





Short Note

Swarming in the storm: Collembola aggregations on sub-Antarctic Marion Island

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Abstract

The intensity and frequency of extreme weather events in rapidly changing environments continue to increase, driving unusual behaviours and posing significant threats to terrestrial ecosystems. In this study, we describe the co-occurrence of 1) Collembola swarming, 2) vegetation die-off and 3) extreme weather events, particularly heavy rainfall and high temperatures, over a 5 day period on sub-Antarctic Marion Island. Taxonomic and molecular evidence confirmed that the Collembola species displaying swarming behaviour was *Ceratophysella denticulata*, an invasive hypogastrurid. Our observations suggest that environmental stressors may have induced vegetation die-off, which, in turn, may have directly or indirectly driven Collembola aggregation. The association of these factors highlights the potential role of Collembola as bioindicators of soil ecosystem responses to climatic extremes, and that the recognition of these interactions can be critical in the prediction and management of ecological responses to changing environments.

Keywords: *Ceratophysella denticulata*; Collembola swarming; extreme weather events; Southern Ocean; sub-Antarctic islands; vegetation die-off

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Introduction

Collembola, commonly known as springtails, are globally distributed microarthropods that are largely terrestrial and often numerically abundant in soil ecosystems. Densities of 10^4 – 10^5 individuals m^{-2} in suitable habitats are common, sometimes reaching considerably greater numbers, with population numbers often exceeding more than half the total number of soil arthropods (Petersen & Luxton 1982, Convey & Smith 1997, Hopkin 1997, Bellini *et al.* 2023). Despite their small size (typically 0.1–3.0 mm), Collembola are important constituents of soil mesofauna, contributing to nutrient cycling and supporting complex food chains by serving as prey to numerous small predatory organisms. They, in turn, feed on microorganisms, fungal hyphae and spores, algae, plant debris, decaying animals and faeces, and, in some cases, they prey on microfaunal groups such as nematodes (Hopkin 1997, Rusek 1998, Salmon *et al.* 2014). In addition, Collembola

play crucial roles in soil ecosystem functioning by regulating soil microbial communities and influencing biochemical processes such as decomposition and carbon sequestration, as well as plant nutrition and growth (Petersen & Luxton 1982, Hopkin 1997, Potapov *et al.* 2020, Bellini *et al.* 2023). Their faeces and other excreted products contribute significantly to humus formation, which improves soil fertility, enhancing nutrient availability and promoting plant growth (Verhoef & Brussaard 1990, Forey *et al.* 2015, Winck *et al.* 2020). The main outcomes of these processes, largely influenced by Collembola density, affect key physical soil properties such as porosity, gaseous and water exchange and stability against erosion (Rusek 1998, Maaß *et al.* 2015, Potapov *et al.* 2020, Bellini *et al.* 2023). Given their key role in soil ecosystems, Collembola have been the focus of studies across fields, including the effects of biological invasions (Potapov *et al.* 2020, Chown *et al.* 2022), biomass shifts due to climate change (Gruss *et al.* 2023), abiotic parameters such as terrain ruggedness, topography and geographical distances (Monsanto *et al.* 2024), soil ecotoxicology and landscape stress and disturbance (Greenslade 2007), responses to urbanization (Qiao *et al.* 2022) and the influence of selective pressures on the mitochondrial genome and adaptive strategies (Monsanto *et al.* 2022).

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Biological invasions can pose significant threats to biodiversity, especially that of sub-Antarctic islands owing to their favourable terrestrial systems and milder temperatures compared to more extreme Antarctic landmasses (Chown *et al.* 1998, Greve *et al.* 2017, Leihy *et al.* 2018). Indigenous fauna are sometimes out-competed or apparently displaced by their invasive counterparts (although this is generally an inference based on the post-invasion dominance of the invasive species in certain habitats where other native species would typically be found; e.g. Convey *et al.* 1999), with consequential impacts on ecosystem functioning and processes (Greenslade 2002, Frenot *et al.* 2005, McGeoch *et al.* 2015, Vega *et al.* 2021). Environmental impact assessments of invasive taxa on indigenous groups have been categorized by Greve *et al.* (2017), and recent quantitative assessments of invasive organisms found that Marion Island hosts a total of 45 established non-native taxa, 25 of which are deemed invasive (Fernández Winzer *et al.* 2025). Of these, five springtail species are considered invasive, in comparison with an overall diversity of 10 native springtails (Janion-Scheepers 2025). Environmental soil variables such as resource availability, temperature and chemistry (e.g. pH, total sodium, exchangeable sodium, total nitrogen, total phosphorous, phosphate, organic carbon, moisture content) and the consequential vegetation/habitat differences strongly affect Collembola assemblages, highlighting microhabitat specificity and adaptive ability (Hopkin 1997, Convey *et al.* 1999, Gabriel *et al.* 2001, Monsanto *et al.* 2022). Notably, the group also exhibits preference for different levels of microhabitat stratification, which are categorized into ecomorphological life-forms, probably driven by factors such as food source and availability, soil type and chemistry, functional ecology and biology/morphology (Rusek 1998, Salmon *et al.* 2014, Potapov *et al.* 2016, Malcicka *et al.* 2017, Monsanto *et al.* 2022). Collembola are broadly defined into six ecomorphological life-forms with major ecological, biological and morphological characteristics - or combinations thereof - that typify each life-form: atmobiotic, epiedaphic, hemiedaphic, euedaphic, myrmecophilous and hydrophilous/aquatic. Atmobi-otic and epiedaphic species are generally larger in size (> 3 mm), possess ocelli, body pigmentation and dorsal patterns, long antennae, well-developed appendages (including furca) and show strong dispersal abilities. Hemiedaphic, euedaphic, myrmecophilous and hydrophilous taxa are usually smaller in size (< 3 mm) and have fewer or no ocelli, little to no body pigmentation with no dorsal patterns, shorter antennae and appendages and reduced or absent furca, and they are therefore poor dispersers (Deharveng *et al.* 2008, Potapov *et al.* 2016, Malcicka *et al.* 2017, Monsanto *et al.* 2022).

Social communication among individuals is necessary to ensure the adequate functioning of a population. Social signalling between organisms can occur via various means, such as chemical, visual, acoustic, tactile or substrate-borne means (Richard & Hunt 2013). Among these, chemical communication through pheromones is the most common, ancient and widespread means of disseminating information (Candolin 2003). Chemical messaging is efficient in most conditions and can be used to convey messages pertaining to health, mate recognition and selection, aggressive behaviour and dominance, defence strategies, microhabitat selection and the search for food (Candolin 2003, Richard & Hunt 2013). Chemical communication among higher-order insects has long been known to be an adaptive feature, such as in mate attraction or enabling the development of aggregation behaviour to collectively respond to and deter predators (Messer *et al.* 2000, Pfander & Zettel 2004, Richard & Hunt 2013).

Aggregation or swarming behaviour has also been noted in more primitive hexapods such as springtails, and in other microarthropods such as mites (Acari). For instance, the Antarctic oribatid mite *Alaskozetes antarcticus* commonly aggregates in multi-instar groups around the edges where embedded rocks or carpet moss vegetation adjoin the ground surface (Block & Convey 1995), or even in abundance on the faeces of the native ducks on Bird Island, South Georgia (T. Martin, personal communication 2002). Although they probably graze on epilithic microalgae in these aggregations, aggregation also appears to be driven by movement towards favourable microhabitats in otherwise-challenging (temperature and desiccation) environments. Sometimes these aggregations form mounds or balls of tightly massed mites several to tens of centimetres across, containing tens to hundreds of thousands of individuals, which could play multiple roles including microhabitat regulation (temperature and water loss) or facilitating mating. These mites do not have native predators in their natural Antarctic habitat, so these visually obvious aggregations may not incur a 'defence' cost. Similarly, Collembola are frequently observed to form aggregations rafting on water and on dead foliage, decaying wood, stone structures and snow surfaces/glaciers, particularly during climatic changes, which can influence the behavioural patterns and community dynamics of populations (Turk 1932, Krediet *et al.* 2023, Susanti *et al.* 2024, Valle *et al.* 2024). Incidences of extremely high densities of up to millions of individuals per square metre of the Antarctic springtail *Cryptopygus antarcticus* have been observed in one of its preferred habitats, the nitrophilous foliose alga *Prasiola crispa* (P. Convey, personal observation from Signy Island in 2024). This, again, is likely to bestow a combination of advantages, including providing a stable and hydrated microhabitat within the folds and thalli of the algal carpet, thereby maximizing access to a preferred food source. These algal mats regularly and progressively dry for periods during the Antarctic summer, sometimes on a daily basis, but live springtails can be retrieved from them even when the mat texture is dry and externally crisp to the touch. Another example of aggregations observed in the Antarctic region is given by the mating swarms of the chironomid midge *Parochlus steinenii* from the Maritime Antarctic South Shetland Islands (Hahn & Reinhardt 2006, Contador Mejias *et al.* 2023). Strongly dominated by males, these swarms are found in densities of more than 5000 individuals in preferred microhabitats such as on the underside of stones, on the sheltered side of rocks and on mosses on the shores of permanent lakes and ponds, and swarms of a few hundred individuals may even be observed floating on the water surface.

Aggregations may have a protective defence function for some springtails, integrating the secretion of active compounds or chemical irritants, thereby providing an energetically more efficient defence mechanism (Hopkin 1997, Bitzer *et al.* 2004, Pfander & Zettel 2004). Whether this is the case in Antarctic or sub-Antarctic springtails is unknown, although, unlike the oribatid *A. antarcticus*, the springtail *C. antarcticus* is the primary prey of the mesostigmatid mite *Gamasellus racovitzai* in the Maritime Antarctic; however, the level of mite predation does not measurably impact the overall springtail population (Usher & Bowring 1984, Lister *et al.* 1988). Evidence of chemical communication (pheromones) has been documented for some collembolans (specifically species of the family Hypogastruridae) that frequently display aggregation/swarming behaviour often noticeable on snow, on melting snow patches or above dead foliage specifically during wet seasons (Turk 1932, Pfander & Zettel 2004, Hågvar 2010, Dányi 2013). Indeed, in Scandinavia, coordinated swarms of

springtails have been documented moving across snow surfaces in winter (commonly known as ‘snow fleas’; Hågvar 2010, Valle *et al.* 2024). However, swarming by collembolans in response to extreme abiotic (climatic) changes in environmental conditions has received relatively little attention globally. In this study, we document springtail swarming observed in two locations during a wet and hot 5 day period on sub-Antarctic Marion Island in the southern Indian Ocean, and we consider the possible causes. These observations are the first of their kind for Marion Island, and we provide a synthesis of the subject of aggregation behaviour in springtails and other invertebrates as applied to the sub-Antarctic and Antarctic regions.

Environmental setting and methodology

The islands that constitute the ‘core’ of the sub-Antarctic region (Fig. 1) are South Georgia, Marion and Prince Edward islands, the archipelagos of Crozet and Kerguelen, Heard and McDonald islands and Macquarie Island (Convey 2020). Marion Island is characterized by hyper-maritime weather conditions, specifically high rainfall (~2200 mm/annum), high frequency of strong winds and low mean annual air temperatures (averaging at 6.3°C), and it has experienced shifts in climatic conditions on both geological and near-contemporary timescales (Rouault *et al.* 2005, Chown & Froneman 2008, le Roux & McGeoch 2008a, Nel *et al.* 2020, 2023,

Rudolph *et al.* 2020). Notably, the mean annual air temperature on Marion Island has increased by 1.7°C since records began in the mid-twentieth century, the highest rate of change for any sub-Antarctic island over the same period (Nel *et al.* 2023). Moreover, the island experiences short-lasting ‘extreme weather events’, such as high-temperature and high-rainfall events (see Kabase 2024), which can have negative impacts on the island’s flora and invertebrate fauna (le Roux & McGeoch 2008b, Nyakatyia & McGeoch 2008, Hedding & Greve 2018, Hugo-Coetzee & le Roux 2018).

Microarthropod aggregation behaviour was observed for the first time on sub-Antarctic Marion Island (the larger of the two islands belonging to the Prince Edward Islands) in April 2019 by S. Schoombie and M. Leitner. This involved a single collembolan species at two locations on the west coast of the island, namely Swartkops (SK; 46°55′33.8″S, 37°35′38.8″E) and Mixed Pickle (MP; 46°52′38.0″S, 37°37′56.2″E). Hundreds of aggregations near SK were observed at the burrow entrances of blue petrels (*Halobaena caerulea*; Fig. 2a), whereas those near MP were at the wet and/or flooded burrow entrances of white-chinned petrels (*Procellaria aequinoctialis*; Fig. 2b,c).

Approximately 80 Collembola specimens were collected at one nest entrance from each of these two sites and stored immediately in absolute ethanol for subsequent taxonomic examination and molecular identification. Twenty individual specimens were photographed using a Zeiss Stemi 305 Stereo Microscope

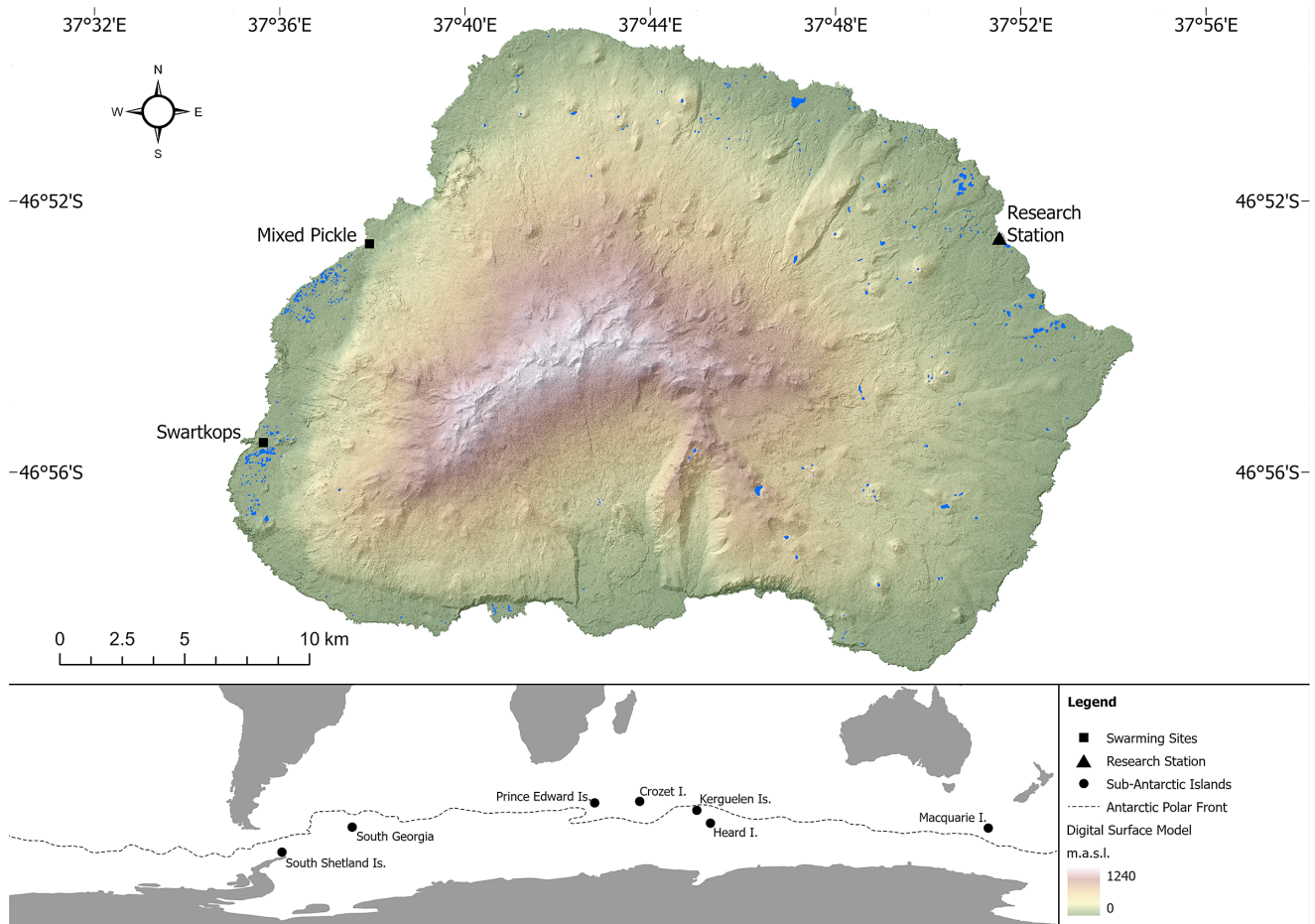


Figure 1. Digital surface model map of Marion Island and its position (represented as Prince Edward Islands) within the Southern Ocean, highlighting the locations (Swartkops and Mixed Pickle) where Collembola aggregations were observed. The inset map shows the positions of sub-Antarctic islands and the Antarctic Polar Front (dashed line). m.a.s.l. = metres above sea level.



Figure 2. Aggregations of springtails of ~20 cm in size at **a.** the burrow entrances of blue petrels at Swartkops, **b.** the wet burrow entrances of white-chinned petrels of ~10 cm in diameter at Mixed Pickle and **c.** floating on the water surface of a flooded white-chinned petrel burrow entrance of ~50 cm in size at Mixed Pickle. **d.** Taxonomic and molecular techniques identified the species forming these aggregations to be the invasive hypogastrurid *Ceratophysella denticulata*.

equipped with an AxioCam ERc 5s microscope camera. The specimens were identified using a taxonomic key for the Collembola of Marion Island (Janion-Scheepers 2025). Taxonomic confirmation was made using molecular sequence data by individually placing ethanol-preserved specimens into 0.2 ml polymerase chain reaction (PCR) tubes and allowing them to air dry at room temperature to remove excess ethanol. The DNA barcoding gene (mitochondrial cytochrome c oxidase subunit I gene, or *COI*) was amplified using the primers described by Folmer *et al.* (1994). A standard PCR master mix was used containing 3 μ l reaction buffer (20 mM TRIS-HCl (pH 8.0), 100 mM NaCl, 0.1 mM EDTA, 1 mM DTT, stabilizers and 50% glycerol), 3 μ l 25 mM MgCl₂, 3 μ l 1 μ M of each dNTP, 3 μ l 10 μ M of both forward and reverse primers, 0.3 μ l Taq polymerase (5 units ml⁻¹) and 14.7 μ l ddH₂O to create a reaction volume of 30 μ l, which was added to each tube. The individual springtails were then homogenized using a pestle, and each PCR tube was placed into a MultiGene OptiMax thermal cycler with the following conditions: initial denaturation at 96°C for 5 min, 40 cycles of 30 s at 96°C for denaturation, 30 s at 48°C for annealing and 50 s at 72°C for extension, followed by a final extension step at 72°C for 10 min. All samples underwent post-PCR clean-up using the Macherey-Nagel NucleoSpin® Gel and PCR Clean-up Kit following the manufacturer's recommendations.

Successful amplifications were confirmed using 2% agarose gel electrophoresis with 0.5X TBE buffer and the GelRed Nucleic Acid Gel Stain (Biotium). PCR products were sequenced with the forward primer on a 3730XL DNA Analyzer (Applied Biosystems). To identify and confirm the species in this study, Basic Local Alignment Search Tools (BLAST) searches were conducted using the GenBank repository based on > 98% identity (Benson *et al.* 2013).

Results and discussion

Collembola aggregations were observed at the burrow entrances of blue petrels and white-chinned petrels at SK and MP, respectively. Ground observations highlighted vegetation alterations at MP with mild vegetation die-off and decay of the native flowering plant *Leptinella plumosa* in the areas near the aggregations (Fig. 2b), and taxonomic and molecular techniques confirmed that the Collembola species was *Ceratophysella denticulata* (Bagnall, 1941; Fig. 2d). At SK, extensive vegetation die-off and decay were observed affecting an area of ~200 m² of *L. plumosa* (Fig. 3a,b), noticeably differing from the typical state of vegetation observed in the area (Fig. 3c,d).

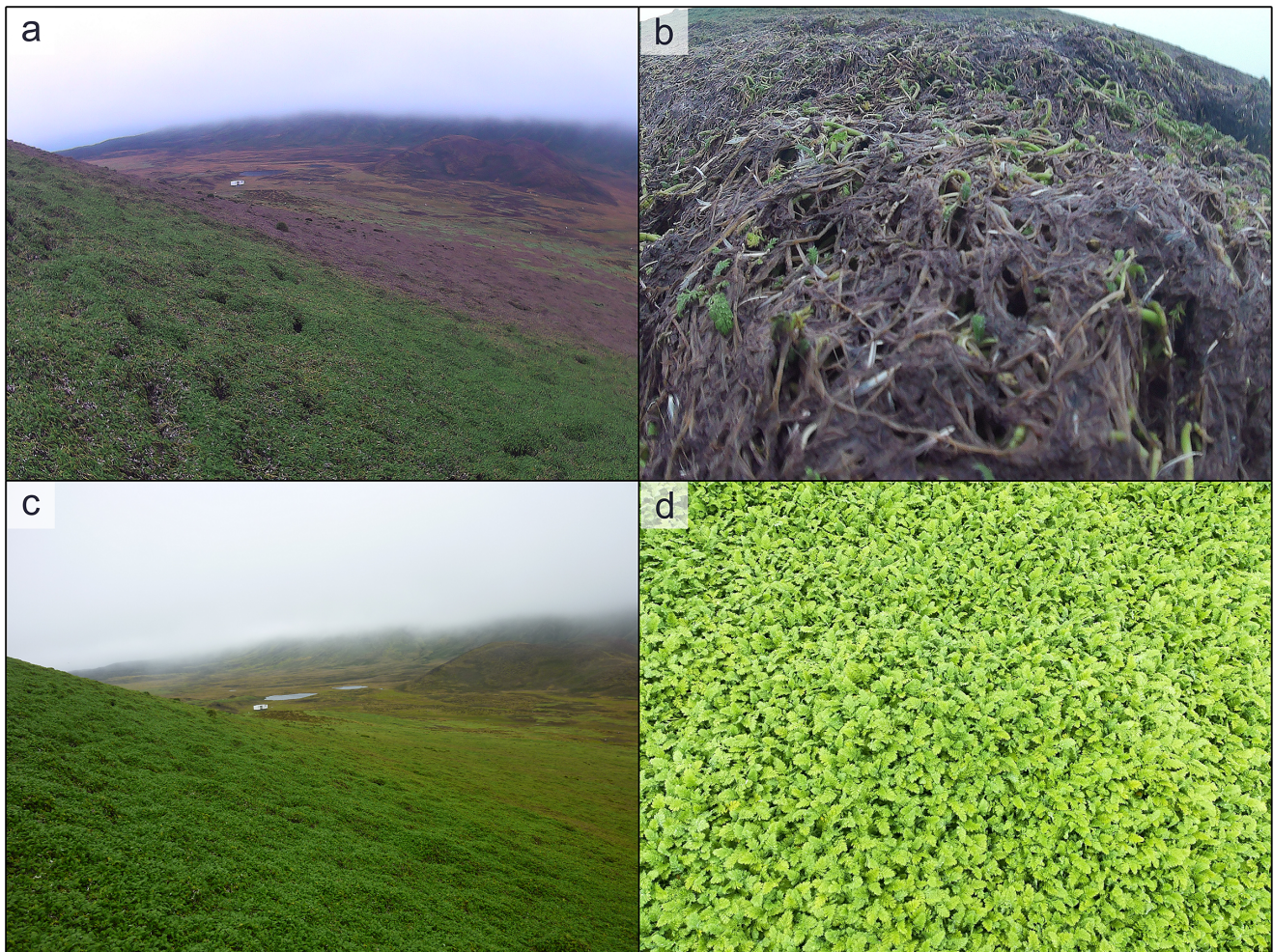


Figure 3. a. & b. Extensive decay of *Leptinella plumosa* of ~200 m² at Swartkops contrasted with **c. & d.** when no vegetation alterations are observed in the area. The photographs for **a.** and **b.** were taken in April 2019, the photograph for **c.** was taken in April 2013 and the photograph for **d.** was taken in January 2020.

The conspicuous Collembola aggregations observed here were found in areas comprising bare ground and poor-health/decaying vegetation in the immediate vicinity of bird nesting burrows, including within their entrances. This may suggest a possible nutrient-related cue, either from the decaying plant material or bird guano, and also raises the possibility of further zoochoric transfer of this already highly invasive springtail if carried in soil or plant material that becomes attached to the birds' plumage. The species forming these aggregations on hyper-maritime Marion Island was confirmed to be the hypogastrurid *C. denticulata* (Bagnall, 1941), which has been documented to be invasive and widely distributed at lower elevations on Marion Island (Gabriel *et al.* 2001, Frenot *et al.* 2005, Hugo *et al.* 2006, Myburgh *et al.* 2007, Slabber *et al.* 2007, Greve *et al.* 2017). Furthermore, this species belongs to the highly invasive family Hypogastruridae (Greenslade 2002), some of whose members are known to be resilient to extreme climatic conditions (Onley *et al.* 2025), and with physiological analyses revealing *C. denticulata* to have a competitive advantage over its indigenous counterparts due to its higher upper lethal temperature and ability to withstand warmer temperatures (Slabber *et al.* 2007). Other members of the Hypogastruridae are also well-known invasive springtails with wide and even global cosmopolitan distributions. These include two representatives of *Hypogastrura*, *Hypogastrura viatica* and

Hypogastrura purpurescens, which are known non-native species on sub-Antarctic South Georgia (Frenot *et al.* 2005, Greenslade & Convey 2012). Additionally, *H. viatica* is widespread and abundant on other sub-Antarctic islands such as Macquarie Island (alongside *C. denticulata*; Greenslade 2018), Kerguelen Island and Possession Island (Baird *et al.* 2019), and on Maritime Antarctic Deception Island (Greenslade *et al.* 2012, Greenslade 2018, Hughes *et al.* 2025). *Hypogastrura viatica* has also been recorded at a location off the coast of the western Antarctic Peninsula, with a recent first-time report (although most probably not established) within Casey Station on the Continental Antarctic coastline (Greenslade 1995, 2002, Greenslade & Convey 2012, Onley *et al.* 2025, Hughes *et al.* 2017). These species are frequently found in dense concentrations, particularly around and under human-made debris.

Previously, Gabriel *et al.* (2001) concluded that native springtail richness and abundance were unaffected by non-native springtails on Marion Island. However, a recent study comparing Marion Island and Macquarie Island with the pristine Heard Island concluded that invasive springtails have the potential to cause detrimental impacts on the native taxa (Chown *et al.* 2022). On the Prince Edward Islands, the current invasion risk potential of non-native springtails on native taxa remains unknown (Fernández Winzer *et al.* 2025). Studies comparing the non-native springtails present on Marion Island and Prince Edward Island previously

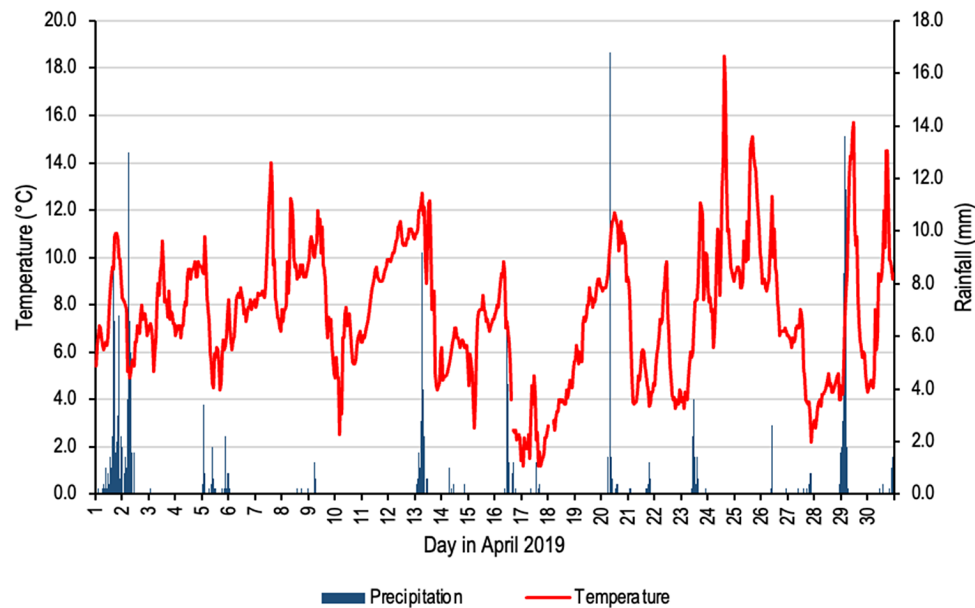


Figure 4. Temperature and precipitation data for Marion Island for April 2019 recorded at the Marion Island research station. Intense rainfall was experienced on 20 April, 5 days before the *Collembola* aggregations were observed and collected on 25 April, when extremely high temperatures were recorded. Hourly weather data were obtained from the South African Weather Service.

confirmed only one on Prince Edward Island: the already globally distributed *C. denticulata*, with densities on Marion Island possibly exceeding 38 000 individuals/m⁻² (Greenslade 2002, Hugo *et al.* 2006). The most recent collections from Prince Edward Island made in November 2023 revealed that a second non-native springtail, *Isotomurus maculatus*, is now present, a species already well-established on Marion Island (Fernández Winzer *et al.* 2025). Genetic analyses of *C. denticulata* and *I. maculatus* revealed single haplotypes across Marion Island, consistent with single invasion events for each species, highlighting the insignificance of propagule pressure and illustrating the high invasion potential of these taxa (Myburgh *et al.* 2007).

In this context, it is notable that both the vegetation die-off and decay and aggregation behaviour of *C. denticulata* were observed after extreme weather conditions, namely warm temperatures and intense rainfall, over a 5 day period between 20 and 25 April 2019 (Fig. 4). Mild vegetation die-off of the flowering plant *L. plumosa* around bird burrows was observed at MP (Fig. 2b), and a considerable extent of vegetation die-off and decay of ~200 m² was observed at SK (Fig. 3a,b), standing in clear contrast to when the area experiences no such die-off and decay (Fig. 3c,d). Although causation cannot be confirmed, environmental stress and subsequent plant decay could produce chemical or physical cues that influence *Collembola* aggregation. Wider botanical research, albeit primarily on crop species, has shown that extreme weather conditions such as heatwaves, droughts and intense rainfall events can impose significant stresses on vegetation (Rosenzweig *et al.* 2002, Lesk *et al.* 2016, Kim *et al.* 2024). Specifically, excess precipitation and waterlogging can impose stresses as a result of submergence, lodging (i.e. weakening of stem and root system and subsequent shifting from an upright position) and the facilitating of pests and pathogens that can benefit from excess water (Thompson *et al.* 2013, Kim *et al.* 2024). Among higher-order taxa, strong evidence of swarming or migratory events linked to climatic episodes, such as storms, floods, atmospheric circulation changes, heatwaves and vegetation alterations, have been extensively documented, with extreme

events potentially causing both population outbreaks or crashes (Harvey *et al.* 2020, Filazzola *et al.* 2021, John *et al.* 2024, Vives-Ingla *et al.* 2025). Additionally, research has suggested that *Collembola* behaviour and community dynamics are also closely linked to extreme weather conditions, with their abundances, species compositions and activity patterns shifting in response to these changes, and with moisture and temperature being the primary drivers (Beet *et al.* 2022, Zhang *et al.* 2022, Krediet *et al.* 2023, Sanders *et al.* 2024, Susanti *et al.* 2024, Li *et al.* 2025). During the decomposition of vegetation, volatile compounds are released that can serve as chemical cues or signals for insects to migrate towards or away from decaying material, and the subsequent secretion of aggregation pheromones in response to decaying vegetation has been reported for social insects (Kojima 2015, Mitaka *et al.* 2024). Although no current research reveals a direct link between vegetation decay and *Collembola* swarming, the co-occurrence of vegetation die-off and decay and aggregations on Marion Island highlights the possible association between vegetation die-off and decomposition and the swarming behaviour of soil microarthropods.

Conclusions

Our findings highlight a plausible connection between *Collembola* aggregation, vegetation die-off and decomposition with extreme weather events recorded on the island. The co-occurrence and interplay of these factors suggest that changes in environmental conditions, especially those brought on by climatic extremes, may significantly influence *Collembola* behaviour and distribution. Such responses may become more noticeable as the intensity and frequency of extreme climatic conditions continue to change. Understanding these interactions is crucial, as they reflect broader ecosystem responses to environmental stress, and they may serve as early bioindicators of soil health and vegetation change. Future studies that recognize these interactions will enhance our ability

to predict and manage ecological impacts in a rapidly changing climate.

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Competing interests. The authors declare none.

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