BOLD:ADZ9063
FCHAR4205-19|Entomobryomorpha|Cambridge Bay|BOLD:ADZ9063
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FCHAR4673-19|Entomobryomorpha|Cambridge Bay|BOLD:AEC0925
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ACHAR2901-18|Folsomia|Victoria Island|BOLD:AEC8159
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FCHAR4464-19|Folsomia|Cambridge Bay|BOLD:AAI2061
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FCHAR4212-19|Folsomia bisetosa|Cambridge Bay|BOLD:ACS8135
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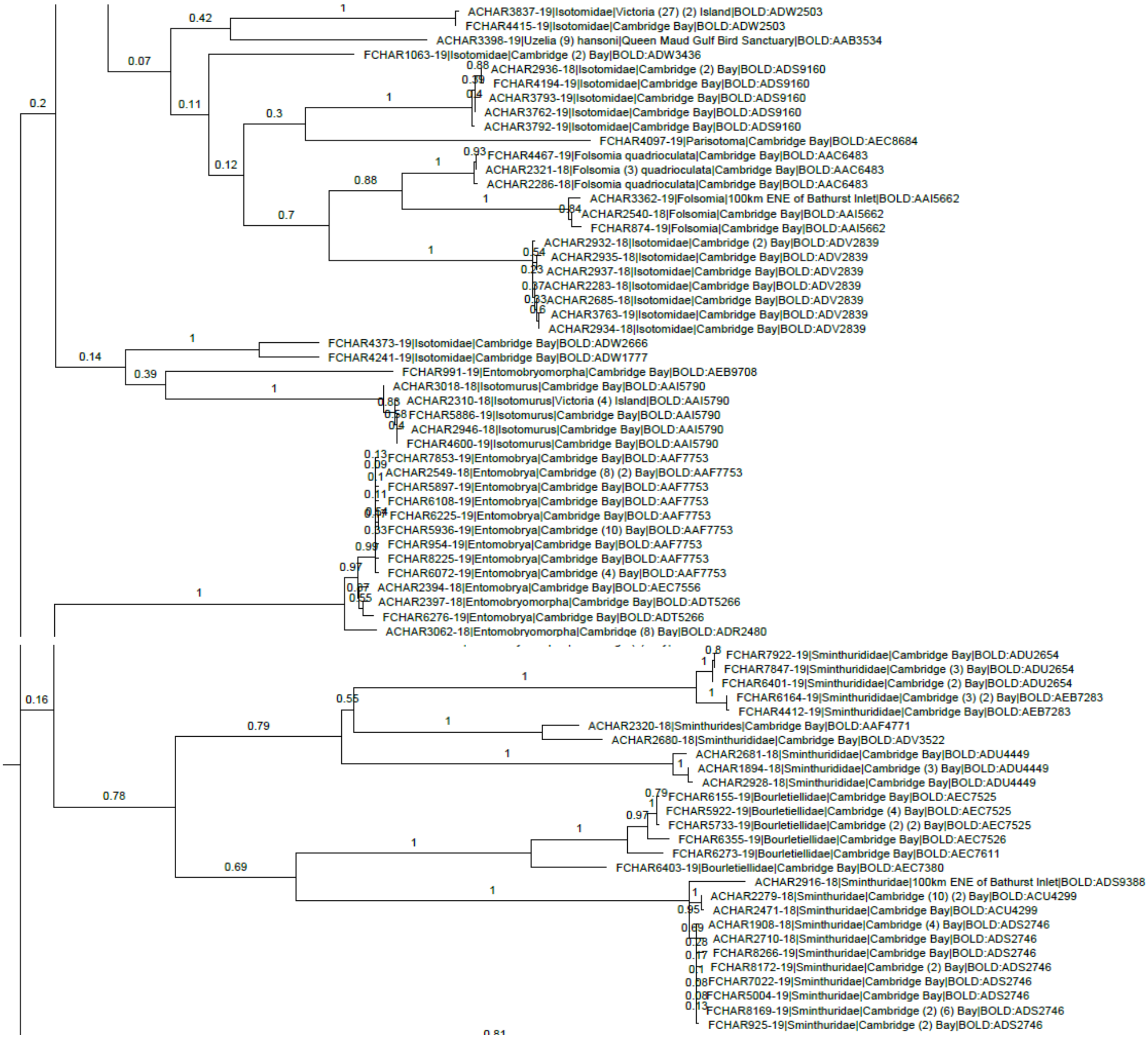
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FCHAR1063-19|Isotomidae|Cambridge (2) Bay|BOLD:ADW3436
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ACHAR2936-18|Isotomidae|Cambridge (2) Bay|BOLD:ADS9160
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FCHAR4194-19|Isotomidae|Cambridge Bay|BOLD:ADS9160
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ACHAR3793-19|Isotomidae|Cambridge Bay|BOLD:ADS9160
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ACHAR3762-19|Isotomidae|Cambridge Bay|BOLD:ADS9160
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FCHAR4467-19|Folsomia quadrioculata|Cambridge Bay|BOLD:AAC6483
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ACHAR2321-18|Folsomia (3) quadrioculata|Cambridge Bay|BOLD:AAC6483
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ACHAR2286-18|Folsomia quadrioculata|Cambridge Bay|BOLD:AAC6483
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ACHAR3362-19|Folsomia|100km ENE of Bathurst Inlet|BOLD:AAI5662
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ACHAR2540-18|Folsomia|Cambridge Bay|BOLD:AAI5662
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FCHAR874-19|Folsomia|Cambridge Bay|BOLD:AAI5662
ACHAR2932-18|Isotomidae|Cambridge (2) Bay|BOLD:ADV2839
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ACHAR2935-18|Isotomidae|Cambridge Bay|BOLD:ADV2839
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ACHAR2937-18|Isotomidae|Cambridge Bay|BOLD:ADV2839
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ACHAR2283-18|Isotomidae|Cambridge Bay|BOLD:ADV2839
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ACHAR2685-18|Isotomidae|Cambridge Bay|BOLD:ADV2839
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ACHAR3763-19|Isotomidae|Cambridge Bay|BOLD:ADV2839
ACHAR2934-18|Isotomidae|Cambridge Bay|BOLD:ADV2839
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FCHAR4373-19|Isotomidae|Cambridge Bay|BOLD:ADW2666
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FCHAR4241-19|Isotomidae|Cambridge Bay|BOLD:ADW1777
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FCHAR991-19|Entomobryomorpha|Cambridge Bay|BOLD:AEB9708
ACHAR3018-18|Isotomurus|Cambridge Bay|BOLD:AAI5790
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ACHAR2310-18|Isotomurus|Victoria (4) Island|BOLD:AAI5790
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FCHAR5886-19|Isotomurus|Cambridge Bay|BOLD:AAI5790
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ACHAR2946-18|Isotomurus|Cambridge Bay|BOLD:AAI5790
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FCHAR7853-19|Entomobrya|Cambridge Bay|BOLD:AAF7753
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ACHAR2549-18|Entomobrya|Cambridge (8) (2) Bay|BOLD:AAF7753
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FCHAR6108-19|Entomobrya|Cambridge Bay|BOLD:AAF7753
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FCHAR6225-19|Entomobrya|Cambridge Bay|BOLD:AAF7753
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FCHAR5936-19|Entomobrya|Cambridge (10) Bay|BOLD:AAF7753
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FCHAR7847-19|Sminthurididae|Cambridge (3) Bay|BOLD:ADU2654
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FCHAR6164-19|Sminthurididae|Cambridge (3) (2) Bay|BOLD:AEB7283
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FCHAR4412-19|Sminthurididae|Cambridge Bay|BOLD:AEB7283
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ACHAR2320-18|Sminthurides|Cambridge Bay|BOLD:AAF4771
ACHAR2680-18|Sminthurididae|Cambridge Bay|BOLD:ADV3522
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FCHAR6273-19|Bourletiellidae|Cambridge Bay|BOLD:AEC7611
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FCHAR6403-19|Bourletiellidae|Cambridge Bay|BOLD:AEC7380
ACHAR2916-18|Sminthuridae|100km ENE of Bathurst Inlet|BOLD:ADS9388
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1
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ACHAR2471-18|Sminthuridae|Cambridge Bay|BOLD:ACU4299
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ACHAR1908-18|Sminthuridae|Cambridge (4) Bay|BOLD:ADS2746
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ACHAR2710-18|Sminthuridae|Cambridge Bay|BOLD:ADS2746
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FCHAR8172-19|Sminthuridae|Cambridge (2) Bay|BOLD:ADS2746
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FCHAR7022-19|Sminthuridae|Cambridge Bay|BOLD:ADS2746
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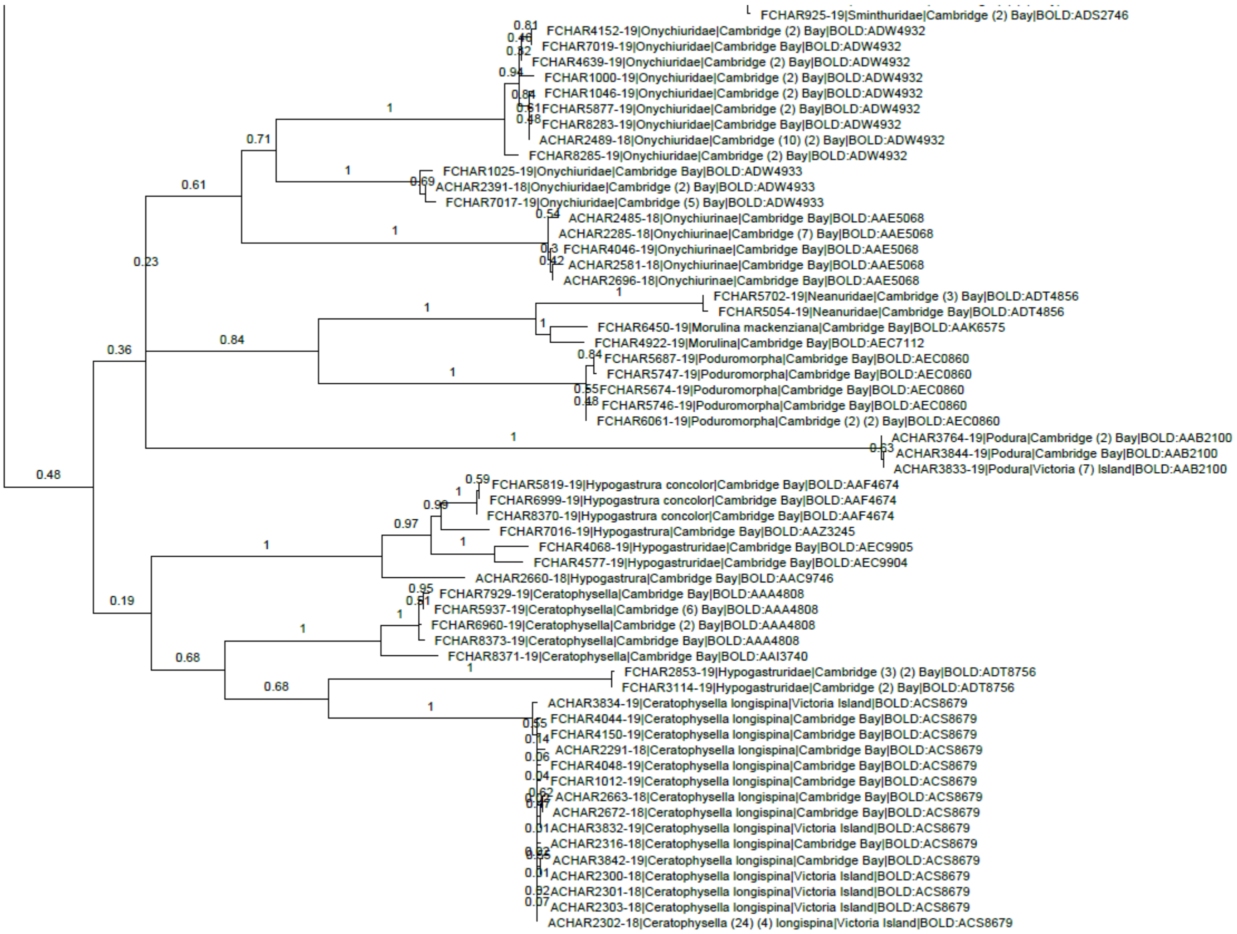
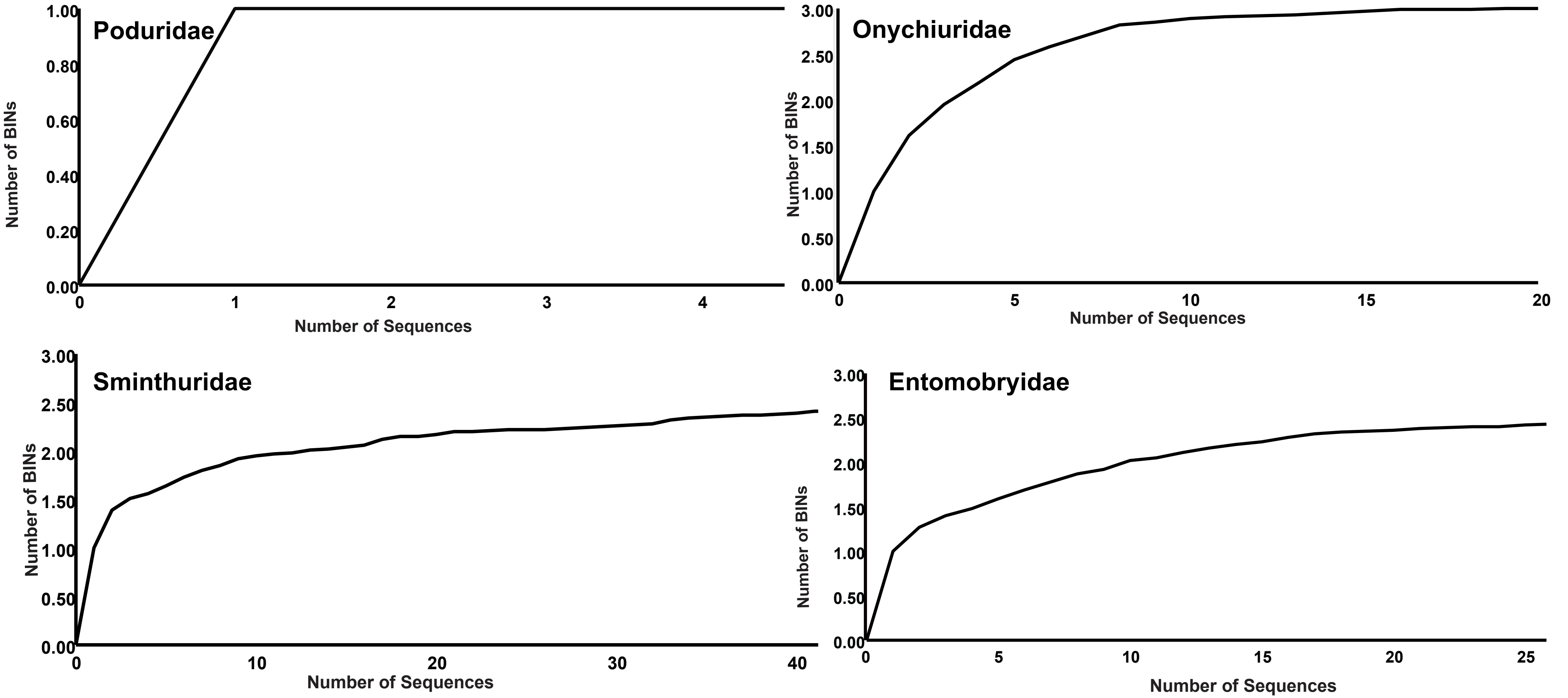
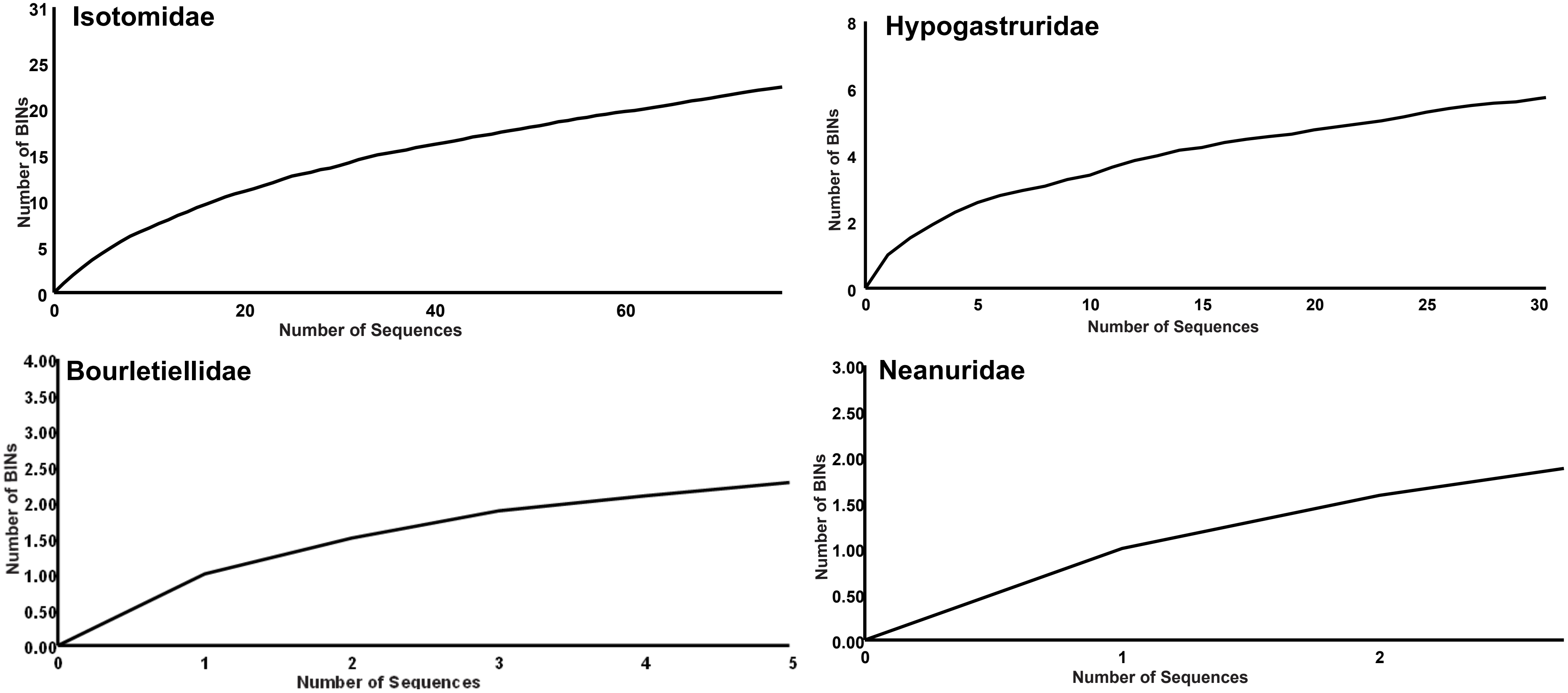


Supplementary Figure 3: Maximum likelihood tree of 204 unique sequences. All bootstrap values are displayed. Sequence labels follow the following convention: BOLD process identification number| Taxonomic identification| Collection location and number of individuals representing each unique sequence in parentheses| BIN number.



Supplementary Figure 4: Species-level accumulation curves based on total number of unique BINs for taxonomic families that have reached or are approaching the asymptote. Number of BINs are provided on the y axis and the number of sequences are on the x axis. The species accumulation curve was calculated using inbuilt software on the boldsystems.org database.



Supplementary Figure 5: Species-level accumulation curves based on total number of unique BINs for taxonomic families that are yet to reach their asymptote. Number of BINs are provided on the y axis and the number of sequences are on the x axis. The species accumulation curve was calculated using inbuilt software on the boldsystems.org database.

Supplementary Figure 6: Map of all sequenced Collembola across the Nunavut (Canada), Northwest Territories (Canada), Alaska, Greenland and Svalbard generated from boldsystems.org. Data for Yukon were unavailable.

CHAPTER IV

Physiology of Collembola from the Canadian Arctic suggests a level of tolerance to warming

Abstract

The Arctic fauna is currently exposed to a range of increasingly variable and extreme environmental conditions driven by climate change, which may pose a particular threat to ectothermic invertebrates including Collembola whose body temperatures largely track that of their environment. However, few studies have examined the physiological tolerances of Arctic Collembola which impairs our ability to predict their resilience to climate change. Here, I assessed the physiological tolerances for five abundant surface-active species of Collembola representing four families (*Isotomurus* sp., *Entomobrya comparata, Podura aquatica, Sminthurides malmgreni*, *Sminthurus aquaticus*) collected from terrestrial and limnetic habitats at Cambridge Bay (Ikaluktutiak) on Victoria Island in the Canadian Arctic. Upper functional thermal limits were measured via critical thermal maxima (CT_{max}) with individuals equilibrated at 10 °C for 15 min and then warmed at a rate of 0.25 °C/min until the onset of muscular spasms. Lower lethal thermal limits measured via supercooling points (SCP) with individuals equilibrated at 0 °C for 15 min and then cooled at a rate of 0.25 °C/min until a visible exotherm at freezing. I also examined the desiccation tolerance of one species by measuring survival time in response to a mild desiccation stress. Sampled individuals had high levels of heat tolerance with mean critical thermal maxima (CT_{max}) all above 30 °C. Overall, individuals exhibited CT_{max} ranging between 26 °C and 41 °C. Most individuals displayed limited cold tolerance, with a majority (64 %) exhibiting SCPs higher than -10 °C. Supercooling points ranged widely between -3.4 to -25.3 °C, with three species exhibiting bimodal distributions of SCPs. Under desiccating conditions, individuals of *E. comparata* survived for up to 13.5 hrs (range: 1.0-13.5 hrs) with 50 % of individuals surviving for less than 9.25 hrs. Accordingly, summer acclimated Collembola currently appear capable of surviving short-term exposure to warmer and drier conditions, although there are high levels of variability both within and among species. The low levels of cold tolerance across species could suggest a vulnerability to sudden summer extremes in cold.

1. Introduction

The Arctic fauna is currently exposed to a range of increasingly variable and extreme environmental conditions driven by climate change (Screen 2014, Vasseur et al. 2014, Christensen et al. 2021). To date, air temperatures in the Arctic have warmed at more than twice the global average, resulting in an increased incidence of temperature extremes (Masson-Delmotte et al. 2021). Warming has also led to a decline in snow-pack accumulation which influences soil moisture and the thermal buffering potential of soils (Convey et al. 2015, Box et al. 2019, Meredith et al. 2019). Collectively, these environmental changes may result in increased physiological stress for soil invertebrates (Hodkinson and Coulson 2004, Koltz et al. 2018b). This could be particularly evident among ectothermic invertebrates such as Collembola which have body temperatures that track that of their environment (Huey and Kingsolver 1989, Sinclair et al. 2016). Collembola are key components of Arctic terrestrial and limnetic food-webs mediating rates of decomposition, plant-microbe interactions, and nutrient cycling (Birkemoe and Liengen 2000, Koltz et al. 2018a, Potapov et al. 2020). Accordingly, any disturbance to the collembolan fauna is likely to cascade through the food-web (Hodkinson et al. 2004, Koltz et al. 2018b). Climate change is already altering patterns of insect emergence (Hodkinson et al. 2013) and abundances (Koltz et al. 2018b, Høye et al. 2021) as well as decreasing individual body sizes at maturity (Bowden et al. 2015).

The proximity of physiological limits to current environmental conditions (e.g. thermal safety margins), levels of acclimation capacity and plasticity can all help inform population response to climate change (Sunday et al. 2014). Physiological studies of Arctic Collembola have largely been limited to *Megaphorura arctica* (formerly *Onychiurus arcticus*) (Holmstrup and Sømme 1998, Worland et al. 1998, Holmstrup 2018b). These studies have highlighted adaptations to extreme Arctic environments including cryoprotective dehydration (Sørensen and Holmstrup 2011). Collembola avoid freezing by either suppressing their freezing point through the accumulation of cryoprotective molecules (e.g. glycerol, trehalose) and supercooling or reducing body water content until they become unfreezable (cryoprotective dehydration) (Cannon and Block 1988, Worland and Block 2003, Sørensen and Holmstrup 2011). Through these mechanisms, Arctic Collembola can display considerable cold tolerance, with individuals of *M. arctica* acclimated at -12.4 °C for seven days tolerating temperatures as low as -30 °C (Holmstrup and Sømme 1998). However, as *M.*

arctica undergoes cryoprotective dehydration, its physiological tolerances are unlikely to be representative of Collembola that survive via supercooling. Arctic Collembola can also display high levels of heat tolerance with *Xenylla humicola* (Hypogastruridae) and *Hypogastrura viatica* (Hypogastruridae) having mean critical thermal maxima of >40 °C (Allen et al. 2016). *Megaphorura arctica* survived brief exposures to 35 °C (Everatt et al. 2014), although heat tolerance varied based on levels of humidity and desiccation stress (Block et al. 1994, Hertzberg and Leinaas 1998). Collembola can be particularly susceptible to desiccation stress as they have a semi-permeable outer integument (Hopkin 1997, Hertzberg and Leinaas 1998). While some Collembola are inherently desiccation tolerant due to their utilisation of cryoprotective dehydration, most are not (Sørensen and Holmstrup 2011). Collembola have been observed following soil moisture profiles seasonally, reinforcing its importance in shaping behavioural and physiological tolerances (Convey and Block 2001, Hayward et al. 2001, Hayward et al. 2004).

Previous studies have provided physiological tolerances for seven species Arctic Collembola (Sørensen and Holmstrup 2011, Everatt et al. 2014, Allen et al. 2016, Holmstrup 2018a). However, expanding physiological studies to a wider range of species and over a broader geographic range would be beneficial as local environmental conditions are known to modulate physiological traits (Sengupta et al. 2016, Sengupta et al. 2017). There are currently over 425 known species of Collembola from the Arctic (Hodkinson et al. 2013). In the Canadian Arctic, 49 morphologically identified species have been recorded (Danks 1990) with potentially as many as 68 putative species on Victoria Island based on mitochondrial cytochrome c oxidase subunit 1 (COI) gene sequences (Danks 1990; Chapter III). The Arctic tundra includes species that dwell deeper in the soil profile as well as surface-active species which are found across terrestrial and limnetic habitats (Hogg and Hebert 2004, Väre et al. 2013, Asmus et al. 2018). Location in the soil profile will influence the environmental conditions that individuals are exposed to and thus the physiological tolerances that are selected for (Liu et al. 2020, Beet et al. 2022, Chapter II). Surface-active springtails are potentially exposed to the greatest fluctuations in temperature and moisture and may therefore have the widest range of physiological tolerances. In a sub-Arctic peatland there was an approximate 10 °C difference in temperatures between surface and deeper soils (Krab et al. 2013). Vegetation can further modify surface microclimates (Convey et al. 2018) while solar insolation can heat the dark surface layers of soil to over 30 °C (Hodkinson 2005).

Assessing the physiological limits for a range of resident Collembola will therefore, aid in predicting the resilience of Arctic taxa and food-webs, to climate change (Beet et al. 2022, Chapter II). Here, we assessed the physiological tolerances for five abundant surface-active species of Collembola (representing four families) collected from terrestrial and limnetic habitats at Cambridge Bay on Victoria Island in the Canadian Arctic. Upper thermal limits were measured via critical thermal maxima ($CT_{\max}$), with lower thermal limits measured via supercooling points (SCP). We also examined the desiccation tolerance of one species by measuring survival time in response to desiccation stress.

2. Methods

2.1 Site description and animal collection

Individual Collembola were collected from near the Canadian High Arctic Research Station (CHARS), in Cambridge Bay/ Ikaluktutiak (also spelled Iqaluktuuttiaq, Ekaluktutiak and ᐃᖃᓗᒃᑑᑦᑎᐊᖅ; 69.1141-105.0472) located on southern Victoria Island (Kilinoyak) in the Kitikmeot Region of Nunavut, Canada. Cambridge Bay is situated amongst a largely flat thermokarst landscape with numerous ponds. Vegetative communities dominated by non-tussock sedge, dwarf-shrubs, lichen covered rocks and moss (Pentinsaari et al. 2020; Chapter III). Sampling was undertaken from 11 July 2019 to 1 August 2019 with individuals collected predominantly within 100 m of the Canadian High Arctic Research Station (Supplementary Fig. 1). Collembola were collected using a hand-made aspirator (constructed using a 1 ml pipette tip, mesh and tubing) from underneath rocks or, for aquatic taxa, netted from the water surface near a pond edge. Collected individuals were placed onto moistened plaster of Paris (poured into 10 ml containers) and returned to the laboratory within approximately 10 minutes of collection and physiological experiments were initiated within 30 minutes thereafter. Microclimate temperatures were obtained using a HOBO Micro Station Data Logger (model H21-002, Onset, Cape Cod, MA, USA) with two thermistor sensors recording temperatures every 10 minutes near the study site. Weather station data including temperature and relative humidity were downloaded from July and August 2019 to provide broader context for the local microclimate data (Source: https://climate.weather.gc.ca/historical_data/search_historic_data_stations_e.html). Species observed and collected in sufficient quantities to facilitate analyses included *Isotomurus* sp. and *Entomobrya comparata* from terrestrial habitats along with *Podura aquatica, Sminthurides malmgreni* and *Sminthurus aquaticus* from the aquatic habitats (Supplementary Fig. 2). Species were identified morphologically, based on Christiansen and Bellinger (1980), with identifications confirmed using cytochrome *c* oxidase subunit 1 (COI) gene sequencing (*sensu* Hebert et al. 2003) through the LifeScanner application (www.lifescanner.net/).

2.2 Physiological Tolerances

Critical thermal maxima ($CT_{\max}$) were measured using a dynamic assay (cf. Jørgensen et al. 2019) in a free-ranging open arena. Critical thermal maxima were measured as they are the upper functional thermal limits that individuals can tolerate. Critical thermal maximum is indicated by the onset of observable muscular spasms/ contractions and "springing" (Sinclair et al. 2006). Measures of $CT_{\max}$ are a proxy for heat tolerances and are informative as survival, reproduction, feeding and activity will all be impaired if individuals are frequently exposed to these stressful temperatures. We measured the $CT_{\max}$ of three species (*E. comparata*, *Isotomurus* sp., and *P. aquatica*). The two Sminthurid species were not assessed for $CT_{\max}$ due to their small size and frequent "springing" at all temperatures which hindered the ability to accurately measure $CT_{\max}$..Each run involved a minimum of 8 individuals (range: 8-36). Multiple species were examined together in each run to ensure that individuals were all exposed to similar conditions. Collembola were placed on moistened filter paper on a copper stage whose temperature was controlled by a custom-built Peltier-effect system (described by Anthony et al. 2019). Four thermocouples were placed in the copper stage and averaged to gain an accurate measure of surface temperature. Thermocouples were monitored using PicoLog software via a Picotech TC-08 thermocouple interface (PicoTechnology, Cambridge, United Kingdom). Collembola were able to move freely around the stage and equilibrated at 10 °C for 15 min. After equilibration Collembola were gradually warmed at a rate of 0.25 °C/min until $CT_{\max}$ was reached. Different studies have used warming rates of 0.05, 0.2, 0.25, 0.5 °C/min, the rate of 0.25 °C/min was chosen as it is an intermediate rate and has been previously used on Polar Collembola (Sinclair et al. 2006, Everatt et al. 2013, Janion-Scheepers et al. 2018). $CT_{\max}$ was determined based on the onset of observable muscular spasms/ contractions or "springing" following vigorous activity at high temperatures. Individuals that had reached $CT_{\max}$ were removed and the corresponding temperature recorded. This was continued until all individuals had reached their $CT_{\max}$. Surviving individuals were returned to the environment with a sub-set of individuals preserved in 100% ethanol. Data were imported to, and analysed in, R v 1.1.423 (RStudio Team 2016). Ggplot2 (Wickham 2016) was used to visualise the data with boxplots and histograms to compare critical thermal maxima across species.

Supercooling points (SCPs) were measured for five species (*Podura aquatica, Entomobrya comparata, Isotomurus sp., Sminthurides malmgreni, Sminthurides aquaticus*). The use of SCPs was based on (Sinclair et al. 2015) and measured as the temperatures at which individuals froze (as a proxy for cold tolerance). Each run included multiple species to ensure they were all exposed to similar conditions. Collected individuals were gently affixed to a thermocouple with a small amount of grease as per Sinclair *et al.* (2015). Individual Collembola and thermocouples were then placed into 1.5 ml tubes. Thermocouples were monitored using PicoLog software via a Picotech TC-08 thermocouple interface

(PicoTechnology, Cambridge, United Kingdom). Tubes were placed into a copper block with 16 1.5 ml tube holes. The copper block was cooled electronically via a peltier system as above. Individuals were equilibrated at 0 °C for 15 min before being gradually cooled at a rate of 0.25 °C/min until all individuals had reached their SCP as evidenced by a visible exotherm (brief spike in temperature due to the release of latent heat at freezing). Different studies have used cooling rates of 0.1 to 0.25 °C/min, I chose a rate of 0.25°C/min as it has been used on Polar Collembola and for consistency and comparison with other studies (Sinclair *et al.* 2006, Sinclair *et al.* 2015; Chapter V). Individual supercooling points were recorded for further analysis. All species were deemed to be freeze intolerant with no signs of recovery following freezing. Data were imported to, and analysed in, R v 1.1.423 (RStudio Team 2016). Ggplot2 (Wickham 2016) was used to visualise the data with boxplots and histograms to compare supercooling points across species.

Desiccation tolerances of *Entomobrya comparata* were evaluated by measuring survival time following exposure to a drought stress. Desiccation tolerance of only *E. comparata* was measured due to the abundance of individuals enabling easier collection and the intention for individuals to be processed for transcriptome analyses in a related study. Individuals were collected at 0900 on the 15/07/2019 with the experiment instigated within 30 minutes of collection. Individual Collembola were placed inside 0.5 ml PCR strip tubes that had multiple holes in them. Tubes of Collembola were then placed inside a small container with desiccating silica gel and kept in an incubator at 10 °C as silica gel is known to reduce relative humidity to 40-60 % (Tétreault and Bégin, 2017). The number of surviving individuals was measured every 15 minutes. A total of 31 individuals were exposed to the desiccation treatment, a further eight control individuals were placed in the same tubes inside a separate replicate container and placed in the 10 °C incubator. Data were imported to, and analysed in, R v 1.1.423 (RStudio Team 2016). The package survival (Therneau 2022) was used to create survival curves from the Kaplan Meier formula. Ggplot2 (Wickham 2016) was used to graph the survival curves.

Figure 1: Map of Canada indicating the location of Cambridge Bay (noted by the blue box) on Victoria Island within Nunavut. Adapted from: Atlas of Canada, https://www.nrcan.gc.ca/earth-sciences/geography/atlas-canada/explore-our-maps/reference-maps/16846

3. Results

We obtained data on the physiological tolerances of five species (*Podura aquatica, Entomobrya comparata, Isotomurus sp., Sminthurides malmgreni, Sminthurus aquaticus*) representing four families (Poduridae, Entomobryidae, Isotomidae Sminthuridae) and three orders (Poduromorpha, Entomobryomorpha, Symphypleona). These species represented a range of body sizes from the smallest *Sminthurides malmgreni* to the largest *Isotomurus* sp. which was approximately four times the length of *S. malmgreni*.

Studied Collembola exhibited high levels of heat tolerance with mean $CT_{\max}$ all above 30 °C. Overall $CT_{\max}$ temperatures ranged between 26 °C and 41 °C (Fig. 2A, Table 1). *Entomobrya comparata* individuals exhibited the highest level of heat tolerance as well as the narrowest range with all individuals exhibiting $CT_{\max}$ between 34 and 41 °C. *Podura aquatica* and *Isotomurus* sp. had similar ranges of critical thermal maxima, both with median $CT_{\max}$ of 32 °C. However, most *Isotomurus* individuals reached their $CT_{\max}$ at 32 °C, while most *P. aquatica* individuals were over 35 °C. The distribution of *E. comparata* and *Isotomurus* sp. $CT_{\max}$ were both broadly normally distributed while the distribution of *P. aquatica* $CT_{\max}$ was skewed towards more heat tolerant individuals (Fig. 2B).

Most individuals we examined displayed limited cold tolerance, with the majority (64 %) exhibiting supercooling points (SCPs) of less than -10 °C. Overall, SCPs ranged widely between -3.4 to -25.3 °C (Fig. 3A, Table 2). With the exception of *E. comparata,* all other species had similar median SCPs of -6.3 to -7.1 °C. The species with the most cold-tolerant individuals were *P. aquatica* and *E. comparata.* While, based on average values (median -6.3 °C), the least cold-tolerant species were *Isotomurus* sp. and *S. aquaticus*. Three out of the five species examined (*E. comparata*, *P. aquatica* and *S. malmgreni*), had bimodal distributions of SCPs with an initial peak around -5 to -7 °C followed by another peak at -15 to -18 °C (Fig. 3B).

Under desiccating conditions, *Entomobrya comparata* individuals survived up to 13.5 hrs at 10 °C (Fig. 4, Table 3). Only one individual was still alive after this time, when the experiment was terminated. Other individuals began dying within one hour of the experiment starting with 50 % of individuals dead by 9.25 hrs and 80 % dead after 11.75 hours (Fig. 4). All eight of the control individuals survived the entire experimental period.

The thermal tolerances of the five species examined consistently exceeded maximum and minimum soil temperatures that were measured throughout the sampling period. Soil temperatures fluctuated on a diurnal cycle, and did not fall below 0 °C. The average surface soil temperature was 8.4 °C, with a maximal daily temperature fluctuation of 10.6 °C (Fig. 5). Peak daily temperatures were generally above 15 °C with a maximum temperature of 19.4 °C. A majority (73 %) of microclimate temperatures were between 4 and 12 °C. Peak air temperatures measured at the Cambridge Bay weather station across July and August 2019 were 21.6 °C and corresponded with minimum relative humidity levels of 44 % (Fig. 6). The average air temperature based on climate station data was 8.1 °C with mean relative humidity of 82.9 %.

Table 1: Summary table of Critical thermal maxima temperatures for three species. N= number of individuals measured. All other metrics refer to $CT_{\max}$ temperatures in °C

***CT*max**	**N**	**Mean**	**Median**	**Min**	**Max**
E. comparata	66	38.3	39	34	41
Isotomurus sp.	23	31.9	32	26	37
P. aquatica	41	31.7	32	26	36
Total	130	35.1	36	26	41

Table 2: Summary table of supercooling point temperatures for three species. N= number of individuals measured. All other metrics refer to supercooling temperature in °C

SCP	**N**	**Mean**	**Median**	**Min**	**Max**
E. comparata	87	-13	-11.8	-24	-3.4
Isotomurus sp.	24	-6.92	-6.35	-15.7	-4.8
P. aquatica	33	-8.93	-6.4	-25.3	-4.9
S. aquaticus	21	-7.22	-6.3	-15.5	-4.9
S. malmgreni	33	9.2	-7.1	-22.3	-5.5
Total	198	-10.3	-7.2	-25.3	-3.4

Table 3: Summary table of survival times in response to a desiccation stress for *Entomobrya comparata.* N= number of individuals, all other metrics refer to survival time in minutes.

Desiccation tolerance	**n**	**Mean**	**Median**	**Min**	**Max**
E. comparata	31	529.5	562.5	60	>810

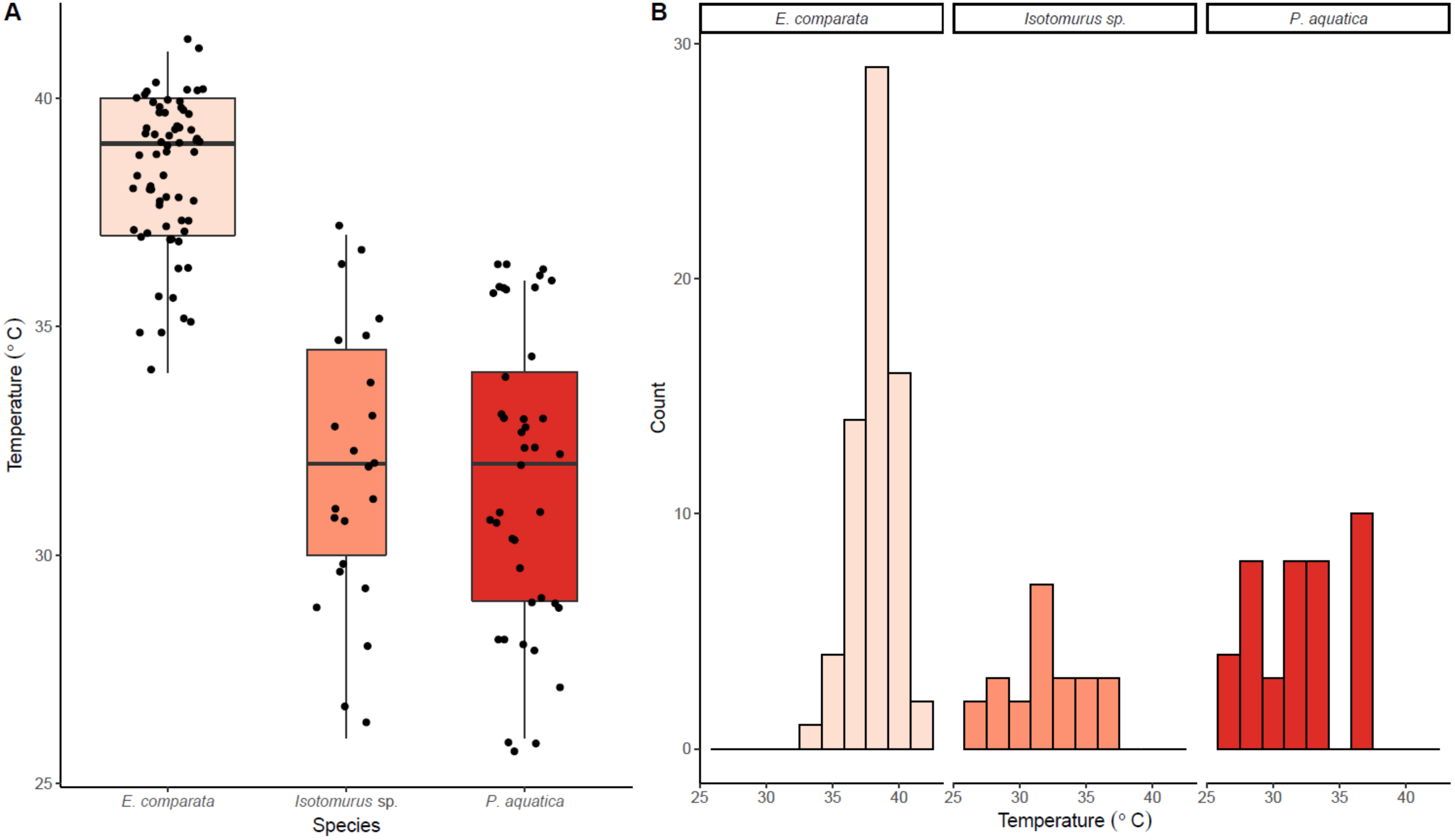


Figure 2: A= Boxplots of the temperatures (°C) at which three species of Collembola (*Entomobrya comparata*, *Isotomurus* sp., *Podura aquatica*) collected from Cambridge Bay, NU reached their critical thermal maxima ($CT_{\max}$ range: 26-41 °C). B= Histograms showing the distribution of critical thermal maxima of three species, with the number of individuals Count) that reached their $CT_{\max}$ at each temperature on the y axis. Temperature in °C, and coloured based on species.

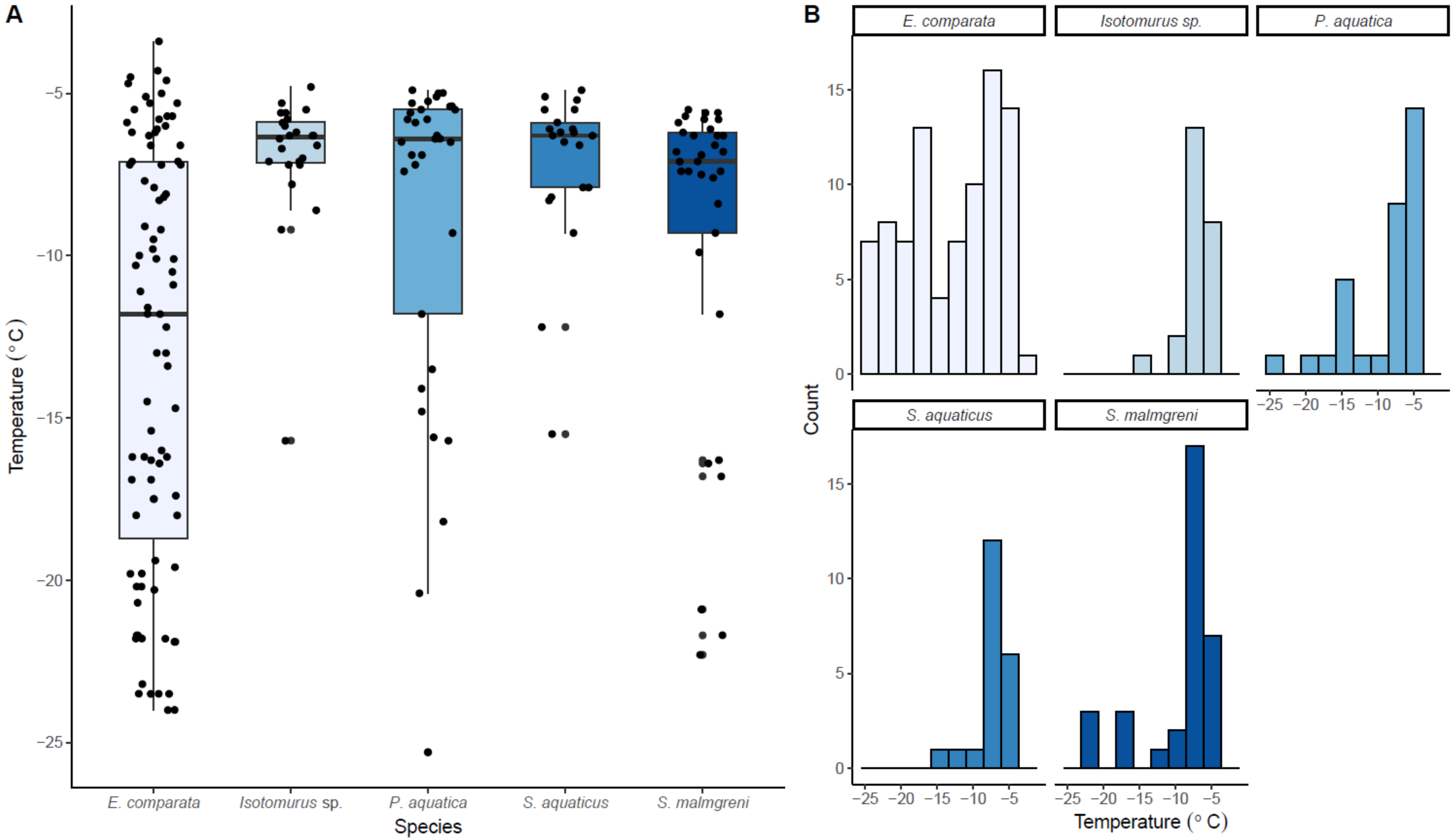


Figure 3: A= Boxplots of the temperatures (°C) at which five species of Collembola (*Entomobrya comparata*, *Isotomurus* sp., *Podura aquatica, Sminthurides aquaticus, Sminthurides malmgreni*) collected from Cambridge Bay, NU reached their supercooling point (SCP range: -3.4 to -25.3). B= Histograms showing the distribution of supercooling points of five species, with the number of individuals (Count) that reached their supercooling point at each temperature on the y axis. Temperature in °C, and coloured based on species.

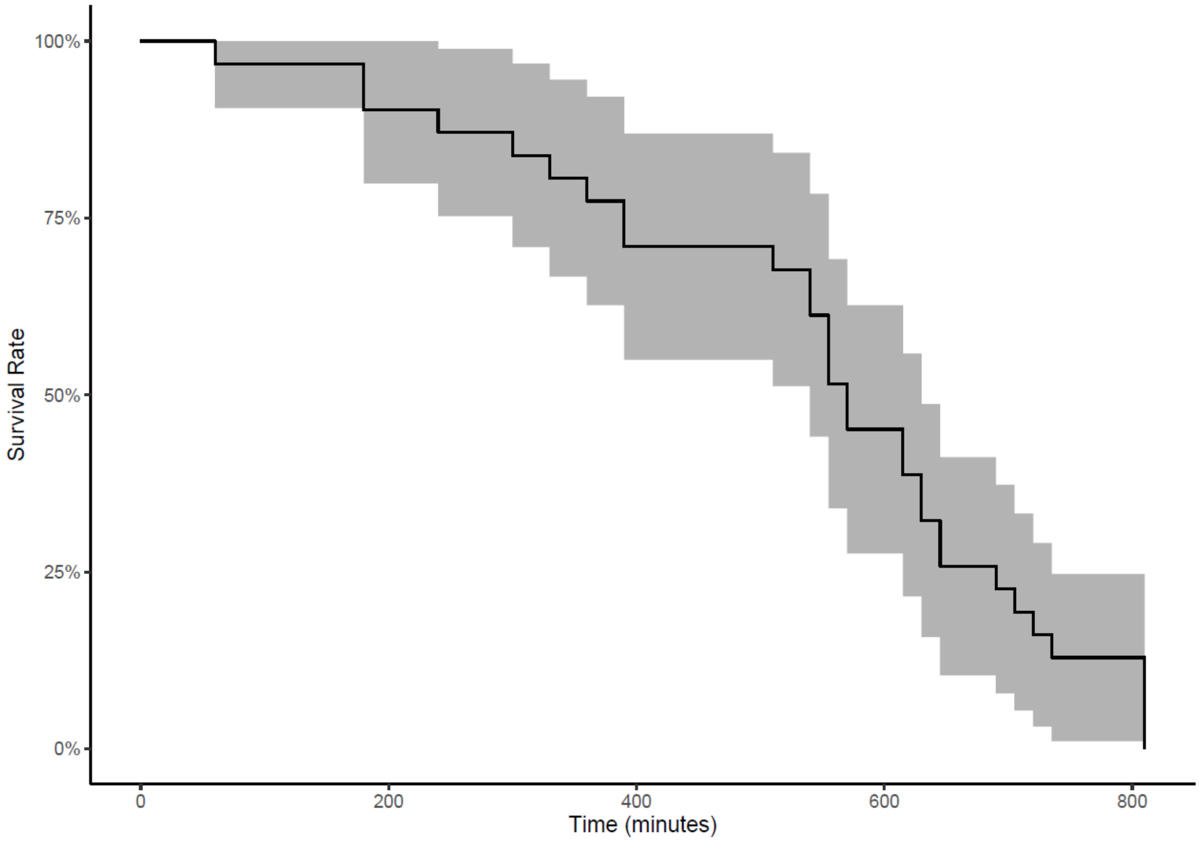


Figure 4: Kaplan-Meier graph of survival rate of *Entomobrya comparata* under desiccating conditions. The black line is the survival rate of measured individuals, the grey area is the 95 % confidence interval.

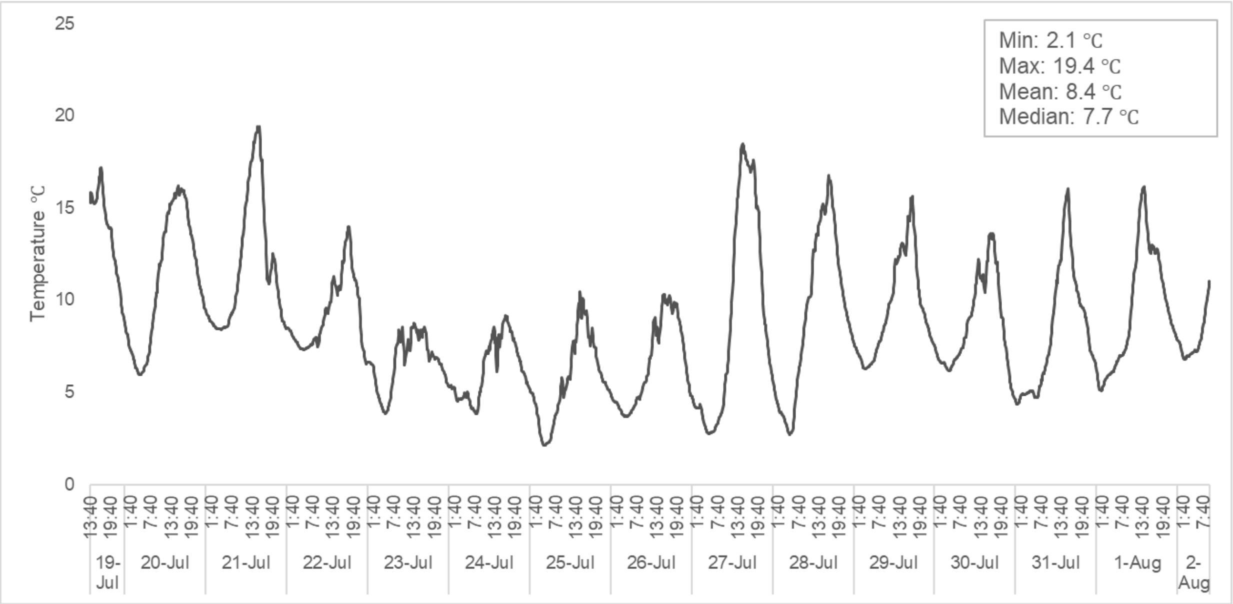


Figure 5: Surface soil microhabitat temperature monitoring near the Canadian High Arctic Research Station at Cambridge Bay, NU from 19 July to 2 August 2019. Summary statistics are displayed in the inset.

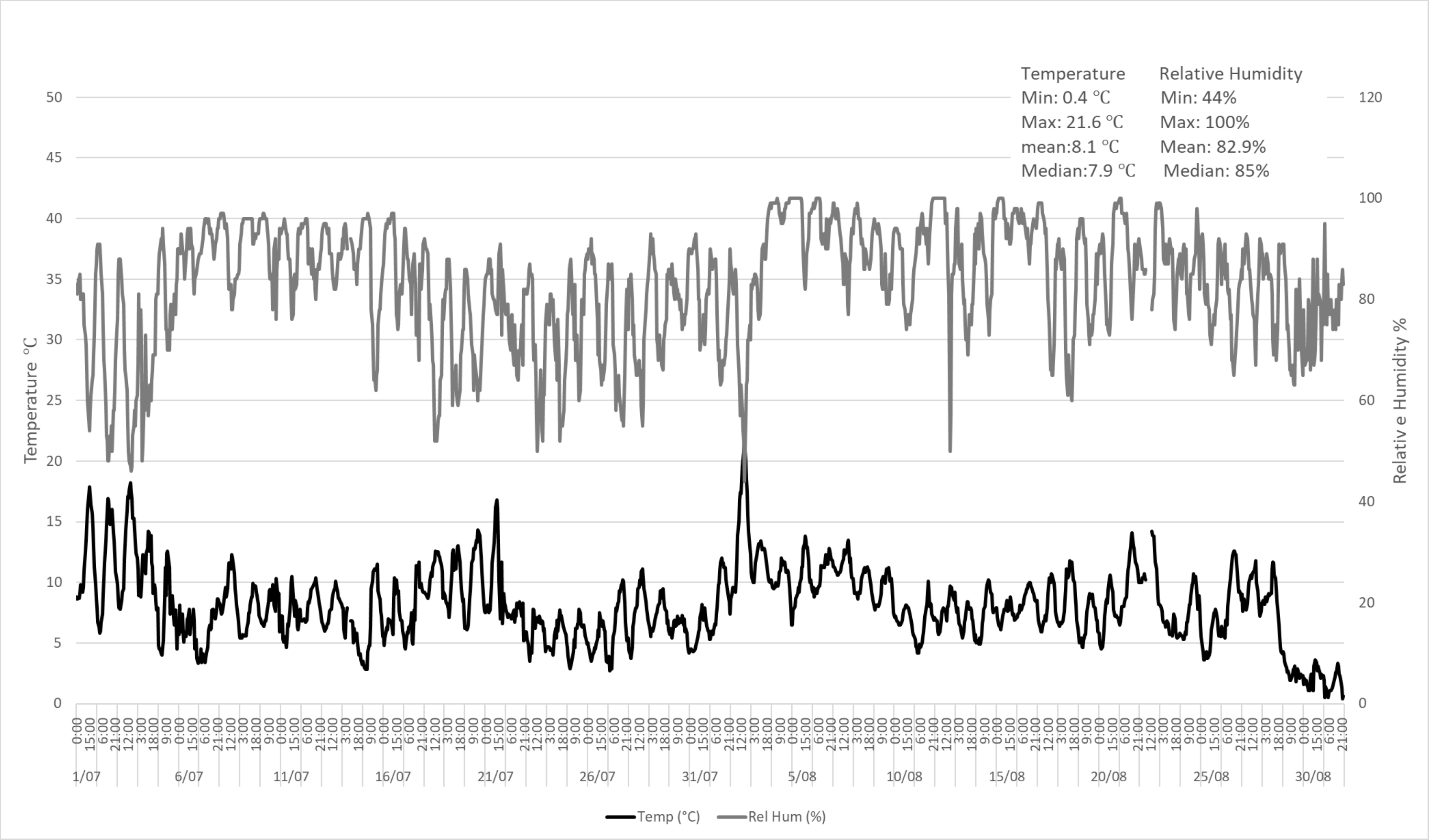


Figure 6: Cambridge Bay weather station data from July to August 2019. Data were collected every hour. The black line represents temperature data in (°C), while the grey line indicates relative humidity (%). Data sourced from: https://climate.weather.gc.ca/historical_data/search_historic_data_stations_e.html

4. Discussion

Our study examined the physiological tolerances of five abundant, widespread surface-active Arctic species. We found that summer-acclimated Arctic Collembola have high levels of heat tolerance but limited cold tolerance. The limnetic Collembola *Podura aquatica* along with *Sminthurides aquaticus* and *S. malmgreni* have a cosmopolitan or Holarctic distribution while *Entomobrya comparata* and *Isotomurus* sp. are Nearctic in origin (Ávila-Jiménez and Coulson 2011, Babenko et al. 2019). The species we examined represented three of the four Collembola orders, four families, a range of body sizes, and contrasting habitats (terrestrial and limnetic), and may broadly represent the physiological tolerances for surface-active species from similar Arctic habitats.

The mean critical thermal maxima ($CT_{\max}$) of all three species were over 30 °C. *Entomobrya comparata* had the highest number of heat tolerant individuals with a maximal observed $CT_{\max}$ of 41 °C. The $CT_{\max}$ of *Podura aquatica* and *Isotomurus* sp. were in line with continental Antarctic species (Chapter V, Sinclair *et al.* 2006) which exist in cooler environments. Both *P. aquatica* and *Isotomurus* sp. although markedly different in body length, exhibited remarkably similar levels of heat tolerance (Supplementary Fig. 1). By comparison, the $CT_{\max}$ of *Entomobrya comparata* individuals which were intermediate in size (relative to the other two species) were higher than some Arctic (Everatt et al. 2014) and Antarctic species (Sinclair et al. 2006, Everatt et al. 2013; Chapter V). *Entomobrya comparata* $CT_{\max}$ were similar to *Seira* spp. from the Cape Floristic region of South Africa which had mean $CT_{\max}$ of over 45 °C (Liu et al. 2020). The intraspecific variation in $CT_{\max}$ could in part be attributed to the presence of cryptic genetic diversity. All of the species tested here were represented by multiple BINs (Chapter III). The minimum $CT_{\max}$ of all species measured here were at least 6 °C above the maximal recorded microclimate temperatures. Local weather station data from July and August of 2019 recorded a maximal temperature of 21.6 °C which was still below all measured minimum $CT_{\max}$. Collectively, this implies a level of resilience to current extreme high temperatures and, potentially, a level of resilience to warming air temperatures. However, multiple studies have demonstrated that Collembola have limited intraspecific variation in heat tolerance, especially when compared to cold tolerance (Slabber et al. 2007, Everatt et al. 2013, Janion Scheepers et al. 2018, Phillips et al. 2020). There was a range of <11 °C in $CT_{\max}$ within each species compared to a maximal range in supercooling points of 21.9 °C. This could imply that there is little adaptive capacity, relative to increasing $CT_{\max}$. While $CT_{\max}$ are indicative of upper functional thermal limits, they are not necessarily representative of survival rates to prolonged raised temperatures. Humidity levels can have a considerable impact on survival rates (Block et al. 1994).

The majority of individuals measured (64 %) had limited cold tolerance with supercooling points (SCPs) higher than -10 °C although there were high levels of variation in SCP within species. The biggest difference in SCP was 21.9 °C between individuals of *S. malmgreni*. Our more comprehensive sampling of *E. comparata* showed a broader range of SCP responses and a higher incidence of more cold tolerant individuals. *Hypogastrua viatica* and *Protaphorura mcfadyeni* originally collected from Svalbard and acclimated at 1.5 °C in the lab had mean supercooling points of -22.0 and -24.2 °C respectively, indicating considerably greater levels of cold tolerance than observed in this study (Holmstrup 2018a). Due to short summer seasons and logistical challenges, many cold tolerance studies for Arctic Collembola have been conducted on lab-cultured specimens (Bahrndorff et al. 2006, Holmstrup 2018a). While informative, these studies likely do not reflect the physiological tolerances of natural summer-acclimated populations, reinforcing the need for wider sampling of field populations.

Three of the five species we examined (*E. comparata*, *P. aquatica* and *S. malmgreni*) exhibited bimodal distributions of SCPs. Bimodal distributions of SCPs are often reflective of the presence of feeding and non-feeding individuals (Worland and Convey 2008). Any food-items present in the gut could serve as ice nucleators and otherwise raise the SCP of feeding individuals (Cannon and Block 1988). *Isotomurus* sp., and *S. aquaticus* predominantly had individuals with SCPs higher than -10 °C. Four of the five species (excepting *E.comparata*), had mean SCPs of higher than -10 °C. Cryoprotective or thermal hysteresis proteins (THPs) that enable lower SCPs are energy intensive to produce. During the experimental period, temperatures did not fall below 0 °C which would reduce the need for such metabolically expensive THPs (Zizzari and Ellers 2011, Klepsatel et al. 2016). Under current summer temperatures, it would be adaptive to have limited cold tolerance. For *Hypogastrura tullbergi* individuals from Svalbard, there was limited evidence for any rapid or diurnal cold tolerance acclimation during summer, relying instead on behavioural responses in the short-term (Hawes et al. 2006).

Individuals of *Entomobrya comparata* demonstrated considerable desiccation tolerance, surviving up to 13.5 hours under desiccating conditions at 10 °C. However, some individuals were more sensitive to desiccating conditions and succumbed in as little as one hour, suggesting high levels of intraspecific variation in desiccation tolerance which may in part be due to base water content levels at the start of the experiment. The level of desiccation stress individuals were exposed to was comparable with minimum levels of relative humidity observed on hot days, indicating that some individuals would need to employ behavioural avoidance or acclimation to survive. Tropical fynbos shrub-dwelling *Seira* spp. exhibited much higher levels of desiccation tolerance with median survival times of 14.9 hours in response to 0 % relative humidity (RH) and 59 hours in response to 76 % RH (Liu et al. 2021). By comparison, less than 50 % of Antarctic *Cryptopygus antarcticus* individuals survived 1.5 hours of desiccation stress at 0 % RH (Elnitsky et al. 2008). This demonstrates that desiccation tolerance can be highly variable among Collembola. Temperate and sub-Arctic studies have shown that 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). Gaining a better understanding of desiccation tolerances is critical as humidity can have a considerable impact on other stressors, particularly heat stress (Bahrndorff et al. 2007, Everatt et al. 2015). For example, at 100% humidity >80% of *Megaphorura arctica* individuals survived a three hour exposure to 30 °C while there were no survivors following exposure to 0% humidity at 25 °C for three hours (Block et al. 1994). Climate change is predicted to reduce winter snowpack and, in turn, summer water availability through reduced snow melt, although such losses may be offset by an increase in rainfall. In addition, higher temperatures will increase rates of soil evaporation collectively increasing desiccation stress (Box et al. 2019). A combination of high air temperatures coupled with low relative humidity could therefore place individual Collembola under considerable stress.

The context of what thermal tolerances are selected for is dependent on the actual microclimate temperatures that individuals are exposed to; and their ability to behaviourally avoid environmental stressors (Beet et al. 2022, Chapter II). Unlike continental Antarctic habitats, the Arctic presents increased opportunities for behavioural mitigation of environmental stressors. In the central Canadian Arctic region there are 640 vascular plants including 137 common species and 34 endemic species (Väre et al. 2013). The combination of shrubs, tussock and moss hedges provide a diversity of microhabitats and increased potential buffering from stressors. In summer, moving into the shade is enough to alleviate the worst of UV, heat and desiccation stress (Hawes et al. 2012, Dahl et al. 2017, Asmus et al. 2018). Collembolan taxa have varied capacity for behavioural mitigation, with the highest capacity found among surface-active species with larger furcula and longer limbs (Hopkin 1997, Krab et al. 2013). All of the species we examined here were surface-active species, with the potential for behavioural mitigation. This could account for the limited cold tolerance capacities we observed.

Our study provides an assessment of the physiological tolerances of Arctic Collembola. The taxa we examined demonstrated a high level of heat and desiccation tolerance, although this did not account for sustained sub-lethal levels of interacting stressors. In order to more fully assess the physiological tolerances of Arctic Collembola, future studies would benefit from: 1) addressing the effects of sub-lethal temperatures on survival and fecundity; 2) examining the influence of plasticity and seasonal acclimation on heat and cold tolerance; and 3) examination of physiological tolerances of taxa which live deeper in the soil profile and may have reduced capacity to behaviourally mitigate harmful temperatures. We suggest that the biggest threats to the resilience of Arctic Collembola are likely to result from a combination of stressors including longer-term increases in air temperatures and changes in relative humidity.

Acknowledgements

Financial support provided through funding of Polar Knowledge Canada Contract 3Y004-210046 to Brent J Sinclair. Field work was carried out at the Canadian High Arctic Research Station, with support from Polar Knowledge Canada.

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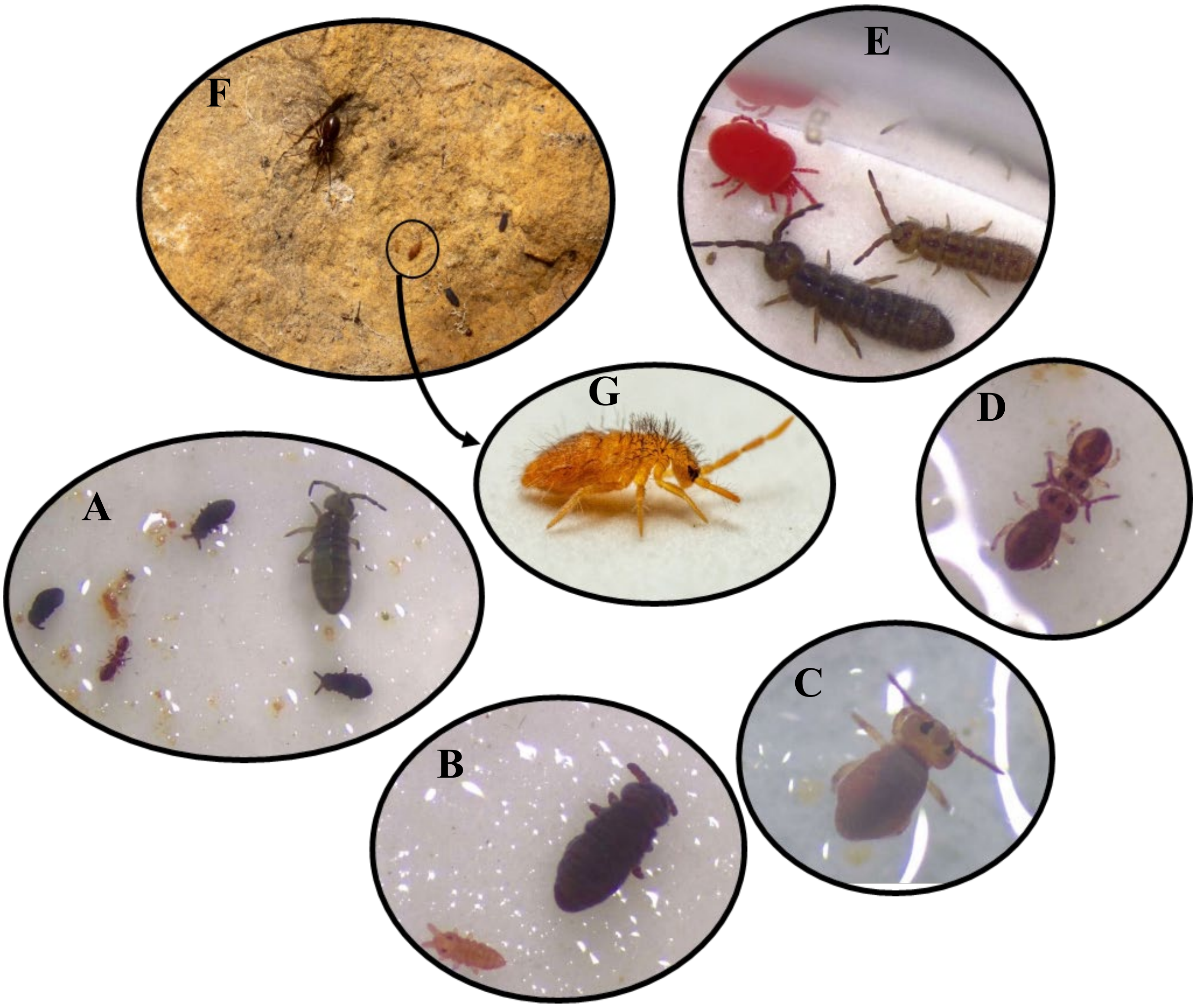
Supplementary Materials

Supplementary Fig. 1: A: Google earth photo of Cambridge Bay township indicating the location of collembola collection locations for physiological analyses. B: Zoomed in google earth photo showing more detail on collection locations. 1= Cambridge Bay High Arctic Research Station. 2= Collection location for *Entomobrya compara* and *Isotomurus* sp. individuals primarily found on the underside of small flat rocks. Also, the location of where the HOBO microclimate station was deployed. 3= Location of a small pond where rafts of Collembola were seen and *Podura aquatica*, *Sminthurides malmgreni* and *Sminthurus aquaticus* individuals were collected from.



Supplementary Fig. 2: Photos of sampled species. A: photo demonstrating size comparison between the large *Isotomurus* sp., *Podura aquatica* and the small *Sminthurides aquaticus*. B: *Podura aquatica* and juvenile. C: *Sminthurides malmgreni*. D: *Sminthurides aquaticus*. E: Two *Isotomurus* sp. individuals and a red velvet mite. F: photo of the underside of a rock where *Entomobrya comparata* (circled) were commonly found along with *Morulina* sp. and a spider. G: *Entomobrya comparata*, photo credit Brent J Smith. Photo credit for all other photos Clare Beet.

CHAPTER V

Fine-scale population genetic structure and thermal tolerance variation in an Antarctic Collembolan*

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* Intended to be published under the same title as: Clare R. Beet Ian D. Hogg, S. Craig Cary, Ian R. McDonald, Brent J. Sinclair

Abstract

Predicting how populations will respond to climate change requires an understanding of how intrinsic organismal traits underly responses to environmental stressors. Here, we consider how genetics and physiology may interact to shape resilience to climate change in Antarctic Collembola. Previous studies have identified two genetically divergent (1.6-2.4 % sequence divergence at the mitochondrial cytochrome c oxidase subunit I (*COI)* gene) populations (X and Y) of the Antarctic collembolan *Gomphiocephalus hodgsoni* and suggested that they may have differing thermal tolerances due to evolution under disparate paleoclimate conditions. Here we hypothesised that among-population genetic differentiation would yield physiological differentiation in tolerances of hot and cold temperatures. To test this, we measured critical thermal maxima (upper functional thermal limit, CT_{max}) and supercooling points (lower thermal limit, SCP) of individuals collected from two locations which broadly served as a proxy for the two genetically divergent populations. Individuals from the X population were collected from a warmer, coastal site versus individuals of the Y population which were collected from a cooler, inland location. We found that individuals from the warmer coastal site had higher upper thermal limits (mean CT_{max} 31.3 °C, range: 19-36 °C) compared to individuals from the cooler inland location (mean CT_{max} 27.2 °C, range: 17-35 °C, p=0.149) although this difference was more attributed to microhabitat temperatures (p=0.0014), suggesting a level of plasticity in heat tolerance. Coastal individuals also had higher mean supercooling points (coastal: -14.3 °C; inland: -22.6 °C, p=0.011), indicating reduced cold tolerance. We conclude that the coastal X population of *G. hodgsoni* exhibit higher levels of heat tolerance and reduced cold tolerance relative to the inland Y population and that the physiological differences we observed have an underlying genetic component.

1. Introduction

Predicting how natural populations will respond to climate change requires an understanding of how intrinsic organismal traits underly responses to environmental stressors (Sunday et al. 2014, Kaunisto et al. 2016, Kellermann and van Heerwaarden 2019). For example, genetic variability within populations will determine the physiological capacity of constituent individuals to survive a novel stress, the capacity of the population to recover from stress, and the capacity a long-term, evolutionary response that will facilitate persistence. Together, these properties determine a population's resilience to environmental change (Beet et al. 2022, Chapter II). Predicting potential resilience requires knowledge of population genetic structure, physiology, and the relationship between them (Somero 2010). Although a few studies link genetic and physiological information across species' geographic ranges (e.g. Kitano et al. 2012, Sengupta et al. 2017, Harada et al. 2019, Pruisscher et al. 2022), our ability to predict resilience in natural populations is still limited. This becomes especially relevant for small, fragmented populations, with potentially limited genetic variability when faced with climate change.

Here, we consider how genetics and physiology may interact to shape resilience to climate change in Antarctic Collembola. Globally, Collembola play key roles as decomposers as well as mediating plant-microbe interactions in soil ecosystems (Hopkin 1997, Caruso et al. 2013, Bardgett and Van Der Putten 2014). Collembola are well-known indicators of environmental change, especially ongoing climate change (Filser 2002, Krab et al. 2013, Høye et al. 2021). Antarctic collembolan populations are highly fragmented on both landscape and local scales which result in high levels of population structure (Hayward et al. 2004, Baird et al. 2020, Collins et al. 2020). Genetically differentiated polar collembolan populations do appear to differ in some physiological parameters including their tolerance of extreme temperatures and desiccation (Bahrndorff et al. 2006), rates of metabolism (McGaughran et al. 2010a), and life history traits (Sengupta et al. 2016, Sengupta et al. 2017). Some terrestrial Antarctic habitats are warming rapidly (Chown *et al.* 2022). This warming is associated with changes in hydrology, the extent of ice-free habitat, and the introduction of non-indigenous species, all of which are likely to have profound impacts on the current fauna (Siegert et al. 2019, Hughes et al. 2020, Chown *et al.* 2022). Thus, there is a pressing need to understand the resilience of Antarctic Collembola to climate change.

Antarctic Collembola experience both extreme high and low temperatures (Sinclair et al. 2006b, Convey et al. 2018), and many Antarctic Collembola are intrinsically tolerant to these stressors (Cannon and Block 1988). For example, Collembola from Northern Victoria Land tolerate temperatures as high as 37 °C and as low as -33 °C (Sinclair et al. 2006b). High temperature tolerance in Collembola can estimated as the critical thermal maximum (CT_{max}), the high temperature where they lose coordination and function (Chown and Nicholson 2004). Because polar Collembola are usually freeze avoidant, the temperature at which they freeze (the supercooling point, SCP), often correlates with the lower lethal temperature (Block 1985, Cannon and Block 1988, Escribano-Álvarez et al. 2022). Terrestrial Antarctic habitat temperatures can change rapidly: as much as up to 30 °C in a day in full sun in habitats with dark rocks (Worland and Convey 2001, Sinclair et al. 2003). In response to this thermal variability, some Collembola exhibit phenotypic plasticity in thermal tolerances on a scale of hours to days (e.g. Sinclair et al. 2003, Worland et al. 2007). Thus, even surviving the summer-active period, Antarctic Collembola require plasticity in their thermal tolerance.

The genetic diversity of Antarctic Collembola has been shaped by the unique biogeography of the continent. The Southern Ocean and circumpolar current have isolated Antarctica from other continents for >26 Ma (Sinclair and Stevens 2006, Pugh and Convey 2008). Consequently, Antarctic Collembola are relictual and all 12 species of Antarctic Collembola are endemic (Wise 1967, Sinclair and Stevens 2006, Hogg et al. 2014). Glaciers and other landscape features are near-insurmountable obstacles restricting collembolan dispersal (Stevens et al. 2007, Collins et al. 2019b, McGaughran et al. 2019), and lead to population fragmentation and genetic divergence at small spatial scales (Frati et al. 2001, Bennett et al. 2016, Collins et al. 2020). Two populations of *Gomphiocephalus hodgsoni* only separated by 10 km differed by 7.3 % COI sequence divergence (Bennett et al. 2016, Beet et al. 2016, Collins et al. 2020). Mitochondrial COI sequences have been evaluated for seven species, with sequence divergences within a species ranging from 1.7 % (between populations of *Kaylathalia klovstadi* 110 km apart between Cape Hallett and Cape Adare) to 14.7 % (between populations of *Cryptopygus terranovus* 66 km apart between Tucker Glacier and Campbell Glacier (Beet et al. 2016, Carapelli et al. 2017, Collins et al. 2019b). The extent to which this inter-population genetic diversity is reflected in among-population physiological divergence has not been explored.

Gomphiocephalus hodgsoni Carpenter (Hypogastruridae) is one of the most widely distributed and abundant species of Antarctic Collembola. *Gomphiocephalus hodgsoni* is present along a 250 km latitudinal gradient in Victoria Land, and is the only Collembolan found in Antarctica's largest ice-free habitat, the McMurdo Dry Valleys (Wise 1967, Hogg et al. 2014). To date, 88 unique cytochrome c oxidase subunit I (*COI*) haplotypes have been described, including three highly divergent (5.9-7.3% *COI* sequence divergence) genetic lineages across their known geographic range (Stevens and Hogg 2003, Beet et al. 2016, Collins et al. 2019b). The two genetically distinct lineages in the McMurdo Dry Valleys probably arose allopatrically when paleo-glacial Lake Washburn expanded and divided Taylor Valley ~23,000 ya (Denton and Hughes 2000, Nolan et al. 2006). This confined one population (Y-lineage) of *G. hodgsoni* to the cooler upper inland area of the Valley (closer to the Antarctic ice-sheet) and the other (X-lineage, 2.4 % *COI* sequence divergence) to the warmer coastal areas (Nolan et al. 2006). Since Lake Washburn disappeared *c.* 8,000 ya, X-lineage individuals have dispersed around the coast and moved inland in the Taylor Valley (Denton and Hughes 2000); by contrast, the Y-lineage appears to have remained in-situ. Y-lineage *G. hodgsoni* were more likely to be caught in pitfall traps at lower temperatures than their X-lineage counterparts (Collins and Hogg 2016), implying low-temperature adaptation in the Y haplotype.

Gomphiocephalus hodgsoni from Marble Point and Ross Island (McMurdo Station) have a thermal preference of 8-11 °C and upper thermal limits of 29.5-33 °C after increasing temperatures at a rate of 2.6 °C an hour over 8.5 hours (Janetschek 1963; Fitzsimons 1971). Current conditions may already approach stressful temperatures: microclimate temperatures on exposed ground and under dark rocks with solar insolation reached 26.2 °C in January 1999 at Cape Bird where *G. hodgsoni* is abundant (B.J. Sinclair unpublished data). Maximal surface temperatures of 23.2 °C have also been reported in the McMurdo Dry Valleys (Gooseff 2022). Supercooling points of *Gomphiocephalus hodgsoni* on Ross Island were low (median of c. -35 °C in the early spring), but bimodal in summer, with a high group median of c. -10 °C (Block 1985, Sinclair and Sjursen 2001). Metabolic rates also varied seasonally, peaking in mid-summer (McGaughran et al. 2009). Thermal tolerances have not been compared among *G. hodgsoni* populations, and variation in plasticity of thermal tolerance has not been compared among Antarctic collembolan populations. Thus, the thermal tolerance consequences of the known population genetic variability in *G. hodgsoni* are unknown.

We hypothesise that genetic differentiation among *Gomphiocephalus hodgsoni* populations will yield physiological differentiation in thermal tolerances. To test this, we collected *G. hodgsoni* individuals from two locations which served as a proxy for the two genetically divergent population. We predicted that individuals from the warmer, coastal X-lineage population of *G. hodgsoni* would be more heat-tolerant (higher $CT_{\max}$), and less cold-tolerant (higher SCP), than individuals from the cooler inland site, where the inland Y-lineage population predominates (X-lineage individuals are present in low numbers). Population differences in thermal tolerances could arise from basal tolerances, plasticity of those tolerances, or a combination of both. In addition to testing whether there were differences in thermal tolerances between the two populations, we examined diel variation in $CT_{\max}$ and SCP to detect potential phenotypic plasticity.

2. Methods

2.1 Site description and animal collection

We collected *Gomphiocephalus hodgsoni* Carpenter (Collembola: Hypogastruridae) from two sites within the McMurdo Dry Valleys: 1) near the Antarctic Specially Protected Area (ASPA 154) at Botany Bay, a coastal site near the terminus of the Mackay Glacier (-77.003889 162.547778, 0-40 m elevation; 5-10 December 2018); and 2) Spaulding Pond, an inland site at the outlet of the Howard glacier in Taylor Valley c. 73 km south of Botany Bay -77.657889 163.120444, 250 m elevation; 13-17 December 2018; Fig. 1). Two mitochondrial cytochrome c oxidase subunit I (*COI*) lineages ("X" and "Y") are known from these sites. At the coastal site only the X lineage is present while both lineages are present at the inland site, although a majority (c. 80 %) of individuals belong to the Y lineage (Nolan et al. 2006, Collins and Hogg 2016), so we assume that samples from the latter will primarily reflect the Y lineage (and note that any conclusions about differences among the lineages are therefore conservative). The X and Y *COI* lineages differed by 1.6-2.4 % sequence divergence (Nolan et al. 2006, Collins and Hogg 2016). Collembola were collected from underneath rocks via aspiration or by tapping individuals off rocks. Individuals were placed onto moist filter paper before being returned to the field laboratory within approximately 10 min of collection. Physiological measurements were initiated within 30 minutes of collection. The age (size) and sex of individuals was not determined (sexing *G. hodgsoni* requires mounting and clearing the specimens); our large samples randomly incorporated a range of different-sized individuals which we assume to be a consistent mix of males and females among treatments.

2.2 Genetic analyses

A total of 95 individuals from both sites (n=2-3 individuals from each experimental run) were photographed and stored in 100% ethanol in a 96 well plate to confirm the mitochondrial lineages present. These plates were sent to the Canadian Centre for DNA barcoding (CCDB), University of Guelph (Ontario, Canada), for genomic DNA extraction, and amplification and sequencing of a *COI* gene fragment (sensu Hebert et al. 2003) in accordance with standard CCDB protocols (see Ivanova et al. 2006 http://ccdb.ca/resources/) using LepFol primers (Hernández-Triana et al. 2014). Photographs, collection information, and sequence data are available from the Barcode of Life DataSystems (BOLD) database (www. boldsystems.org; Ratnasingham and Hebert 2013) in dataset DS-GHPHYS. A total of 83 out of 95 individuals were successfully sequenced (87%). Sequences were downloaded and aligned using

MUSCLE and trimmed in Geneious v.11.1.5 (https://www.geneious.com). An overall alignment of 654 bp including 83 sequences was reduced to 16 unique sequences in Geneious using the “find unique sequences” function to simplify downstream analyses with the number of individuals for each unique sequence provided in parentheses. This alignment of sequences was then compared with the sequences previously reported in Collins and Hogg (2016) to maintain the same designations for reported sequences. Any new, unique sequences were labelled with the BOLD process identification number. A phylogenetic tree was created to visualise the genetic relationships among all individuals sequenced from both locations. Due to the small number of sequences involved and the similarity of the sequences, a neighbour joining tree was deemed sufficient to examine the relationships between the two genetic lineages. The alignment of 16 unique sequences was uploaded to MEGA version X 10.0.5 (Kumar et al. 2018). The default Kimura 2- parameter model (Kimura 1980) of evolution was selected with all other default settings maintained and 1000 bootstrap replications selected. The resulting tree was edited in FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) with bootstrap values over 70 displayed due to the small number of branches on the tree. Assignment to the X or Y lineage was made by comparing sequences to those reported in Collins and Hogg (2016).

2.3 Microclimate monitoring

We recorded under-rock temperatures at 10 min intervals during the sampling period (HOBO model H21-002, Onset, Cape Cod, MA, USA with two thermistor sensors; we averaged the values from the two probes). At the coastal Botany Bay site, the HOBO logger was placed approximately 15 m uphill of the established campsite, amongst the boulders. The two thermistors were placed under separate small rocks (<30 cm in length) (surrounded by boulders >1 m in length) which were representative of microhabitats Collembola were most collected from. At Spaulding Pond, the HOBO logger was placed five metres from the eastern edge of Spaulding Pond with the two thermistor probes placed under small rocks (<30 cm in length, surrounded by exposed sand). Each sampling site was close to a long-term weather station, from which we obtained longer-term air temperatures. The Botany Bay weather station was c. 20 m from our collection sites (https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/climate/?cid=nrcs142p2_053771), and the Spaulding Pond climate station was at the Howard Glacier, c. 1.5 km from the collection site (-77.67120 163.07730, 465 m elevation, Doran and Fountain 2022: https://mcm.lternet.edu/content/mcmurdo-dry-valleys-meteorological-station-locations).

2.4 Thermal tolerance measurements

We measured the CT_{max} of *G. hodgsoni* using a dynamic assay (cf. Jørgensen et al. 2019) *G. hodgsoni* free-ranging in an open arena. We placed *G. hodgsoni* of mixed size to free range on moistened filter paper on a copper stage whose temperature was controlled by a custom-built Peltier-effect system (described by Anthony et al. 2019). Measurements from four 36-Gauge type-T thermocouples (OMEGA, Laval, Quebec, Canada) affixed to the stage and interfaced to a computer via a PicoTech TC-08 and Picolog software (v 5.24.2 PicoTechnology, Cambridge, United Kingdom), were averaged to approximate body temperature of the Collembola. We equilibrated individuals at 10 °C for 15 min before warming them at 0.25 °C min^{-1} until all had reached their CT_{max} (defined as the onset of observable muscular spasms/ contractions, cf. Sinclair et al. 2006). As each individual reached its CT_{max}, the temperature was recorded and it was removed from the stage. The number of individuals included in each experimental run varied depending on how many individuals were found prior to each experiment. At Botany Bay sample sizes for each experimental run ranged from 16-91 (median = 33; 6 runs, total n=274). At Spaulding Pond sample sizes for each experimental run ranged from 23-66 (median = 37.5; 10 runs, total n=412) (Table 1). Two to three individuals from each physiology run were preserved in 100 % ethanol for *COI* sequencing to confirm presence of X and Y haplotypes at each site. The haplotype of every individual used in CT_{max} experiments was not determined, and site was used as a proxy for the two X and Y lineages. Surviving individuals were returned to their collection site. To encompass diel variation in CT_{max}, we conducted measurements stratified across the day: 1100-1130 (n=6 runs, 316 individuals total), 1300-1730 (n= 5, 236 individuals total), 2300-0030 (n=4 runs, 134 individuals total) (Table 1).

We measured supercooling points of individual Collembola as described by Sinclair et al. (2015). Briefly, we affixed Collembola (n=15/run) to individual thermocouples with petroleum jelly. Each thermocouple was suspended in a 1.5 ml microcentrifuge tube which was placed into a hole in a Peltier-cooled copper block (dimensions: 1.9 mm diameter, 2 mm depth) (see also Anthony et al. 2019, Duell et al. 2022). We equilibrated each group of Collembola at 0 °C for 15 min before cooling them at 0.25 °C min^{-1} until all individuals froze. We recorded thermocouple temperatures continuously using TC-08 and Picolog software (as above), and identified the SCP as the lowest temperature immediately prior to the exotherm that indicated freezing (Sinclair et al. 2015). A total of 37 individuals were successfully measured at the coastal site and 65 individuals at the inland site (Table 2). To encompass diel variation, we stratified SCP measurements for the following periods: 1130 (one run at the inland site only, n=14), 1300-1830 (two runs at each site, n=48), and 2200-2300 (one run at the coastal site, two at the inland site, n=40), for a total of 102 individuals across both sites (Table 2).

2.5 Data analysis

All statistical analyses were conducted in R v 1.1.423 (RStudio Team 2016). To determine whether individuals from the warmer, coastal X-lineage population of *G. hodgsoni* would be more heat-tolerant (higher CT_{max}), but less cold-tolerant (higher SCP), than individuals from the cooler, inland Y-lineage population Ggplot2 (Wickham et al. 2016) was used to visualise the data with violin plots. Histograms were used to compare critical thermal maxima and supercooling points across sites. Summary stats (minimum, maximum, mean and median temperatures) were produced for CT_{max} and SCPs between the two sites and for each experimental run. We compared CT_{max} and SCP between the two collection sites (as a proxy for the two mitochondrial lineages) using linear mixed effects models using the lme4 function (Bates et al. 2014) with date as a random effect to account for any temporal variation. All models were checked for homoscedasticity and normality of model residuals. To determine whether there was any plasticity in thermal tolerances and whether one site (as a proxy for each genetic lineage) was more plastic than another, we looked at ratios of high and low supercooling points at each site. SCPs were classified as high if they were above -15 °C. The cut off point of -15 °C was set by visually assessing a histogram of all SCP data for an obvious break between modes. We constructed linear mixed effect models using the lme4 function (Bates et al. 2014). We used an AIC-based model selection approach to determine the best set of predictors for each model (Akaike 1981). Boxplots of each CT_{max} and SCP run were also created using Ggplot2 (Wickham 2016) to visualise any plasticity in thermal tolerances across sampling times (Supplementary Materials).

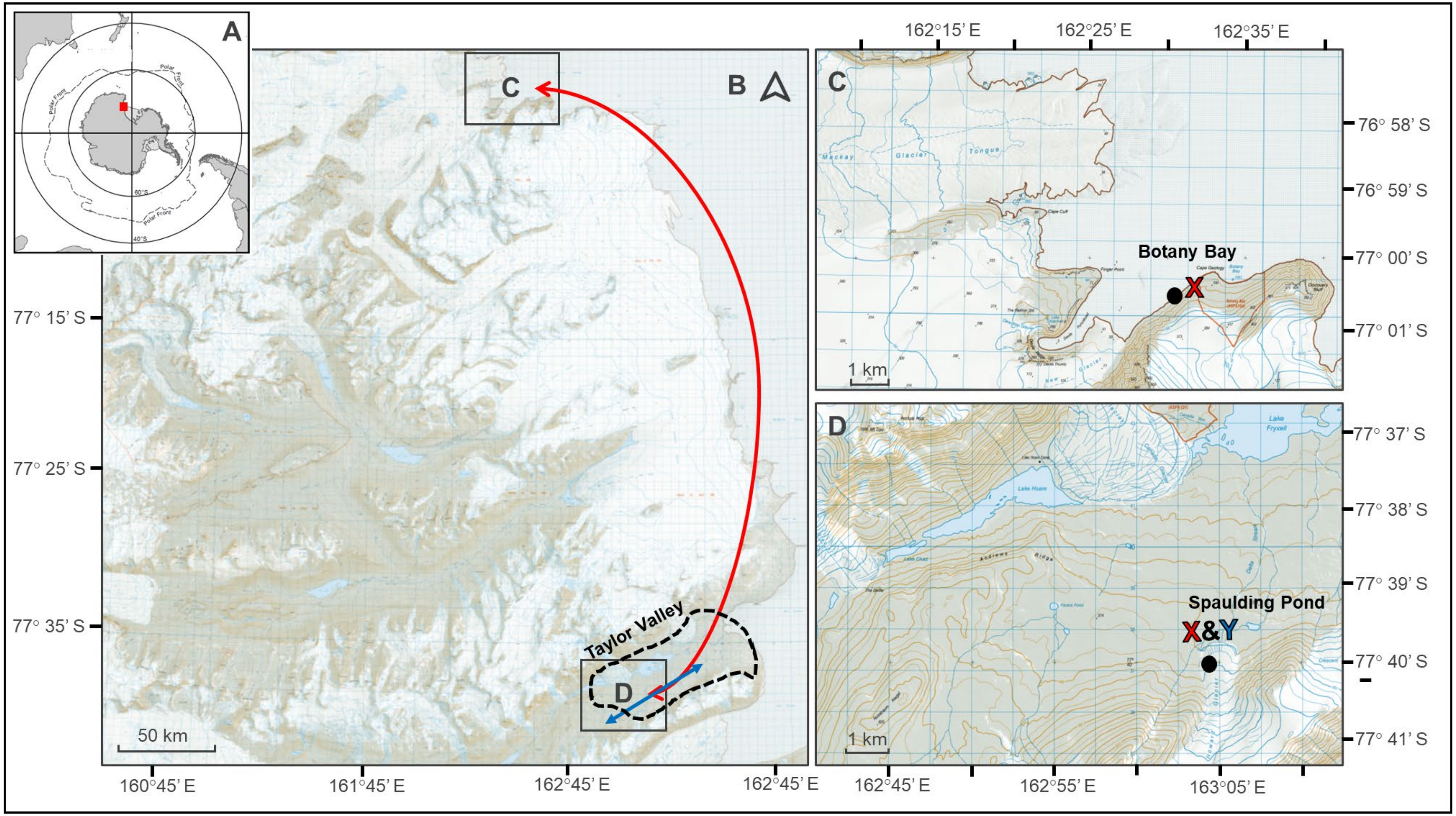
A
Polar Front
60°S
40°S
B
C
D
Taylor Valley
50 km
77° 15' S
77° 25' S
77° 35' S
160°45' E
161°45' E
162°45' E
162°45' E
162°15' E
162°25' E
162°35' E
76° 58' S
76° 59' S
77° 00' S
77° 01' S
Mackay Glacier Tongue
Botany Bay
X
1 km
Lake Hoare
Lake Fryxell
Andrews Ridge
Spaulding Pond
X&Y
77° 37' S
77° 38' S
77° 39' S
77° 40' S
77° 41' S
162°45' E
162°55' E
163°05' E

Figure 1: A= overview map of Antarctica with the red square in the Ross Sea region indicating the area of the McMurdo Dry Valleys found in B. B= Topographic map of McMurdro Dry Valleys with inserts highlighting the two sampling sites at the outflow of the Mackay Glacier (C) and in Taylor Valley (D). White areas indicate glaciated areas, brown indicates areas with exposed soil, blue areas indicate streams and lakes. The dashed line indicates the approximate shoreline of paleoglacial Lake Washburn in Taylor Valley. The red arrow indicates the distribution of the X lineage of the collembolan *Gomphiocephalus hodgsoni* which is found predominantly on the coast while the blue arrow shows that the Y lineage of *G. hodgsoni* is more commonly found inland. The arrows in Taylor Valley indicates that there is overlap in the distributions of X and Y lineages. The extent of Lake Washburn and distribution of the two lineages is taken from Nolan *et al.* (2006). C = Coastal Botany Bay site at the outflow of the Mackay Glacier home to the X lineage of *G. hodgsoni*, with BB demarking the sampling location. The black circle indicates the approximate site of the Botany Bay weather station. D = the inland Y site at Spaulding Pond in Taylor Valley with an SP demarking the sampling location. The black circle indicates the site of the Howard Glacier weather station. Antarctic overview map adapted from https://data.aad.gov.au/aadc/mapcat/display_map.cfm?map_id=13137. Topographic maps sourced from

3. Results

3.1 Genetic analyses

The sequenced individuals represented a total of 16 haplotypes corresponding to two distinct lineages which diverged by a maximum of 2.1% (divergence range: 1-13 base-pairs) (Fig. 2). All sequenced coastal individuals (n=30) were of the X-lineage, comprising six haplotypes differing by 1-6 base pairs. Inland individuals were predominantly of the Y-lineage (n= 46 of 53) with the remaining individuals (n=7) aligned with the X-lineage. The seven inland X-lineage individuals were all genetically distinct from coastal X-lineage individuals and clustered together in a sub-group of the X-lineage consisting of three haplotypes (Fig. 2). Individuals from the Y-lineage included seven haplotypes, six of which differed only by a single base-pair (the 7th haplotype differed by two base-pairs).

3.2 Microclimate temperatures

Soil surface temperatures across both sites were similar during the sampling periods although the coastal Botany Bay site had higher maximum temperatures (Fig. 3). Surface soil microclimate temperatures showed a consistent diel pattern with peak coastal temperatures usually at 1400-1500. The timing of temperature peaks was more variable at the inland Spaulding Pond site, occurring between 1030 and 1730 (Fig. 3). Across both sites, microclimate temperatures only briefly dipped below 0 °C (generally between 0200 and 0800) with minimum temperatures of -1.3 and -0.9 °C observed at Botany Bay and Spaulding Pond respectively (Fig. 3). The amplitude of diel peaks was dependant on weather, with snow providing more thermal buffering to top-soils (temperatures on 8th and 9th of December at Botany Bay did not fall below 0 °C). Climate station data from Botany Bay and Howard Glacier suggested that Botany Bay tends to be a warmer site although the Howard Glacier climate station is situated atop the glacier further from the collection sites surveyed in this study. Average air temperatures from the climate station at Howard Glacier were -6.2 °C from December 2017 to January 2018 (Doran and Fountain 2019)

3.3 Physiological measurements

Upper thermal limits

The $CT_{\max}$ measurements from *G. hodgsoni* from both coastal and inland sites were highly variable and differed by up to 19 °C between individuals with an overall range of 17 to 36 °C (Table 1). The majority (96.7 %) of observations ranged between 20 °C and 35 °C (Fig. 4A). However, across both sites minimum $CT_{\max}$ temperatures were consistently above maximum recorded microclimate temperatures, indicating that the thermal limits of *G. hodgsoni* at these sites exceeded the temperature extremes they were exposed to. The similar range in CT_{max} values across both sites obscures the variability observed both within and across experimental samples (Fig. S1A, S2) especially at the inland site with the mean CT_{max} of each experimental run ranging between 22.2-31.5 °C. By comparison, CT_{max} at the coastal site had narrower ranges with mean maxima for each experimental run only ranging between 28.0-32.9 °C (Table 1).

At the coastal site, CT_{max} measurements were skewed toward higher temperatures (Fig. 4B) At the inland Spaulding Pond site there was a more even distribution of CT_{max} values (Fig. 4B). The distribution of coastal CT_{max} observations were weakly bimodal (with peaks at 25 and 34 °C) while inland CT_{max} were weakly trimodal (with peaks at 21, 25 and 33 °C) (Fig. 4B). The coastal population had on average higher upper functional thermal limits (mean CT_{max}: 31.7 °C) compared to the inland population (mean CT_{max}: 27.5 °C) (Table 1). The visible difference in CT_{max} between the inland and coastal sites, was not statistically significant (p=0.149), based on the linear mixed effects model. However, we found that microhabitat temperature at time of sampling had a significant effect ($p = 0.0014$) on the critical thermal maxima of *G. hodgsoni* in addition to a combination of site and microhabitat temperature ($p = 0.0029$) (Fig. 4B, Table 3).

Lower thermal limits

Supercooling points (SCPs) among *G. hodgsoni* from both sites ranged from -2.7 to -31.6 °C. At the inland site, SCPs were broadly unimodal, while at the coastal site they were bimodal. At the coastal site SCPs were weakly skewed towards high group individuals (less cold tolerant) with freezing most frequently observed at -7 °C (Fig. 5A). By contrast, inland SCPs skewed were more heavily toward low group (more cold-tolerant) individuals with freezing most commonly recorded at -28 °C (Fig. 5B). At Spaulding Pond the ratio of high group to low group individuals was 9:56 while at Botany Bay it was 21:16 (Table 4). The minimum and maximum SCPs across both sites were similar. However, the inland site had a higher incidence of more cold tolerant individuals. The contrast in supercooling points between both sites is shown in Figure 5A with most coastal SCPs above -20 °C and most inland SCPs below -20 °C. The coastal individuals had significantly higher supercooling points in comparison to the inland (i.e. predominantly Y) individuals (coastal mean: -14.6 °C; inland mean: -22.7 °C; $p = 0.011$) (Table 2). Unlike the CT_{max} measurements, microhabitat temperature alone did not have a significant effect on the supercooling points of *G. hodgsoni* ($p = 0.1108$) while a combination of site and microhabitat temperature was significant ($p = 0.0308$) (Table 3).

Table 1: Minimum, maximum and mean CT_{max} recordings for each sampling time across Botany Bay and Spaulding Pond. All CT_{max} values are in °C.

Site	**Sample**	**Sampling Date**	**Sampling Time**	**Min**	**Max**	**Mean**	**Median**	**N**
Botany Bay	BBM7	7/12/2018	1100	20	35	32.3	34	91
	BBE7	7/12/2018	0030	20	36	31.6	32.5	16
	BBA8	8/12/2018	1400	25	34	28	28	23
	BBE8	8/12/2018	2330	25	35	32.2	33	34
	BBA9	9/12/2018	1500	19	35	30.5	25.5	32
	BBM10	10/12/2018	1130	20	35	32.9	34	78
Overall				**19**	**36**	**31.7**	**34**	**274**
Spaulding Pond	SPM13	13/12/2018	1100	17	31	26.1	27	23
	SPA13	13/12/2018	1500	18	34	26.1	26	34
	SPE13	13/12/2018	2300	17	31	24.8	25	32
	SPM14	14/12/2018	1100	18	31	24.6	25	41
	SPM16	16/12/2018	1130	17	29	22.2	21	28
	SPA16	16/12/2018	1730	18	35	26.7	27	66
	SPE16	16/12/2018	2300	17	35	28.7	31	52
	SPM17	17/12/2018	1100	20	35	31.5	33	55
	SPA17	17/12/2018	1300	17	35	29.2	32	32
	SPA17B	17/12/2018	1530	20	35	30.6	32	49
Overall				**17**	**35**	**27.5**	**27**	**412**

Table 2: Minimum, maximum and mean SCP recordings for each sampling time across Botany Bay and Spaulding Pond. All SCP values are in °C.

Site	Sample	Sampling Date	Sampling Time	Min	Max	Mean	Median	N
Botany Bay	BBE5	5/12/2018	2300	-19.7	-2.7	-9.8	-8.7	12
	BBA6	6/12/2018	1400	-26.3	-3.6	-14.9	-17.4	12
	BBA10	10/12/2018	1430	-31.6	-6.3	-17.5	-14.8	13
Overall				**-31.6**	**-2.7**	**-14.6**	**-13.6**	**37**
Spaulding Pond	SPA14	14/12/2018	1500	-28.4	-6	-19.4	-22.9	12
	SPE14	14/12/2018	2230	-28.6	-18.9	-25.3	-25.8	14
	SPM15	15/12/2018	1100	-31.3	-3.9	-23.4	-26.2	14
	SPE15	15/12/2018	2200	-30.1	-5	-22.8	-24.1	14
	SPA17	17/12/2018	1830	-28.5	-8.7	-21.7	-24.4	11
Overall				**-31.3**	**-3.9**	**-22.7**	**-25.1**	**65**

Table 3: Summary of linear mixed effects models conducted on CT_{max} and SCP data (response variables). AIC criteria were used to select the most appropriate model. Significant p-values are bolded. Microhabitat temperature refers to the temperature at sampling time.

Response Variable	Fixed effect	Estimate ± SE	t-value	p-value	Random Effect
CT_{max} temperature					Date
	Intercept	30.146 ± 1.42	21.26	0.000	
	Site	-3.290 ± 1.99	-1.66	0.149	
	Intercept	25.549 ± 1.48	17.25	0.000	
	Microhabitat temperature	-0.329 ± 0.103	3.20	**0.0014**	
	Intercept Site + Microhabitat temperature	25.596 ± 2.06	12.89	0.000	
	Site	-1.816 ± 2.43	-0.75	0.483	
	Microhabitat temperature	-0.314 ± 0.105	2.99	**0.0029**	
SCP temperature					Date
	Intercept	-14.564 ± 1.37	-10.61	0.000	
	Site	-8.050 ± 1.80	-4.48	**0.011**	
	Intercept	-21.982 ± 3.04	-7.24	0.000	
	Microhabitat	0.556 ± 0.345	1.61	0.111	
	Intercept Site + Microhabitat temperature	-14.919 ± 2.54	-5.87	0.000	
	Site	-7.832 ± 2.39	-3.27	**0.0308**	
	Microhabitat temperature	0.046 ± 0.25	0.19	0.850	

Table 4: Summary of number of individuals with high group (higher than -15 °C) and low group (lower than -15 °C) supercooling points for both sites divided by sampling time.

Site	**Time**	**High Group**	**Low Group**
SP	Morning	2	12
BB	Afternoon	12	13
SP	Afternoon	6	17
SP	Evening	1	27
BB	Evening	9	3
	SP Total	9	56
	BB Total	21	16
	Total	30	72

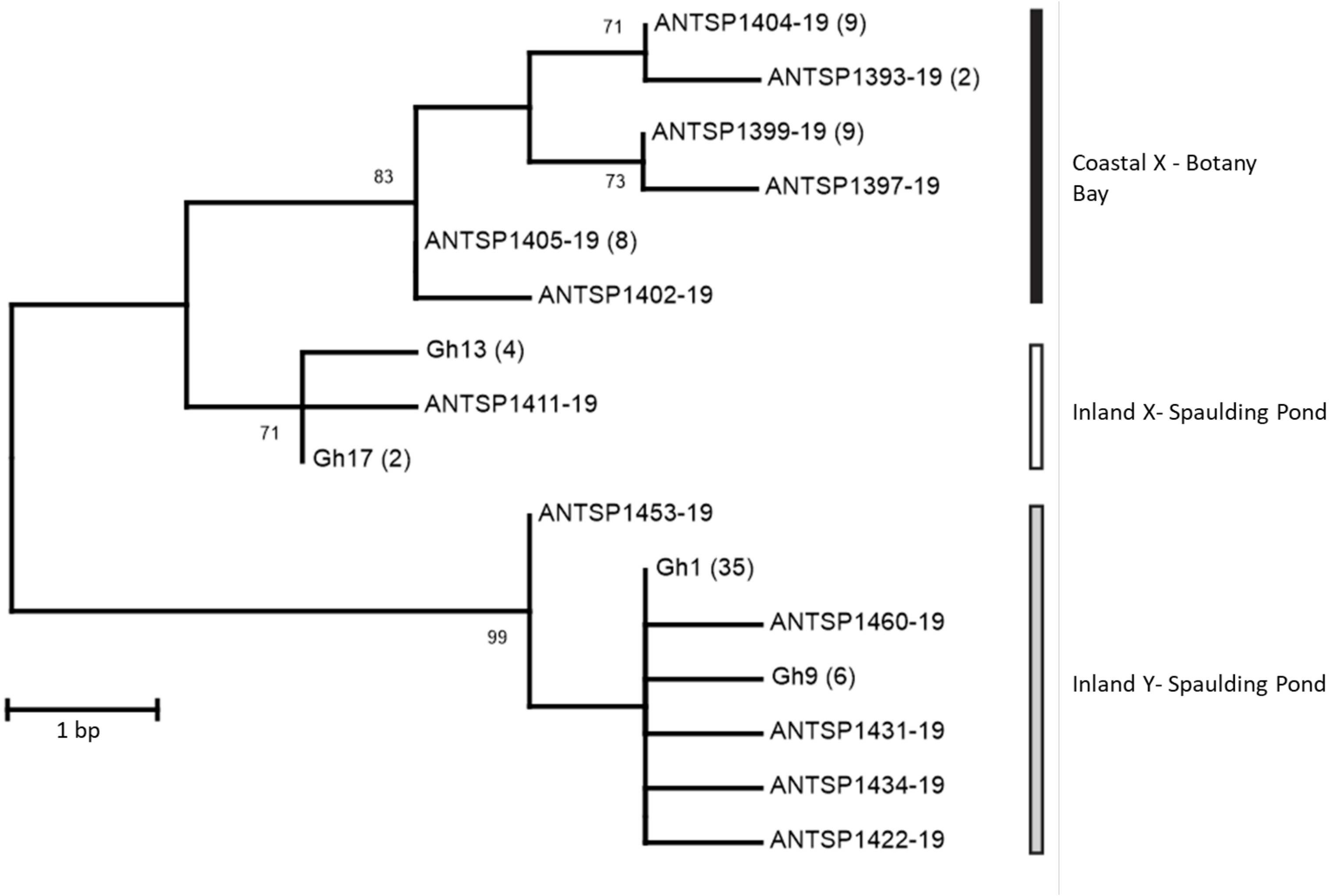

Figure 2: Neighbour joining tree of all unique sequences from Botany Bay and Spaulding Pond. Gh haplotype codes used where they match sequences reported in Collins and Hogg 2016. Other sequence codes used are process ID codes of sequences on BOLD. Numbers in parentheses refer to the number of sequences of that haplotype. Bars on the side refer to the *COI* XY lineage and sampling site

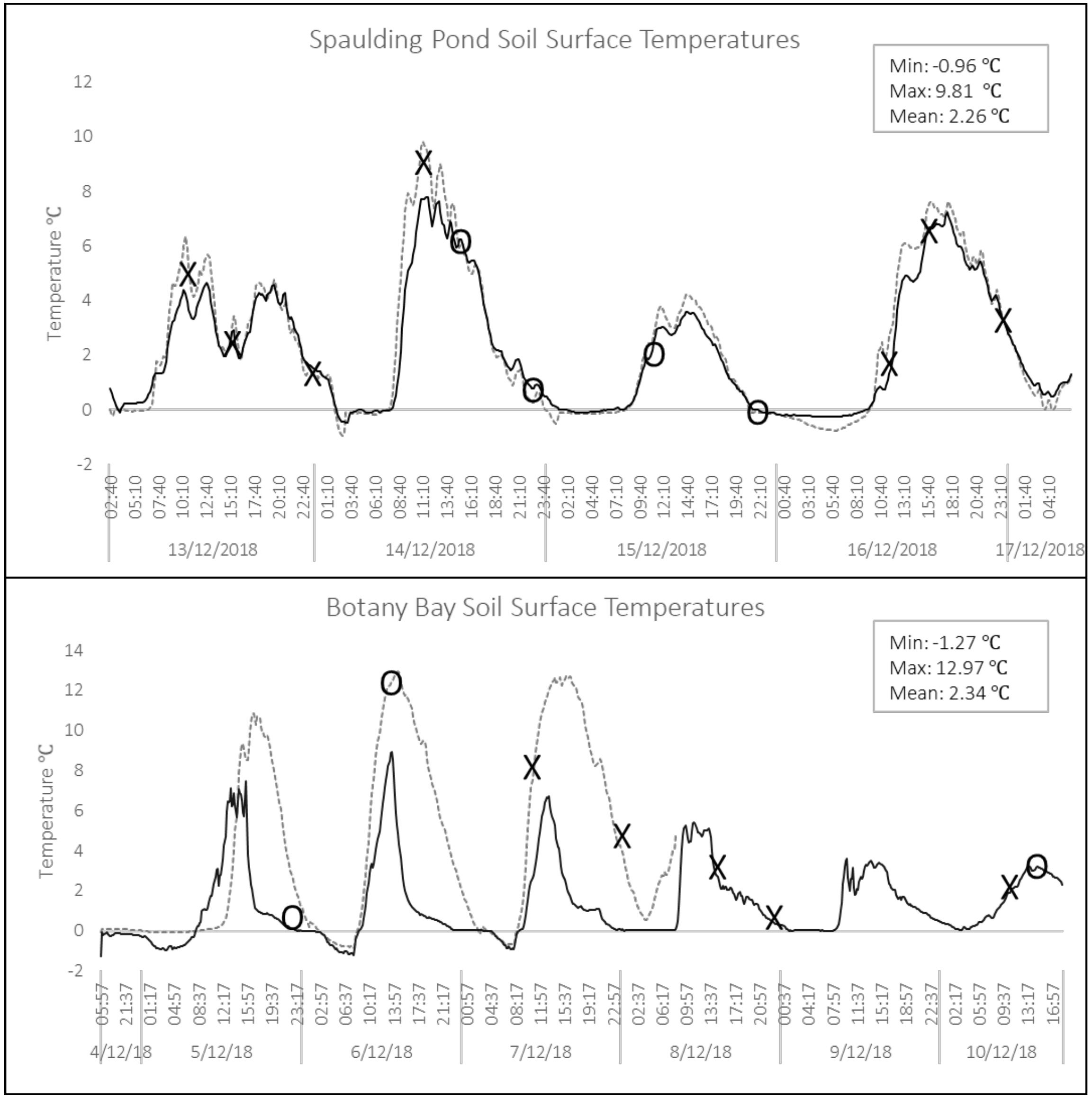

Figure 3: Microhabitat surface temperature monitoring at Botany Bay and Spaulding Pond using two HOBO temperature probes recording every 10 minutes at each site. X symbol is noted at sampling times for $CT_{\max}$ experiments while O denotes sampling for SCP experiments. Temperature monitoring at Spaulding Pond is missing the last few hours from the 17/12/2018 during which time 3 $CT_{\max}$ and one SCP experiment were conducted.

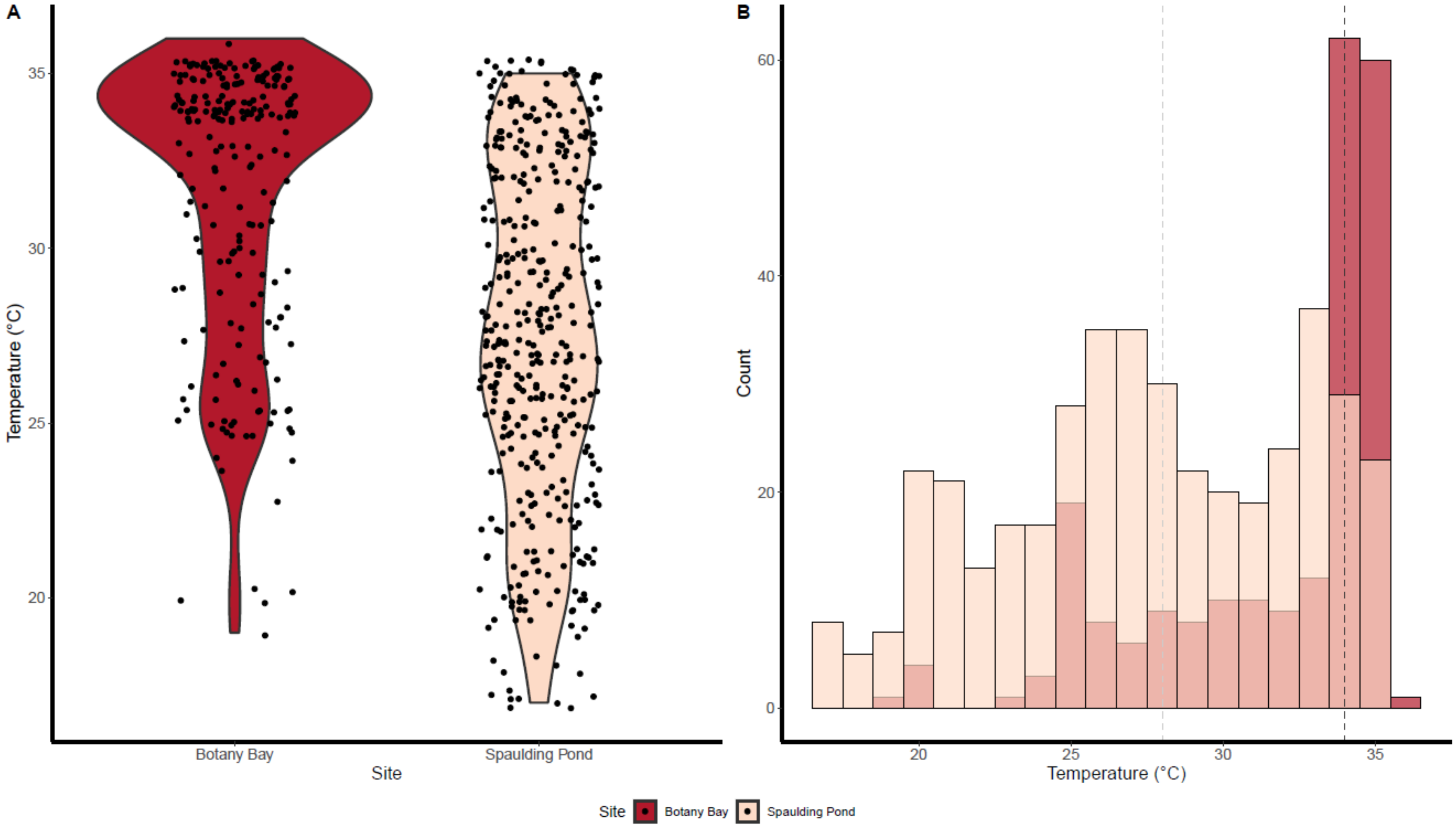

Figure 4: A = Violin plots with overlaid plot of all data points showing the overall distribution of critical thermal maxima ($CT_{\max}$) observations at Botany Bay and Spaulding Pond. B = Histogram with overall $CT_{\max}$ data from both sites overlaid atop each other for better comparison. Dashed lines indicate the mean $CT_{\max}$ for each site. Bars colourised by site with the inland Spaulding Pond site in the light red and the coastal Botany Bay site in darker red. The intermediate red colour is where observations from both sites overlap.

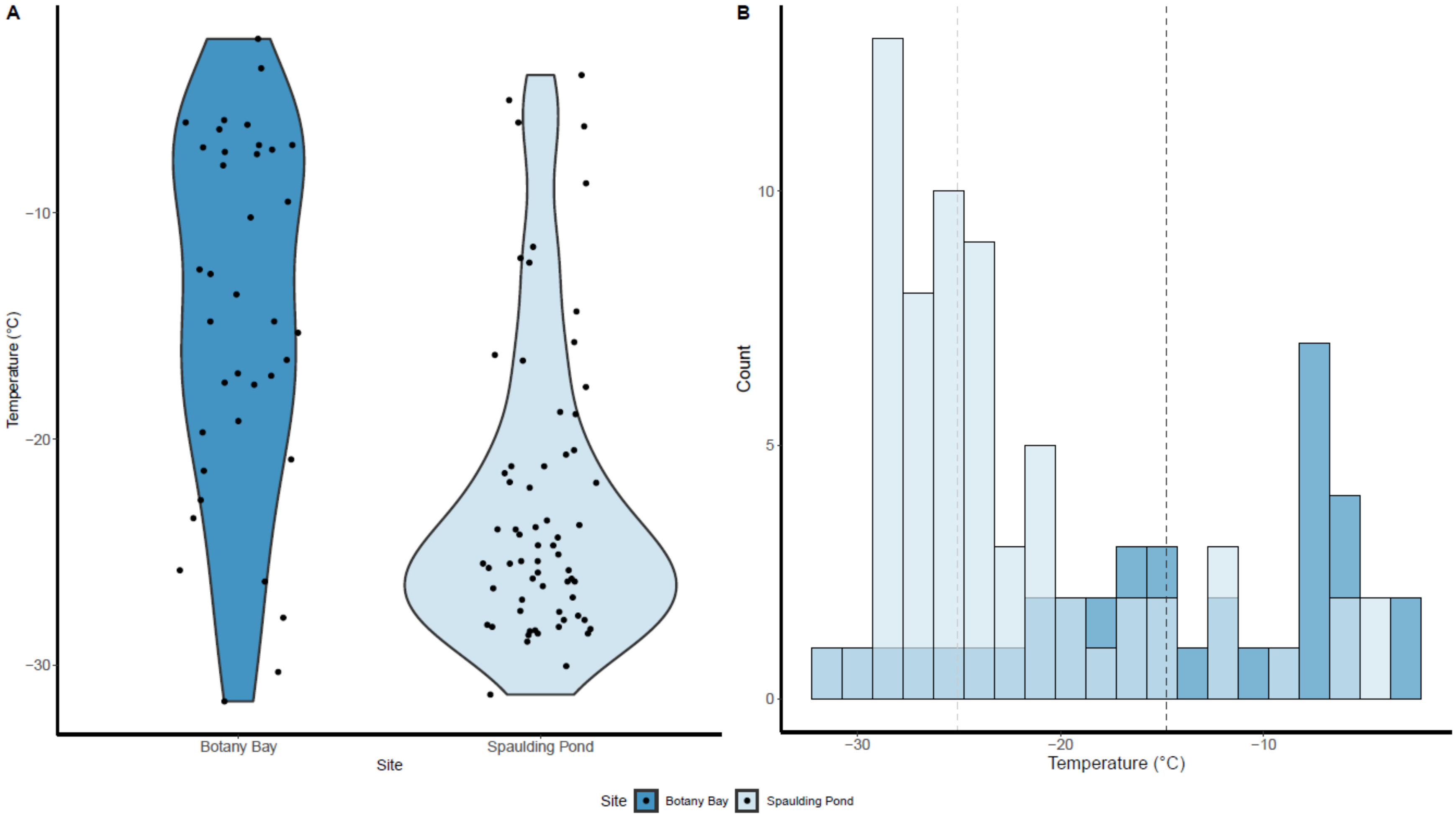

Figure 5: A = Violin plots with overlaid plot of all data points showing the overall distribution of supercooling point (SCP) observations at Botany Bay and Spaulding Pond. Temperature is in °C. B= Histogram with overall SCP data from both sites overlaid atop each other for better comparison. Dashed lines indicate the mean SCP for each site. Bars colourised by site with the inland Spaulding Pond site in the light blue and the coastal Botany Bay site in darker blue. The intermediate blue colour is where observations from both sites overlap.

4. Discussion

Based on a comparison of the thermal tolerances for genetically divergent populations of *Gomphiocephalus hodgsoni*, we found that individuals collected from warmer coastal and cooler inland locations, were associated with differences in physiological tolerances of hot and cold temperatures. We found higher levels of genetic diversity at the inland Spaulding Pond site relative to the coastal Botany Bay site. A total of 19 haplotypes have been identified at the inland site alone (Collins and Hogg 2016), with Gh1 (of the Y lineage) remaining the most abundant haplotype comprising 66 % of all inland sequences. Six of the haplotypes we found (representing six individuals) had not been previously detected in earlier studies, although they only differed by a single base-pair. Individuals of the predominantly coastal X lineage (first identified in Nolan et al. 2006, Collins and Hogg 2016) were present at both locations, although those haplotypes from the inland site were genetically distinct from the coastal individuals. The presence of both genetic lineages at the inland site may suggest the population has the potential for greater variation in physiological tolerances and is pre-adapted to climate variability as populations with higher genetic diversity tend to house genetic variants able to survive new or altered environmental stressors (Somero 2010).

All individuals we assessed had thermal tolerances that exceeded the microclimate temperatures observed at both the coastal and inland sites. Microclimate temperatures across both sites were similar during the sampling period. However, they do not fully represent the thermal environment experienced by *Gomphiocephalus hodgsoni*. The temperature under a dark rock warmed by the sun is unlikely to be the same as the temperature under bare soil, or in the shade of a boulder (Young et al. 1997, Sinclair et al. 2006a). The coastal Botany Bay site had greater potential for behavioural thermoregulation and/or avoidance with a more complex physical environment with a range of rock sizes (from pebbles to large boulders) and high vegetative coverage including mosses, lichen, and liverwort (Seppelt et al. 2010). Collembola at Botany Bay are often seen moving around on the surfaces of rocks on warm days indicating a level of local-scale dispersal and potential for behavioural thermoregulation. By comparison, Spaulding Pond was a predominantly exposed site with only smaller-sized rocks (<30 cm) and vegetative communities limited to cyanobacterial mats along the edges of ponds. Landscape heterogeneity creates a diversity of thermal niches which Collembola can potentially exploit through behaviour (Hopkin 1997, Sunday et al. 2014). However, the thermoregulatory behaviour of Collembola in natural Antarctic systems has not been directly assessed. Further field- and laboratory-based experimental approaches are needed to determine the extent to which Collembola can behaviourally avoid environmental extremes, which in turn will dictate the physiological tolerances selected for. It is possible that the exposed inland site has resulted in selection for more cold tolerant individuals while the diversity of thermal niches at the coastal site has partially mitigated selection pressures (Sunday et al. 2014, Liu et al. 2020, Liu et al. 2021).

More individuals with higher $CT_{\max}$ were found at the coastal Botany Bay site, reflecting a higher degree of heat tolerance among the coastal population. While the $CT_{\max}$ of coastal individuals was weakly bimodal with a small peak at 25 °C, there was a clear skew towards individuals with $CT_{\max}$ of over 33 °C. There were higher levels of variation in heat tolerance between individuals at the inland site relative to the coastal site, which could be due to the presence of both haplotypes at the inland site. In future, DNA sequencing of individuals after the $CT_{\max}$ is recorded could enable a better assessment of these relationships. The minimum $CT_{\max}$ temperatures observed in our study were all lower than those measured for three species of Collembola from Cape Hallett (located approximately 640 km north of Taylor Valley) – all of which were above 25 °C, with the minimum $CT_{\max}$ of *Kaylathalia klovstadi* recorded at 31.5 °C (Sinclair et al. 2006b). However, summer microclimate temperatures at Cape Hallett still exceeded the $CT_{\max}$ for two out of the three extant species (Sinclair et al. 2006b). The maximal $CT_{\max}$ temperatures recorded here of 35 and 36 °C were similar to those seen among sub-tropical species (Liu et al. 2020) with several Australian Collembola exhibiting critical thermal maxima in the range of 30-35 °C (Janion-Scheepers et al. 2018). These upper functional thermal limits are considerable when considering some of the highest $CT_{\max}$ recorded for Collembola were 45-47 °C among species of *Seira* (Entomobryidae) found in the Cape Floristic Region of South Africa (Liu et al. 2020). Variation in $CT_{\max}$ between our two sites was largely attributed to variation in microclimate temperatures at the time of collection, indicating a level of environmental responsiveness and phenotypic plasticity in heat tolerance of *Gomphiocephalus hodgsoni*. Previous studies (Slabber et al. 2007, Everatt et al. 2013a), have suggested that while acclimation and plasticity in heat tolerances for polar Collembola are limited relative to cold tolerance, they still have an influence. The degree of plasticity in heat tolerances we observed is likely limited, with lethal temperatures remaining upwards of 30-35 °C. These data suggest *Gomphiocephalus hodgsoni* may be able to survive brief exposures to high temperature extremes, although persistent exposure to sub-lethal temperatures is likely to have a larger negative influence than temporary extremes (Colinet et al. 2015). For example, under controlled conditions, survival of *Cryptopygus antarcticus* individuals maintained at 10 °C declined to ~30 % after 20 days with less than 10 % surviving more than 30 days (Everatt et al. 2013b). Sub-lethal impacts may include cessation of feeding, heightened metabolic demands, and consequential declines in maturation and reproduction which are all likely to contribute to declines in fitness and overall resistance to further stress (Marshall and Sinclair 2012, Colinet et al. 2015, Dillon et al. 2016).

The differential distributions of supercooling points between the inland and coastal sites support the hypothesis that genetic diversity arising from historical glacial processes has contributed to evolutionary adaptation in cold tolerances among populations of *G. hodgsoni. Gomphiocephalus hodgsoni* supercooling points ranged between -2.7 to -31.6 °C similar to absolute ranges identified among populations on Ross Island (Sinclair and Sjursen 2001). While ranges of supercooling points were similar between our inland and coastal locations, the distribution of supercooling points was bimodal at the coastal site and mostly unimodal at the inland site. Bimodal supercooling points have previously been observed, whereby populations can be split into "high-group" and "low-group" individuals (Worland and Convey 2001, Sinclair et al. 2003). In the Maritime Antarctic, higher supercooling points were found to occur among actively feeding individuals as a consequence of having food particles within the gut which served as ice nucleators (Block 1985, Worland and Convey 2001, Worland and Convey 2008). We found evidence for population-level variation in cold tolerance with the distribution skewed toward high-SCP-group (less cold tolerant) individuals at the coastal Botany Bay site and more low-SCP-group (more cold tolerant) individuals at the inland Spaulding Pond site. This may indicate that more of the coastal population is actively feeding and putting energy into growth, maturation and reproduction rather than restricting feeding and/or expending energy into producing metabolically expensive cryoprotectant molecules.

Variation in the proportions of Antarctic Collembola in high and low SCP groups has been shown to shift in accord with diurnal temperature fluctuations for two of the three species studied at Cape Hallett (Sinclair et al. 2003). We found no clear patterns of diurnal variation among *G. hodgsoni* at either site, similar to *Friesea gretae* (previously F. grisea) from Cape Hallett (Sinclair et al. 2003, Carapelli et al. 2020). One possible explanation is that individuals may behaviourally mitigate daily temperature fluctuations by migrating to more favourable microhabitats as seen among Collembola from Greenland (Fox and Stroud 1986, Hopkin 1997). Diurnal patterns of surface activity among *G. hodgsoni* have been observed at Spaulding Pond with an absence of individuals in pitfall traps during cooler evening periods (Collins and Hogg 2016). Seasonality in supercooling points was observed among *G. hodgsoni* at Cape Bird (located approximately 95 km from Spaulding Pond), with median SCPs rising from -38.4 °C in late October to -28.4 °C in late December (Sinclair and Sjursen 2001). Increased sampling at different time periods and over longer time-scales, coupled with dissection to determine feeding status could help better determine levels of cold tolerance plasticity among these populations.

In summary, our study provides evidence linking fine-scale genetic diversity and physiological tolerances as well the relative roles of evolutionary adaptation and phenotypic plasticity in shaping resilience for an Antarctic collembolan. Understanding the resilience of Antarctic biota, and Collembola in particular, can help determine vulnerability of current populations to climate change induced stressors and displacement risk either by other extant populations or by non-indigenous species (Vega et al. 2021). Differential thermal tolerances among closely related yet genetically distinct populations of *G. hodgsoni* highlight the potential that, as temperatures rise, warm-adapted individuals (e.g. coastal, X-lineage) may have a selective advantage relative to more cold-adapted individuals (inland, Y-lineage) leading to overall changes in population genetic structure and variability. The continued survival of Antarctic Collembola in a warming world may further depend on the presence of refugia and the ability of individuals to disperse (Pugh and Convey 2008). The degree of behavioural moderation employed by Collembola to adverse environmental conditions will be critical to ascertaining the consequences of rising temperatures associated with climate change. With only a single species of Collembola across the whole McMurdo Dry Valleys region, the loss of a distinct population and its inherent genetic structure is likely to impair the future resilience of this species. Monitoring the relative proportions of the two haplotypes at the inland site may provide a sensitive method to track climate change and/or ongoing evolution. Future studies conducting genome and transcriptome sequencing are needed to provide a more mechanistic understanding of the genetic basis underlying these differential thermotolerances. Furthermore, future work should focus on the impacts of multiple interacting stressors on genetically distinct populations and the effects of prolonged sub-lethal stressors.

Acknowledgments

Financial support provided through funding from the New Zealand Antarctic Research Institute to IDH; New Zealand Ministry of Business Industry and Enterprise to SCC, IDH, IRM., and Polar Knowledge Canada Contract 3Y004-210046 to BJS. Thank you to Susan Anthony for organising the physiology device. Logistic support was kindly provided by Antarctica New Zealand. This manuscript is part of the PhD thesis of CRB. We are extremely grateful to the two PhD thesis examiners for their valuable and constructive comments which helped improve this manuscript.

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Supplementary Materials

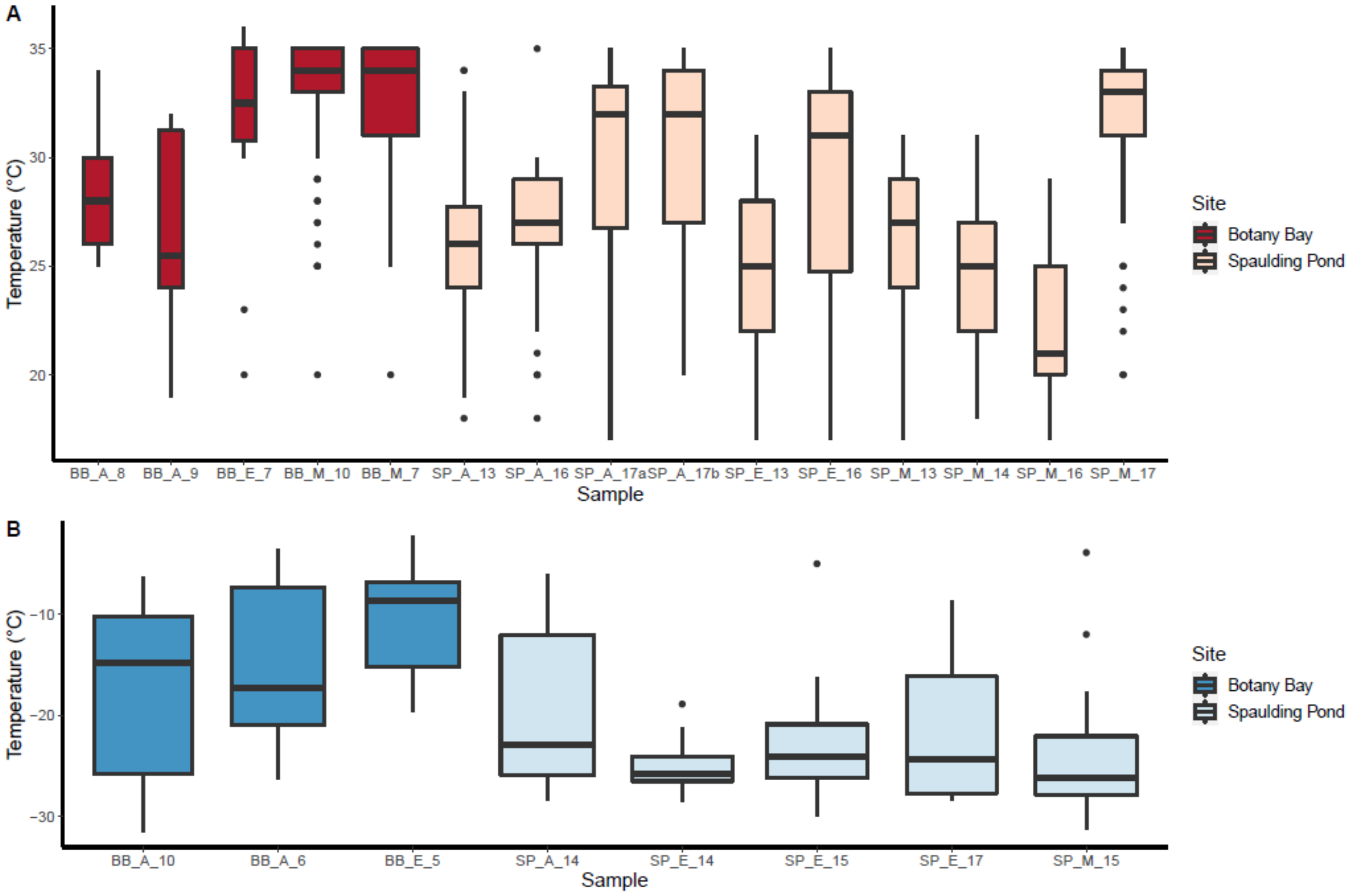

Figure S1: A= Boxplots of each heat tolerance CT_{max} experimental run (sample) exhibiting the variability within and between experimental runs. Experimental run (sample) naming convention follows as site_time of day_date. Sites BB=Botany Bay, SP=Spaulding Pond; time of day M=morning, A=afternoon, E=evening. The date is a day in December 2018. B= Boxplots of each cold tolerance supercooling point experimental run (sample)

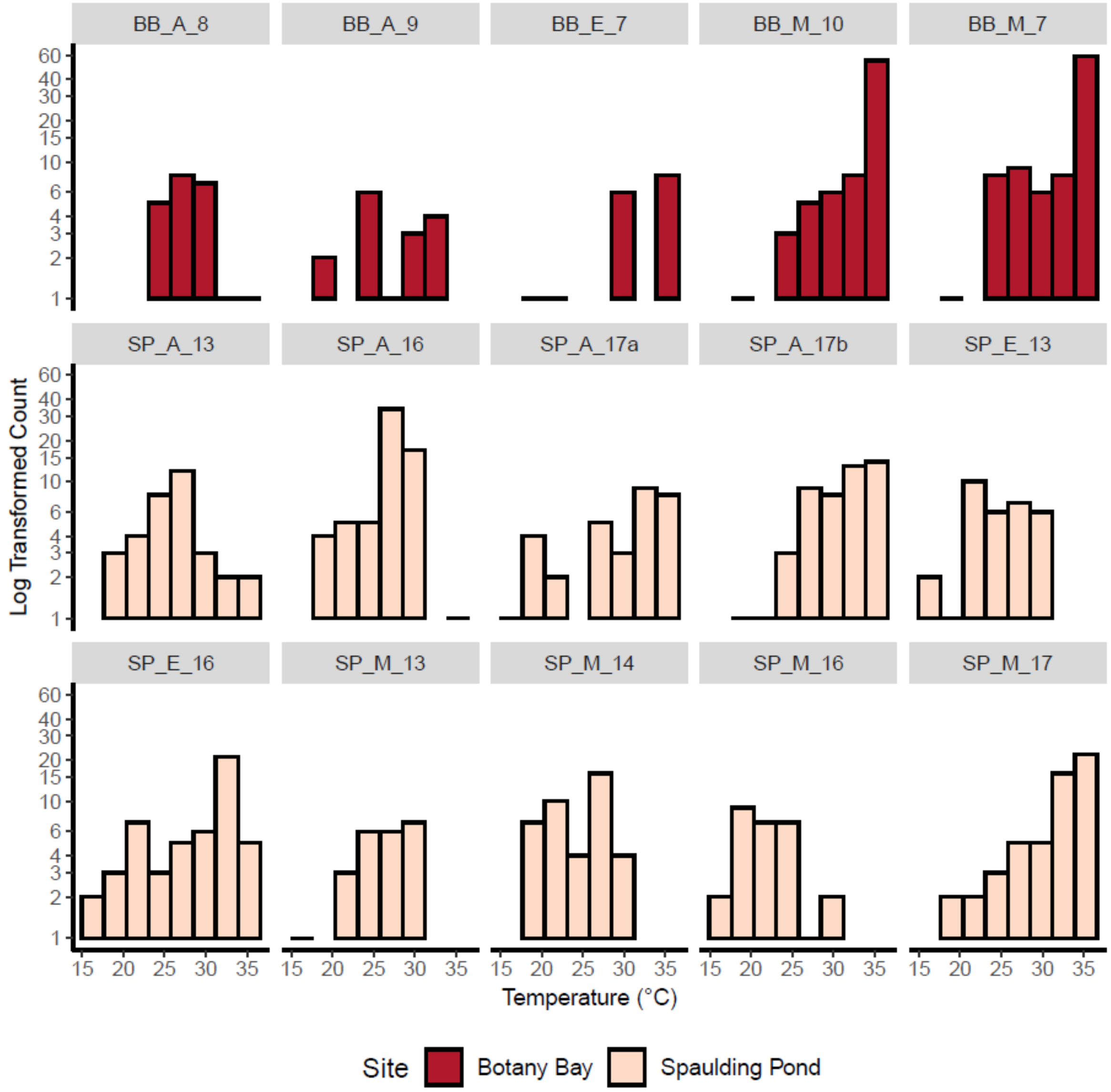

Figure S2: A= Histograms of each heat tolerance critical thermal maxima experimental run (sample) exhibiting the variability within and between experimental runs. The temperature refers to the temperature at which individuals reached their critical thermal maxima.The number of individuals in each run is log transformed due to the variability in sample size. Experimental run (sample) naming convention follows as site_time of day_date. Sites BB=Botany Bay, SP=Spaulding Pond; time of day M=morning, A=afternoon, E=evening. The date is a day in December 2018.

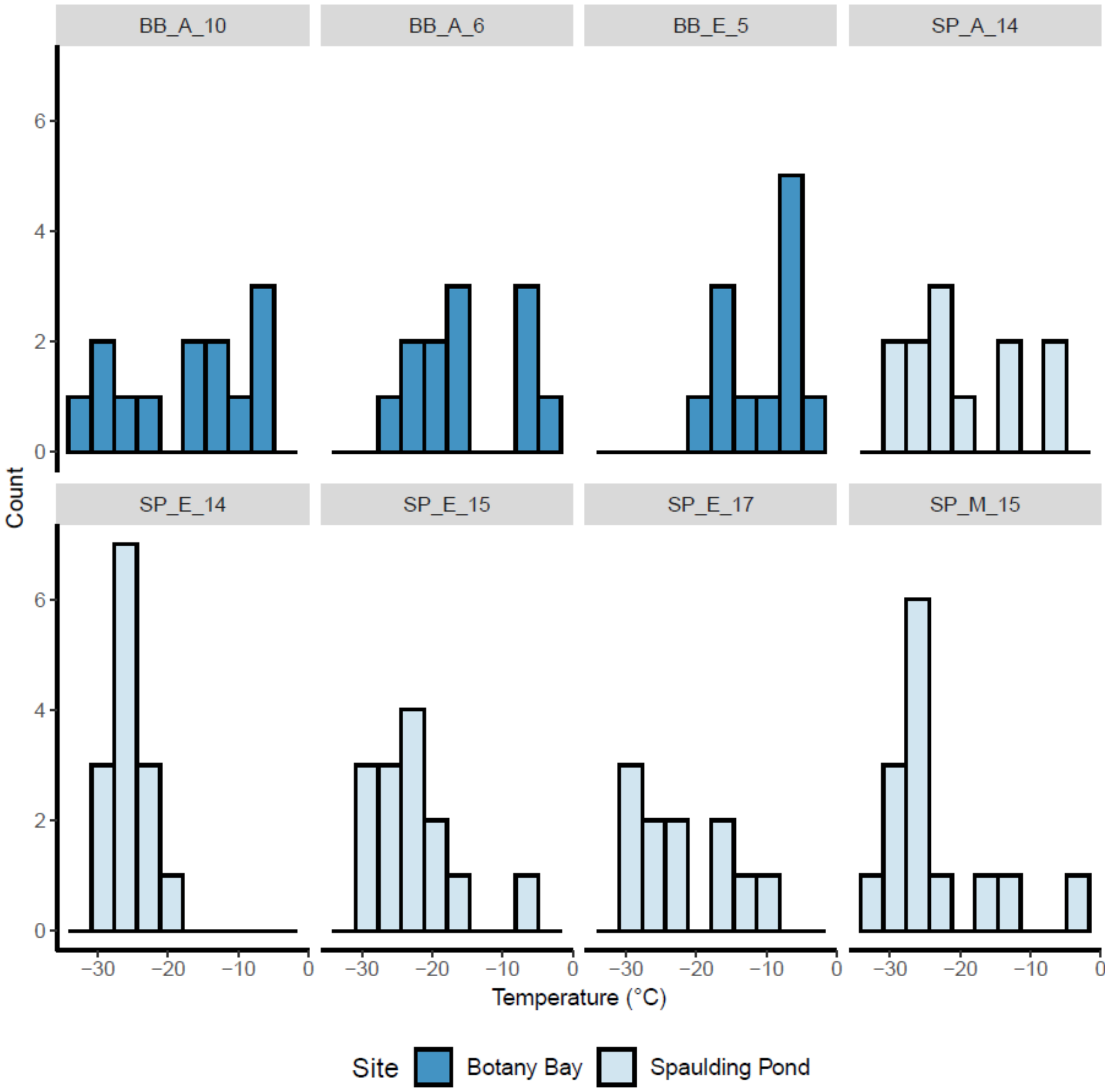

Figure S3: A= Histograms of each cold tolerance, supercooling point experimental run (sample) exhibiting the variability within and between experimental runs. The temperature refers to the temperature at which individuals reached their supercooling point and froze. The number of individuals in each run is log transformed due to the variability in sample size. Experimental run (sample) naming convention follows as site_time of day_date. Sites BB=Botany Bay, SP=Spaulding Pond; time of day M=morning, A=afternoon, E=evening. The date is a day in December 2018.

CHAPTER VI

Thesis Conclusions

Climate change is already having visible impacts on polar ecosystems (Hodkinson et al. 2013, Koltz et al. 2018, Høye et al. 2021). It is therefore urgent to assess the resilience of polar fauna to environmental changes. Resilience is defined as the capacity to limit the impact of a disturbance to ensure survival (resistance), and the ability to recover accordingly (recovery) (Holling 1973, Nimmo et al. 2015, Ingrisch and Bahn 2018). In my thesis, I focussed on the resilience of polar Collembola at different spatial (two polar regions), and relevant temporal scales in addition to different taxonomic (population and species) levels. From a temporal perspective, the role of long-term geological processes in structuring the highly endemic Antarctic Collembola fauna (Sinclair and Stevens 2006, Pugh and Convey 2008) was contrasted with the relatively recent history of the Arctic fauna and the legacy of those processes in shaping current and future resilience (Danks 1990, Hodkinson et al. 2013).

The chapters in my thesis addressed several current research needs including the provision of baseline genetic diversity and physiology data for Arctic Collembola along with integrative studies that compare genetics and physiology between Collembola populations. My first research chapter (Chapter II), provided a synthetic review of multiple aspects of polar collembolan resilience to climate change and to help focus ongoing research. Chapter III established the baseline genetic diversity of Collembola from the central Canadian Arctic and examined patterns of genetic connectivity with other locations in the Arctic. Chapter IV provided data on the physiological (cold, heat, drought) tolerances for five Arctic species. My final research (Chapter V) provided data on the heat and cold tolerances for two evolutionarily divergent populations of *G. hodgsoni* in the McMurdo Dry Valleys of Antarctica.

My first research chapter (Chapter II) highlighted that 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 (Beet et al. 2022, Chapter II). The biggest threats to the ongoing resistance of polar Collembola are increasing levels of dispersal (gene flow) (Nielsen and Wall 2013, Convey and Peck 2019), increased mean and extreme temperatures (Vasseur et al. 2014, Christensen et al. 2021), drought (Box et al. 2019), changing biotic interactions (Høye et al. 2021), and the expansion of non-indigenous species (Hughes et al. 2020, Chown et al. 2022). If resistance is insufficient, numerous studies have highlighted that while some species can recover from disturbances quickly, complete community-level recovery is exceedingly slow (Dunger et al. 2004, Hodkinson et al. 2004, Malmström 2012). 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 pace of climate change (Malmström 2012, Thakur et al. 2017, Aupic-Samain et al. 2021). Ultimately, diverse communities are more likely to have species or populations with individuals that are able to resist or recover from disturbances (Somero 2010). While much of the Arctic has comparatively high levels of genetic (and species) diversity and phenotypic plasticity; areas of Antarctica have extremely low levels of species diversity and are potentially vulnerable to climate change (Hodkinson et al. 2013, Collins et al. 2019).

In the second research chapter (Chapter III) a total of 512 individuals was sequenced and 68 Barcode Index Numbers (BINs; as a surrogate of putative species diversity) were found. There were eight morphologically-based species (identified based on comparison with reference sequences; Hogg and Hebert 2004, Babenko 2005, Porco et al. 2014), which were represented by multiple BINs with mitochondrial *COI* sequence divergences ranging from 1.28 – 18.39 %. Molecular clock calibrations of 3.54 % My^{-1} (Katz et al. 2018) suggested that the majority of multi-BIN species diverged 1.8-0.5 Mya during the Pleistocene when ice-sheets covered much of the Arctic (Dyke 2004, Gowan 2013, Lacelle et al. 2018). The timing of divergences for Collembola populations could indicate the presence of local cryptic refugia during this glacial period (England and Bradley 1978, Thomas et al. 2008). Comparison with available BOLD records, showed that 29 BINs (42 %) were currently unique to our study area on Victoria Island, 20 (29 %) clustered together with individuals collected from lower latitude mainland Canada sites, 21 (31 %) were shared with other locations on the Canadian Arctic Archipelago, seven (10 %) were shared with Greenland and Svalbard and a single BIN contained individuals collected from Herschel Island near the border between the Yukon and Alaska. The fact that there are shared BINs with locations primarily to the east (but not the west), could potentially support an east to west rafting dispersal route with additional mixing among the archipelago as well as northward migrations from lower latitude populations.

In the third research chapter (Chapter IV), sampled individuals of three species (*Entomobrya comparata*, *Isotomurus* sp., *Podura aquatica*) exhibited high levels of heat tolerance with mean critical thermal maxima (CT_{max}) all above 30 °C. Overall CT_{max} temperatures ranged between 26 °C and 41 °C, with the highest tolerances comparable with tropical Collembola (Liu et al. 2020). Most individuals displayed limited cold tolerance, with a majority (64 %) exhibiting supercooling points of less than -10 °C. Cold tolerances ranged widely between -3.4 to -25.3 °C, with three out of five species exhibiting a bimodal distribution of supercooling points, indicating active foraging (Cannon and Block 1988, Worland and Convey 2008). Under desiccating conditions, *Entomobrya comparata* individuals tolerated up to 13.5 hrs (range: 60-810 minutes) with 50 % of individuals surviving for less than 9.25 hrs. The desiccation stress that experimental individuals experienced was in line with minimum levels of relative humidity observed on warm days at my study site, indicating that some individuals would need to employ behavioural avoidance or acclimation to survive. Based on these findings, summer acclimated Collembola appear well placed to survive a level of warming. I conclude that the biggest threats to the resilience of Arctic Collembola are likely to be a combination of sustained heat and desiccation stress.

In the final research chapter (Chapter V) I integrated the genetic and physiological approaches of the previous two chapters (Chapter III, IV) to compare the resilience of two closely related, yet genetically distinct populations of Antarctic Collembola. I found that *Gomphiocephalus hodgsoni* individuals from the warmer coastal site had higher upper thermal limits (mean CT_{max} 31.3 °C) compared to individuals from the cooler inland location (mean CT_{max} 27.2 °C). Coastal individuals also had higher mean supercooling points (coastal: -14.3 °C; inland: -22.6 °C), indicating reduced cold tolerance. The physiological differences I observed were likely to have an underlying genetic component (Nolan et al. 2006, Collins and Hogg 2015). Accordingly, I concluded that in a warming climate, warm-adapted individuals are likely to have a selective advantage leading to changes in population genetic structure, a decline in genetic diversity, and associated decline in resilience to environmental changes.

Collectively, my thesis chapters (II, III, IV, V) demonstrated that across both polar regions Collembola can exhibit remarkably high levels of physiological tolerance with Antarctic individuals exhibiting a thermal range of >60 °C (Chapter V) and Arctic individuals exhibiting upper thermal limits comparable with tropical species (Chapter IV; Liu et al. 2020). Together, my research indicates that polar Collembola could exhibit high levels of resistance to climate change associated warming. In the central Canadian Arctic, I examined the genetic diversity for an estimated 68 species (based on BINs) with maximal divergences of 1.28 – 18.39 % between morphologically-based species (Chapter III). In the Antarctic, I was focussing on two populations (separated by 2.4 % COI sequence divergence) of the only springtail species found in the largest ice-free area of Antarctica (Chapter V). I found that the genetic diversity of Collembola at each polar region was similarly influenced by past glacial histories although the Arctic fauna has maintained higher levels of shared genetic diversity with surrounding habitats (Ávila-Jiménez and Coulson 2011, Collins and Hogg 2015, Collins et al. 2020). The different levels of habitat connectivity are likely to influence recovery potential following disturbances. In the Arctic, the presence of genetically similar populations from lower latitude areas and neighbouring Arctic islands suggests that any local population losses may be able to recover through dispersal. By comparison, in the Antarctic the low levels of diversity and connectivity mean that the impacts of disturbances are likely to be persistent. Together, my thesis chapters have identified that the biggest threats to the ongoing resistance of polar Collembola are sustained and extreme heat stress, desiccation stress, changing biotic interactions, and the arrival and spread of invasive species. Despite this, polar Collembola exhibit considerable levels of genetic diversity and physiological tolerances that may make them pre-adapted and resistant to some climate change induced environmental changes.

CHAPTER VI

Future Research

Profitable areas of research that would benefit from immediate attention include: 1) improved morphological work and associated reference DNA barcoding for the Arctic fauna; 2) determining the degree of seasonality and plasticity in Arctic thermal tolerance limits; 3) using genome and transcriptome sequencing to understand the genetic and physiological mechanisms of polar Collembola responses to stressors and their interactions; 4) evaluating the behavioural avoidance capacity of polar Collembola to stressors in natural systems; and 5) employing molecular tools to catalogue the diets of a broad array of species and life stages.

Based on results from Chapter III, further morphological work and associated reference DNA barcoding will help to better characterise the species diversity present in the central Canadian Arctic. This work would help to assess the level of cryptic genetic and species diversity to improve future abilities to identify species (e.g. sampling based on environmental DNA). This would also allow for further wide-scale approaches to measuring Collembola diversity and aid in monitoring efforts that aim to detect changes in community composition in response to climate change (sensu Høye et al. 2021). Future studies would also benefit from monitoring of temporal variability in diversity (sensu Bardgett and Van Der Putten 2014), in order to detect interannual variability versus any directional changes in species diversity.

There is an ongoing need to characterise thermal tolerance limits for Arctic Collembola across a range of life stages and at different times throughout the summer season in addition to acclimation and seasonal experiments to help determine the degree of plasticity in thermal tolerance limits. It is important to examine the tolerances across life-stages to determine whether juveniles are more sensitive to stressors which if so could result in population declines. Chapter IV showed that the Collembola from the central Canadian Arctic had high levels of heat tolerance. Future research should focus on survival rates following exposure to sustained heat stress and combinations of stressors to test the boundaries of heat tolerance (Kaunisto et al. 2016). The cold tolerance capacities I observed were, in theory, too high for surviving the Arctic winter. It is thus critical to determine whether seasonal acclimation of cold tolerances occurs or whether microhabitat selection is the main method employed to mitigate winter cold. This could become more important as snow pack and its associated thermal buffering capacity declines and the Arctic winters warm (Bokhorst et al. 2012, Williams et al. 2015).

In the Antarctic, future research should target acclimation and plasticity to better understand the role of seasonality in thermal tolerances and overall resistance capacities of the Antarctic Collembola (Chapter V). Understanding the relative contributions of phenotypic plasticity and evolutionary adaptation to thermal tolerances can help inform their adaptive potential in the face of climate change. For example, if populations are highly plastic they may be better able to adapt to changing environmental conditions compared to populations that have evolved based on paleoclimate conditions. My work has established that two populations of an Antarctic Collembola differ based on mitochondrial *COI* sequence and physiological tolerances of hot and cold temperatures. Genome and transcriptome sequencing (sensu Dunning et al. 2014, Cucini et al. 2021) are needed to understand the genetic and physiological mechanisms underlying differential physiological phenotypes. Furthermore, monitoring shifts in patterns of thermal tolerance or proportions of genetic populations of these sentinel species could be employed to detect the early effects of climate change on Antarctic biological systems.

The context of what physiological tolerances are selected for is predicated on the actual microclimate that individuals are exposed to. If individuals can successfully avoid climate change induced stressors they may not have to adapt physiologically to maintain high levels of resistance. Research on behavioural avoidance of stressors in natural environments would be beneficial.

Descriptive data on the ecology of polar Collembola including the feeding habits of different species and life stages are needed to develop a more mechanistic understanding of terrestrial invertebrate food-webs and the flexibility of the interactions therein. Detailed research into food-web interactions could also aid in better characterising competitive and predatory relationships between Collembola which have a direct influence on fitness and resilience particularly if food availability or quality changes (Aupic-Samain et al. 2021, Doucette et al. 2022). Molecular tools could be used to catalogue the diets of a broad array of species and life stages (Anslan et al. 2016, Potapov et al. 2020)

My thesis research as well as these suggested avenues for future research will help to further understand the role of polar Collembola in mediating the resilience of wider polar ecosystems to climate change.

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