Assemblage level variation in springtail lower lethal temperature: the role of invasive species on sub-Antarctic Marion Island

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Abstract. It is widely held both in the physiological literature, and more generally, that the average characteristics of species within an assemblage differ among sites. Such generalizations should be based on investigations of whole assemblages at sites, but this is rarely done. Here, such a study is undertaken for virtually the full assemblage of springtails found at sub-Antarctic Marion Island, by investigating supercooling points (SCPs) of 12 of the 16 species that occur there. Assemblage level variation tends to be less than that documented for assemblages across northern hemisphere sites but similar to that found at some Antarctic locations. Across this set of species, the mean SCPs of the indigenous species (mean $\pm$ SE = -17.2 ± 0.4 °C) do not differ significantly from that of the invasive species (-16.3 ± 0.7 °C). Overall, the introduction of several species to the island does not appear to have led to functional homogenization (for this trait). By combining the assemblage-level SCP data with information on the abundances of the species in each of four major habitats, it is also shown that severe but uncommon low temperature events could substantially alter species relative abundances. By resetting assemblage trajectories, such events could play an important role in the terrestrial system at the island.

Key words. Biological invasion, cold hardiness, functional homogenization, macrophysiology, relative abundance.

Introduction

It has long been thought that, in extra-tropical environments, physical factors are of prime importantance for limiting the abundance and richness of species. This idea, which stretches back to Darwin, as well as explorations by Schmalhausen (1949) and Fischer (1960), is now established in concepts such as adversity selection (Southwood, 1988). More recently, the tropical (niche) conservatism hypothesis has promoted the idea that tropical organisms typically do not disperse into temperate regions because they cannot tolerate, and rarely evolve, resistance to adverse physical conditions, and especially low temperature (Wiens & Graham, 2005).

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In other words, physiological tolerances vary systematically through space in a consistent, reasonably predictable fashion.

At least for lower temperature thresholds, much work appears to support this notion (Prosser, 1986; Spicer & Gaston, 1999; Sinclair *et al.*, 2003a). Most of the data on which this generality is based originate from studies at the interspecific level. That is, a comparison is made of a group of species for which each species has a physiological trait measure (although, more recently, some ecologists now consider that a range-based climate envelope = physiological tolerance; Bonier *et al.*, 2007) and some measure of geographic position (Gaston *et al.*, 2008). Similar work is also often undertaken at the intraspecific level (Spicer & Gaston, 1999). However, the idea that physiological tolerances of a group of organisms generally vary between locations or major areas is one that should be tested at the assemblage level because this is the level at which any generality concerning differences in tolerances among areas is being made

(Gaston *et al.*, 2008). In other words, if it is argued that tropical species are typically less cold hardy than temperate ones, then the formal argument is that the average value of the character traits (i.e. averaged across all species in each assemblage) that are used to establish cold hardiness [such as supercooling point (SCP) and/or lower lethal temperature] differ significantly among the two sites (or more correctly the two assemblages, each of which can also be characterized by a single geographic location or a general statement about geographic position, such as a given latitudinal or altitudinal band). The rationale can be applied more generally to statements about the average characteristics (e.g. upper thermal limits, desiccation resistance, standard metabolic rate) of any two or more assemblages over a cline of any size (e.g. altitudinal, latitudinal or depth clines).

Studies of the variation in average characteristics of assemblages among sites are nonetheless uncommon. Those that have been conducted are usually associated with investigations of functional traits in plant assemblages and their responses to particular kinds of environmental settings (Fonseca *et al.*, 2000) or in studies of morphology in animals as a proxy for function in an ecological setting (Gilbert, 1985; Price *et al.*, 2000). Rarely are they undertaken for traits that would be recognized as explicitly physiological, such as lower lethal temperatures, metabolic rates, ultraviolet tolerance or desiccation resistance (although see Leinaas, 1981, 2002; Block, 1982; Sinclair *et al.*, 2006) and then often species means are reported, rather than the mean and variance for the assemblage. In the few cases where assemblage level data are available, it is clear that variation in the trait of interest at a particular site or across a range of sites can be much more substantial than might be expected on the basis of generalizations about spatial variation in the mean value of a trait. For example, in one of the few studies reporting assemblage level data, Addo-Bediako *et al.* (2000) show that not only does the mean SCP in insects decline with latitude, but also variance in SCP increases. This is ascribed to an increase in the range of behavioural and physiological strategies adopted by insects to survive low temperatures as conditions become more severe. Nonetheless, the generality of this phenomenon remains unclear.

One way to remedy this situation is to increase the frequency with which assemblage-level investigations are undertaken, despite the obvious difficulty that, in most assemblages, many species are rare (Gaston, 1994; McNab, 2003). Notwithstanding the challenges associated with undertaking them, such studies are essential for understanding how variation in physiological traits is partitioned through space as well as the ecological implications of this. Not only would they provide more robust tests of ideas such as the tropical conservatism hypothesis, but also they could provide further insight into the ways in which assemblages are altered by current anthropogenic change (Chown *et al.*, 2004; Chown & Gaston, 2008). For example, among the many environmental changes associated with the introduction of non-indigenous species, homogenization (or differentiation) of assemblages is of substantial concern (McKinney & Lockwood, 1999; McKinney, 2008). Although most work in this field deals

with taxonomic homogenization/differentiation, it is suggested that changes in functional similarity may also be of considerable significance (Olden, 2006). For example, these changes might alter the way in which an entire assemblage responds to other perturbations, such as those associated with climate change or pollution (Stachowicz *et al.*, 2002; Piola & Johnston, 2006; Chown *et al.*, 2007). However, this would depend to a large extent on the way in which the addition of non-indigenous species affects the mean and variance of the traits of interest at the assemblage level.

In the present study, an assemblage-level investigation of lower lethal temperature is provided in springtails from sub-Antarctic Marion Island aiming not only to establish ways in which this might be done, but also to investigate the extent to which invasive alien species may alter this characteristic of the assemblage. Although mean annual temperatures at the island are increasing (le Roux & McGeoch, 2008), this warming is being accompanied by an increase in clear skies and the severity and frequency of freezing events (Chown & Froneman, 2008). In consequence, this physiological trait is ecologically relevant.

Materials and methods

Study site and animals

Sub-Antarctic Marion Island (46°54′S, 37°45′E) has a cool, wet and windy climate that varies considerably with the island's elevation (1230 m a.s.l.) and has been showing substantial change over the last 50 years (Chown & Froneman, 2008). Sixteen species of springtail have been recorded from the island, of which five are introduced (Deharveng, 1981; Gabriel *et al.*, 2001).

Individuals of 12 of the 16 sixteen species of springtails (Table 1) were collected during April 2008, during the day and usually on relatively dry days after previous rain. Some

Table 1. Mean ± SE (°C) supercooling points of the 12 springtail species investigated in the present study.

Species	*n*	Mean ± SE
Indigenous		
Isotoma marionensis	20	−14.4 ± 1.3
Sminthurinus granulosis	16	−18.5 ± 1.7
Cryptopygus antarcticus travei	35	−16.3 ± 1.3
Cryptopygus tricuspis	33	−17.1 ± 0.9
Tullbergia bisetosa	46	−17.8 ± 0.7
Sminthurinus tuberculatus	20	−13.5 ± 1.1
Cryptopygus dubius	28	−21.0 ± 0.9
Invasive		
Megalothorax sp.	14	−18.5 ± 1.5
Ceratophysella denticulata	19	−21.2 ± 0.8
Isotomurus cf. palustris	20	−12.9 ± 1.4
Pogonognathellus flavescens	25	−11.6 ± 0.8
Parisotoma notabilis	18	−19.1 ± 1.4

species were collected in the field using an aspirator, whereas, for others, plant material known to contain particular springtail species was returned to the laboratory where the springtails were extracted using a sieve over a tray. Some species were more difficult to find than others: *Frisea tilbrooki* and *Katianna marionensis* are rare on Marion Island (Gabriel *et al.*, 2001). *Cryptopygus caecus* was also difficult to collect and *Hypogastrura viatica* has not been seen subsequent to an initial report by Deharveng (1981). Specimens collected in the field were placed into 30-mL plastic vials with moist Plaster-of-Paris substrates and small amounts of detritus as a food source and for shelter. They were returned to the laboratory within 3 h of collection. Both laboratory- and field-collected specimens were sorted to species level and kept in small plastic contain- ers (diameter 4 cm) with a base of moist Plaster-of-Paris mixed with charcoal, at 5 °C (LD 12 : 12 h) in temperature- controlled incubators (LABCON, South Africa; accurate to ± 1 °C) for 24 h. Because the aim of the study was to examine variation in lower lethal-temperature in field-collected animals, multiple acclimation treatments were not adopted (for such work on several of these species, see Slabber *et al.*, 2007).

SCP determinations

Cold hardiness was measured as the SCP (or crystalliza- tion temperature; Chown & Nicolson, 2004) of the individu- als of each species. Although it is well known that lower lethal temperatures may either lie above or below the SCP (Bale, 1987; Sinclair *et al.*, 2003b), investigation of several of the species studied here, namely *Pogonognathellus flavescens*, *Isotomurus cf. palustris*, *Ceratophysella denticulata*, *Cryptopygus antarcticus travei* and *Tullbergia bisetosa* has shown that the lower lethal temperature established over a period of several hours (i.e. a brief exposure, rather than one of weeks or months) and SCP are equivalent (Slabber *et al.*, 2007) as is the case for many other species (Sømme, 1982; Cannon & Block, 1988; Sinclair & Sjursen, 2001; Sinclair *et al.*, 2003a). It has also been shown that SCP varies with season, moult, acclimation treatment and diurnal temperature fluctuations (Cannon & Block, 1988; Worland & Convey, 2001; Sinclair *et al.*, 2003c; Worland *et al.*, 2006; Slabber *et al.*, 2007). In the present study, work was conducted within a single season (i.e. the onset of the sub-Antarctic winter, acknowledging that seasonal variation in climate on Marion island is small; le Roux, 2008) using a single holding protocol to retain differences related to field conditions and considering moult to be a natural source of variation that might influence the survival likelihood of individuals within an assemblage. Consequently, detailed influence of this variation was not explored. Rather, the characterization of assemblage-level properties at the onset of winter was investigated.

SCP were determined using a Mettler-Toledo Differential Scanning Calorimeter (DSC) 820 (Mettler-Toledo Ltd, U.K.) incorporating a mechanical intra-cooler (Lab-Plant Ltd, U.K.) capable of cooling to −60 °C. The system was calibrated with indium (melting point 156.6 °C, enthalpy 28.71 J g⁻¹) and gallium (melting point 29.8 1 °C, enthalpy of 79.3 J g⁻¹).

Calibration was regularly checked by measuring the melting point of 0.5 µL drops of high-performance liquid chomatog- raphy grade water. Data generated by the DSC were analysed using the STARe software package (Mettler-Toledo Ltd). Six to 20 animals were placed in a sealed aluminium pan (40 µL) and cooled at a rate of 1 °C min⁻¹ from +5 to −30 °C. Previous investigation of five of the species under study (see above) showed that a change in cooling rate did not affect the SCP (Slabber *et al.*, 2007) and this is true also for other springtail species (Cannon, 1983; Worland, 2005). The SCP was taken as the lowest point reached before the exotherm produced by the latent heat of freezing of the animal's body fluid (Worland, 2005).

Statistical analysis

Assemblage level analyses can potentially be undertaken in two ways. Most commonly, trait mean values for each species are obtained and the assemblage then characterized using standard measures of central tendency and variance (Addo- Bediako *et al.*, 2000; Gaston *et al.*, 2008; Greve *et al.*, 2008). For comparison of the present results with those obtained in other studies, this approach was also adopted here. Differences between the SCP means of the indigenous and invasive species were also investigated, to determine the extent to which the results obtained by Slabber *et al.* (2007) generalize, using a generalized linear model assuming a Poisson distribution and an identity link function as imple- mented in Statistica version 8 (StatSoft, Tulsa, Oklahoma) (Sinclair *et al.*, 2006). Differences between SCPs for differ- ent species were also assessed assuming a Poisson distribu- tion and using an identity link function as implemented in Statistica, version 8.

A second analysis was undertaken to determine the extent of individual-level variation within the assemblage because SCP values vary considerably within a given species at a given time (Cannon & Block, 1988; Sinclair *et al.*, 2003a). The aim was to determine the extent to which the characteristics of the assemblage at this level are altered by the presence of invasive species (i.e. how much is functional diversity in this trait altered) and to determine whether particular low-temperature events are likely to alter the relative abundances of springtail species in the field. The outcomes of low temperature events play out at the level of the population rather than the species (Bale, 1987; Sinclair, 2001). Therefore, understanding how assemblages might be altered via interactions between different environmental change drivers must be explored at this level (Brook *et al.*, 2008).

For this approach, frequency distributions of the SCPs across the entire assemblage were constructed using the approaches recommended by Scott (1979). This procedure was repeated separately for the indigenous and non-indigenous assemblages, using the class number and limits of the full analysis. In each case, the mean, variance, maxima and minima, skewness and kurtosis were calculated, and the latter was tested for significance using *t*-statistics (Quinn & Keough, 2002). The frequency distributions of the SCP values for the

indigenous and invasive species were also compared using a Kolmogorov–Smirnov two-sample test.

The likely change in the abundance (and relative abundance) of indigenous and invasive species was also investigated. First, the proportion of the sample of individuals surviving a particular temperature was calculated for each species. These values were then multiplied by the species abundances in four major habitats investigated by Gabriel *et al.* (2001), namely *Poa cookii* tussock grassland, *Azorella selago* cushion plants, *Jamesoniella*-dominated mires and high-altitude mires. The difference between the original and low temperature-affected assemblages was then inspected visually using rank-abundance plots (Magurran, 2004). The temperatures selected for the comparisons were based on a long-term soil tempera-ture record (2002–2007) for nine sites (0–800 m a.s.l.) at Marion Island (Slabber *et al.*, 2007) and, specifically, these were −6 °C and −12 °C. As an extreme temperature, we included −16 °C because it lies close to the mean of the assemblage-level frequency distributions. Owing to the diffi-culty of finding C. *caecus*, SCP data for C*ryptopygus tricuspis* were used for this species, acknowledging the potential for differences between the species, although they are closely related (Stevens *et al.*, 2006).

Results

Mean ± SE SCP of the assemblage was −16.9 ± 3.14 °C and varied between −21.3 °C in *C. denticulata* and −11.6 °C in *P. flavescens* (Table 1). Significant differences in SCPs were found among species ($\chi^2 = 70.59$, $P = 0.001$). The indigenous species showed a slightly narrower range in SCP (−13.6 to −21.0 °C), but no difference was found between the groups using the species means ($\chi^2 = 0.012$, $P = 0.913$). This lack of difference was maintained when the species values were examined including only data below −12 °C ($\chi^2 = 0.082$, $P = 0.7703$).

At the individual level, a much larger range in SCP values was found (Fig. 1). The distributions did not appear to differ between the indigenous and introduced species, and this was borne out by the two-sample Kolmogorov–Smirnov test ($P > 0.10$). Unsurprisingly, the statistical descriptions of the two distributions did not differ to any large extent (Table 2) and neither of the distributions showed significant skewness, although both were significantly platykurtic, perhaps unsur-prising given their bimodal distributions. Although distributions are frequently divided into high and low group individuals and analysed further (Block, 1982; Sømme & Block, 1982; Sinclair *et al.*, 2006), this was not performed in the present study because preliminary analyses indicated that no further differences among the two groups of species would be found and because changes in the relative proportions of individuals in the groups were not the subject of investigation (for such an approach, see Klok & Chown, 1998; Sinclair *et al.*, 2006).

Assuming that the relative proportions of individuals surviving −6 °C and −12 °C in the laboratory would be reflected in the field, it is clear that the higher temperature has relatively little impact on the relative abundances of the
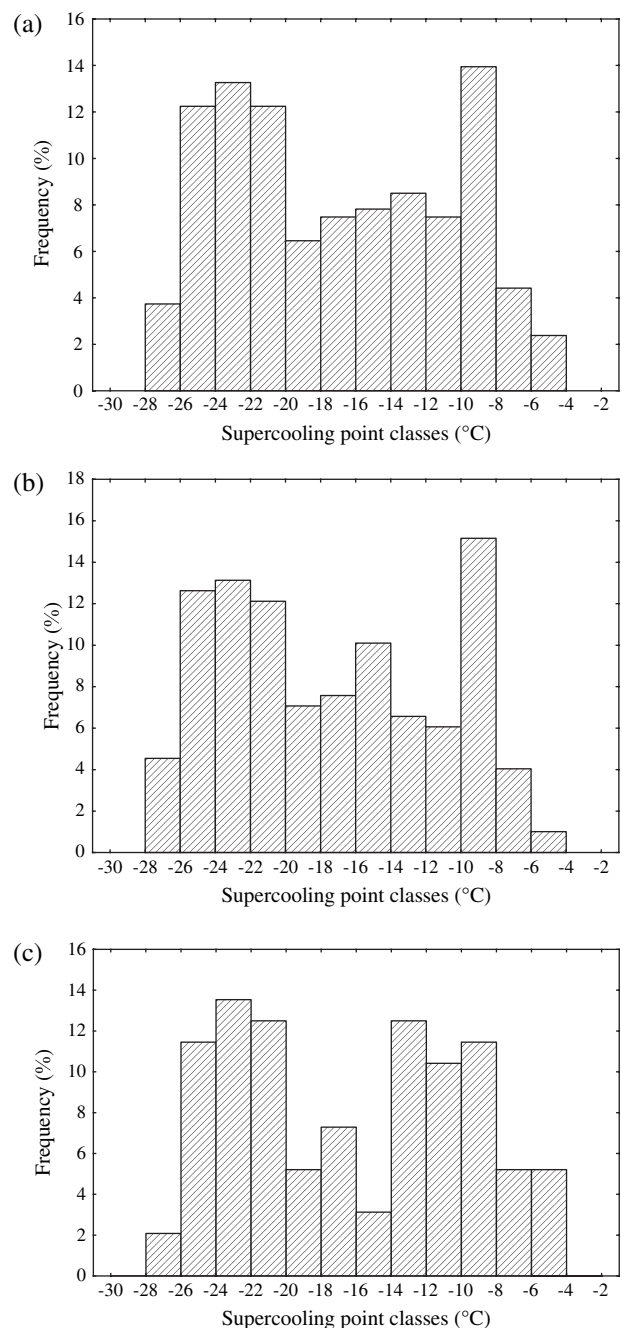
Fig. 1. Frequency distributions of the supercooling points for: (a) all springtail species investigated, (b) indigenous species only and (c) invasive species only.

species concerned within each of the four habitat types inves-tigated (Fig. 2). By contrast, −12 °C has a much more marked influence, changing the relative rankings of several of the species concerned. These included changes in rank among the indigenous and invasive species. For example, in the *P. cookii* tussock grassland, the indigenous *Sminthurinus tuberculatus* and invasive *Parisotoma notabilis* switched relative rankings, with substantial changes in abundance of the former by

Table 2. Summary statistics for the frequency distributions of supercooling points for the springtail assemblages on Marion Island, including data from all the species investigated, the indigenous species only and the invasive species only.

	All species	Indigenous	Invasive
n	294	198	96
Mean	−16.9	−17.2	−16.3
Median	−17.4	−17.9	−16.5
SE	0.367	0.441	0.657
Min	−27.3	−27.3	−26.7
Max	−4.8	−5.5	−4.8
Range	22.5	21.8	21.9
Skewness	0.179083	0.212610	0.101534
SE Skewness	0.142135	0.172778	0.246210
Kurtosis	−1.30773*	−1.28178*	−1.36935*
SE Kurtosis	0.28332	0.343885	0.487732

*Significance of kurtosis ($P < 0.05$) as determined using a *t*-test.

comparison with the latter species (Fig. 2a). Inspection of the frequency distributions suggested that splitting the distributions at −16 °C would reasonably differentiate between high and low group individuals (Block, 1982; Sinclair *et al.*, 2003c). Using this temperature as a cut-off for population survival in a similar way results in much more dramatic changes to the relative abundance rankings of the species in each of the habitats investigated (Fig. 2).

Discussion

The assemblage approach adopted in the present study is unusual by the standards of most modern, comparative work. However, as pointed out by Gaston *et al.* (2008), this is the only approach that can justifiably support a conclusion that assemblages differ on average in some characteristic among areas. Moreover, it is also the only approach that can enable generalizations to be developed of the different ways in which major groups of organisms might deal with similar environmental stresses (Bartholomew, 1987; Rubinstein, 1992; Huey *et al.*, 2002), a theme of considerable importance given current environmental change. Although it might be tempting to argue that the responses of each species are so contingent on conditions that generalization is precluded, this is frequently not the case, with generalizations often emerging at broader spatial and temporal scales (Lawton, 1999; Chown *et al.*, 2003; Hodkinson, 2003).

In this particular instance, the range of mean SCP values recorded for the species is similar to the lower lethal temperature variation recorded by Addo-Bediako *et al.* (2000) for a latitudinal band encompassing 40–60 °S (Fig. 2a). By contrast, it is much narrower than for a similar area in the Northern hemisphere, although this may be a result of the larger number of species studied in the latter case. The range of values found in the present study is also similar to that that recorded by Sinclair *et al.* (2006) for a much colder, Antarctic continental site at Cape Hallett (−14.6 to −25.8 °C). However, the typical median values of the Cape Hallett species are lower than

those found here. Moreover, Sinclair *et al.* (2006) note that their study was conducted in the austral summer and conclude that winter SCP values in the species that they examined are likely to be much lower. A similar range of SCP values to that found in the present study is also recorded for springtails at the maritime Antarctic Signy Island (Sømme & Block, 1982) but, again, the average values are lower than those found here. The present data thus suggest that the generalization that springtails are more cold tolerant at higher latitudes appears to be supported at the assemblage level, although work on temperate and tropical assemblages is required to fully support this conclusion.

Based on an investigation of 12 of the 16 species found on Marion Island, no differences are found, using species means, between the indigenous and invasive species present on the island. This outcome is different from that of previous a study by Slabber *et al.* (2007) using a smaller subset of species. However, that study shows that differences among the groups are most pronounced at the lowest acclimation temperatures, and less extensive after higher temperature acclimations. Nonetheless, both the mean data and the data from the individual level, as presented here, suggest that the two groups of species do not differ systematically in their SCPs, at least under the conditions in the field at this time of year. Consequently, it is reasonable to conclude that, at least from the perspective of this trait, invasion by the introduced species, which are mostly European in origin (Gabriel *et al.*, 2001) has not contributed to functional homogenization or differentiation (Olden, 2006). Strictly speaking, such a conclusion requires comparison with another site, and perhaps the most striking one to be made is with nearby Prince Edward Island (19 km distant), which is free of introduced springtail species with the exception of *C. denticulata* (Hugo *et al.*, 2006). If little difference in SCP is assumed among populations on the two islands, then the introduction of the four additional non-native species to Marion Island has made little difference to the assemblage frequency distribution for SCP. Of course, this does not mean that other functional traits might not have changed, and this would appear to be the case for upper thermal tolerance, direction of thermal plasticity in desiccation resistance, and possibly also egg development rates (Chown *et al.*, 2007; Slabber *et al.*, 2007; Janion, 2008).

Despite the overall similarity in frequency distributions among the two groups, it is clear that, after a severe low temperature event (e.g. −12 to −16 °C) substantial differences in the relative abundances of the different springtail species would be found, with this also varying among habitats. Such events, although uncommon, are likely to be important in structuring assemblages via their differential effects on populations (Parmesan *et al.*, 2000; Lee *et al.*, 2009). Clearly, survival of such an event is not the only factor likely to influence subsequent community dynamics, given that growth rates of each species, resource availability and interactions are all important. However, if any form of assembly rules operate in these systems, then changes in abundance may reset the assemblage trajectory (Drake, 1990; Weiher & Keddy, 1995).

An important question is how frequent low temperature events of the kind explored in the present study are likely to be on Marion Island. Microclimate data collected for the
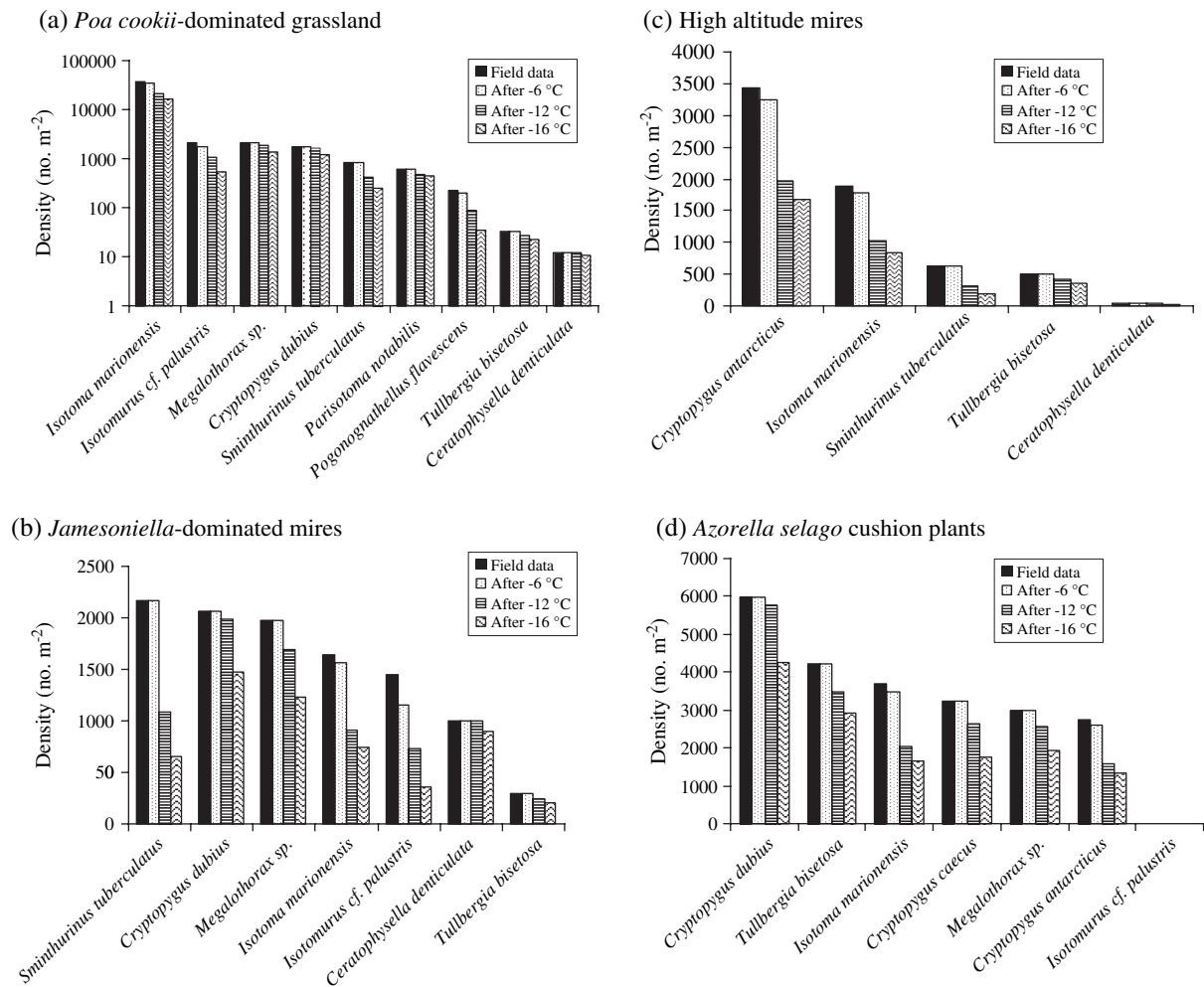
Fig. 2. Abundances (expressed as density, number of individuals per metre^2) of springtail species in (a) *Poa cookii*-dominated grassland, (b) *Jamesoniella*-dominated mires, (c) high altitude mires and (d) *Azorella selago* cushion plants. In each case, the field data provided by Gabriel *et al.* (2001) are shown first, and then how low temperature events of increasing severity would affect abundances. In all cases, abundances decline, but the change in density of species relative to each other changes in several instances.

island in the range 0–800 m over several years suggest that, from 200 m upwards, events where temperatures decline to these levels (approximately −13 °C) are likely to be reasonably uncommon, occurring perhaps once every 3–5 years, with increasing frequency at higher elevations (Boelhouwers *et al.*, 2003, Slabber *et al.*, 2007; Lee *et al.*, 2009). At sea level, such events seem entirely unlikely. Nonetheless, as noted above, uncommon, although extreme, events may have substantial effects on populations.

A further consideration is the extent to which populations may alter their lower lethal temperatures (or SCPs) in anticipation of extreme events. Acclimation ability (over a 1-week period) is known for three of the invasive (*P. flavescens*, *Isotomurus cf. palustris* and *C. denticulata*) and two of the indigenous species (*C. antarcticus* and *T. bisetosa*) examined in the present study. Typically, acclimation ability in SCP is small and does not differ among the indigenous and invasive species, suggesting that such a response is not likely to be

important, at least in these springtail species (Slabber *et al.*, 2007). However, if such a population-level approach is to be adopted for understanding the likely effect of low temperature events on other springtail species or invertebrates, both short- and long-term variation in hardening and acclimation ability would have to be considered (Klok & Chown, 1998; Worland & Convey, 2001; Hoffmann *et al.*, 2003; Sinclair *et al.*, 2003c). For several species of terrestrial arthropods across a range of groups on Marion Island, the acclimation ability in SCPs is not well developed (Deere *et al.*, 2006; Slabber *et al.*, 2007; Marais *et al.*, 2009), which may be a consequence of the unpredictability of changing conditions on the island (Deere & Chown, 2006). However, in other species, this is not the case (Klok & Chown, 1998; Slabber & Chown, 2004, 2005).

In conclusion, the present study shows that an assemblage-level investigation of a physiological trait is a useful way to explore the ecological consequences of trait variation, particularly for ecological characteristics that are an emergent property

of assemblages (such as species rank abundance distributions). Moreover, the approach can provide an additional route for understanding the environmental context of physiological traits, and such an approach is growing in importance, as emphasized most notably by Baust & Rojas (1985) and by Bale (1987).

Acknowledgements

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