

# ECOGRAPHY

## Research article

### Colonizing polar environments: thermal niche evolution in Collembola

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Temperature is a primary driver to define the ecophysiological activity and performance of ectotherms. Thus, thermal tolerance limits have a profound effect in determining geographic ranges. In regions with extreme cold temperatures, lower thermal limits of species are a key physiological trait for survival. Moreover, thermal niche breadth also plays an important role in allowing organisms to withstand climatic variability and confers species with broader potential to establish in new regions. Here we study the evolution of thermal tolerance limits among Collembola (Arthropoda) and explore how they are affected by the colonization of polar environments. In addition, we test the hypothesis that globally invasive species are more eurythermal than non-invasive ones. Critical thermal limits ( $CT_{min}$  and  $CT_{max}$ ), classic measurements of thermal tolerance, were compiled from the literature and complemented with experimental assays for springtail species. Genetic data of the mitochondrial gene cytochrome oxidase subunit 1 (COI) was used to assemble a phylogeny. Our results show that polar springtails have lower  $CT_{min}$  and lower  $CT_{max}$  compared to species from temperate and tropical regions, consistent with the Polar pressure hypothesis. We found no phylogenetic signal for  $CT_{max}$ , but low values of phylogenetic signal for  $CT_{min}$ . Globally invasive species do not have significantly broader thermal tolerance breadth ( $CT_{range}$ ) than non-invasive ones, thus not supporting the predictions of the Eurythermality hypothesis. We conclude that polar springtails have evolved their thermal niches in order to adapt to extremely cold environments, which has led to decreasing both upper and lower thermal tolerance limits.

Keywords: Antarctica, cold tolerance, critical thermal limits, ectotherms, invasive species, phylogenetic signal



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## Introduction

The geographic distribution of species can be explained by niche theory (Grinnell 1917, Hutchinson 1957), in which the interactions of species with the environment (abiotic factors), other species (biotic factors), and evolutionary processes acting through time, modulate the geographic and/or niche space where they can live (Holt 2009). The ecological and physiological traits that allow species to persist in a certain niche can be conserved to some extent across the phylogeny, which is called niche conservatism (Harvey and Pagel 1991, Wiens and Graham 2005). Phylogenetic niche conservatism, which has profound consequences for the ecology and conservation of species (Wiens et al. 2010), requires that niche-related traits change very slowly over evolutionary time within a clade (Webb et al. 2002). Evidence for niche lability, i.e. rapid niche evolution, also exists for some traits so that phylogenetically closer species are not necessarily ecologically similar across all niche dimensions (Losos et al. 2003, Knouft et al. 2006, Kamilar and Cooper 2013). Climate (especially temperature), both past and present, is highlighted as a primary driver modulating the niche of species (Araújo et al. 2013, Sunday et al. 2019).

Upper and lower thermal limits, between which species can maintain their physiological functions, and their evolutionary changes, have been identified as key determinants of species' geographic ranges (Huey and Kingsolver 1989). Species' thermal limits are subject to selective pressures from the environment, although upper limits in general tend to evolve more slowly than lower limits (Donoghue and Moore 2003, Araújo et al. 2013, Bennett et al. 2021). Indeed, studies with insects indicate that strategies to withstand extreme cold temperatures play a major role in determining geographical distributions (Bale 2002, Sinclair et al. 2003a, b). The difference between upper and lower thermal limits defines thermal tolerance breadth, which can vary depending on climatic stability (Pallarés et al. 2019) or temperature of the region to which species are adapted (Payne and Smith 2017). At the biogeographic level, species with broader thermal tolerance breadth (i.e. eurythermal species) are expected to display larger geographical ranges (Gaston and Spicer 2001, Calosi et al. 2010, Bozinovic et al. 2011). In contrast, the opposite (i.e. narrow thermal tolerance breadth leading to restricted geographic ranges) is expected for stenothermal species. This is the case, for instance, of several Antarctic marine species that are limited to occupy polar latitudes in the Southern Hemisphere because of thermal specialization (Gaston et al. 2009, Peck and Conway 2000, Pörtner 2002). Yet, some Antarctic terrestrial species, such as some invertebrates, have greater physiological flexibility (defined as the ability to cope with both rapid and lasting environmental changes) (Peck 2005).

Springtails (Collembola) are a group of hexapods that are widely distributed throughout all continents, including Antarctica, and is one of the most abundant groups of edaphic fauna worldwide (Rusek 1998, Potapov et al. 2020). These invertebrates play an important role in soil nutrient cycling

(Filser 2002, Potapov et al. 2020), especially in polar regions (Addison and Parkinson 1978, Bokhorst et al. 2007) where springtails constitute a significant proportion in edaphic microarthropod communities (MacLean 1975). Based on the oldest fossil found so far, the evolutionary origin of this taxonomic group dates back to the Devonian (Greenslade and Whalley 1986). Although fossils of springtails are more abundant from later geological periods (Sánchez-García and Engel 2017), it is known that the group had well diversified at least in the latter part of the Mesozoic (Sánchez-García and Engel 2017). Across the evolutionary history of Collembola, spanning ca 400 Myr, the Earth's climate has alternated between warm and glacial periods (Scotese et al. 2021). Such paleoclimatic changes caused much of the geographical isolation and biological dispersal processes that have largely contributed to shape the biogeography and evolution of several taxa in Antarctica (Stevens et al. 2006, Convey et al. 2008, Bennett et al. 2016). For these reasons, springtails are an interesting group to study the evolution of thermal tolerances.

A recent global-extent scientific review has detected that there is a bias towards the study of thermal tolerances of springtails from cold and polar regions, compared to the less studied tropical species (Escribano-Álvarez et al. 2022). The soils of polar environments, such as those of Antarctica, are subject to strong freezing and thawing process of the ice-sheets (Blume et al. 2002), which in turn leads to low-diversity edaphic ecosystems (Convey 2001). Extremely low temperatures have acted as an environmental filter to colonization and adaptation processes in Antarctica (Convey 1997), but the current increase of global temperatures is contributing to weaken this natural barrier (Convey and Peck 2019). Climate change not only favours the expansion of ice-free habitats (Lee et al. 2017), but warmer soil temperatures also make these habitats increasingly suitable for the establishment of non-native species (Duffy et al. 2017, Pertierra et al. 2022) and favour range expansions of pre-established alien springtail species in the Antarctic Peninsula region (Vega et al. 2021). Considering that eurythermality is one of the traits most often associated with invasion success (Zerebecki and Sorte 2011, Kelley 2014), eurythermal species of soil arthropods might have a competitive advantage in new ice-free areas (Duffy and Lee 2019, Pertierra et al. 2022).

The aim of this work is to explore the interspecific variation in thermal tolerance limits of Collembola in a phylogenetically explicit context. Specifically, we focus on addressing two hypotheses. First, since extremely cold environments exert selective pressures on lower thermal limits, we postulate that polar species would have their tolerance limits shifted to withstand lower temperatures – the Polar pressure hypothesis (Convey 1997). To evaluate this hypothesis, we test whether differences exist between polar and extra-polar springtails (i.e. those that inhabit temperate and tropical regions of the planet) in terms of their upper and lower thermal tolerance limits ( $CT_{max}$  and  $CT_{min}$ ). Second, we conduct a global-scale comparison of physiological thermal tolerances between invasive (anywhere in the world) and non-invasive species as a test of the Eurithermality hypothesis (Rejmánek and Richardson

1996, Kelley 2014). While non-invasive species are expected to be more stenothermic and well-adapted to survive within their native thermal range, invasives would be more cosmopolitan (eurythermal) as a result of adaptations to broader ancestral thermal regimes which may have favoured their invasion success.

## Material and methods

### Data collection and thermal tolerance assays

Critical thermal limits (CTL) of a total of 65 species of springtails (Collembola) were retrieved from the review by [Escribano-Álvarez et al. \(2022\)](#).  $CT_{max}$  and  $CT_{min}$  are classic measurements of physiological thermal tolerance ([Cowles and Bogert 1944](#), [Terblanche et al. 2007](#)), as well as a relevant metric in studies aimed to address climate change impacts in ectotherms ([Deutsch et al. 2008](#), [Clusella-Trullas et al. 2021](#)). In our database (Supporting information), we first collated information for  $CT_{max}$ ,  $CT_{min}$  and  $CT_{range}$  (calculated as the difference between  $CT_{max}$  and  $CT_{min}$ ), the locality where specimens were sampled, the status invasive/non-invasive (the invasive status was considered for species that have been cited in the literature as invasive in any region of the planet) and the methodology used in each experiment. We generated additional experimental CT profiles for four Antarctic species (*Cryptopygus antarcticus*, *Friesea grisea*, *Folsomotoma octooculata* and *Hypogastrura viatica*). Springtails used for experimentation were collected from King George Island (62°02'S, 58°21'W) and Deception Island (62°58'S, 60°39'W), Antarctic Peninsula, in February 2020. Field sampling was carried out by taking a soil sample with a 10 cm deep core. Extractions of the specimens were performed with a Berlese-Tullgren funnel. The springtails were held at 4°C (0:24 L:D) in plastic tubes with a moistened Plaster-of-Paris substrate during 48 h before starting thermal tolerance assays in the laboratories of both the Uruguayan Artigas Station and the Gabriel de Castilla Spanish Station. CTL were determined following a standard methodology as described in e.g. [Chown et al. \(2009\)](#) and [Janion-Scheepers et al. \(2018\)](#). Several individuals of each species (minimum of six, maximum 53; Supporting information) were placed in plastic tubes with Plaster-of-Paris substrates saturated with water to avoid desiccation. Thermal tolerances were measured with a Julabo F34 programmable circulator (Julabo GmbH) adjusted to a ramping rate curve of 0.05°C per minute, as indicated in the literature ([Terblanche et al. 2007](#)). The substrate temperature was monitored with a type K thermocouple, using a digital data logger (Model Lascar EL-GFX-DTC, RS Pro). After experiments, springtails were identified using a microscope (Olympus CX40RF200).

### Phylogenetic tree reconstruction

To examine evolutionary processes, we reconstructed a phylogenetic tree for our set of 69 species of springtails using the

mitochondrial gene cytochrome oxidase subunit 1 (COI). We used COI sequences based on the study of [Janion-Scheepers et al. \(2018\)](#). The sequences (658 base pairs) were downloaded from Bold System ([www.boldsystems.org](http://www.boldsystems.org)) and Genbank database ([www.ncbi.nlm.gov/genbank](http://www.ncbi.nlm.gov/genbank)). The mitochondrial sequences (COI) of the species *Parajapyx emeryanus*, *Tricampa rileyi* and *Pedetontus submutans* were used as an outgroup, since they are close groups to Collembola ([Kjer et al. 2006](#)). The sequences were aligned using a clustalW algorithm ([Thompson et al. 1994](#)) and the evolutionary models of the sequences (GTR + G) were selected according to the lowest Akaike's information criterion (AICc) using Mega ver. 11.0.11. We used a relaxed lognormal molecular clock, and the tree was time-calibrated using the following oldest fossil species of Collembola: Entomobryidae: *Pemobrya mirabilis* (275 Mya); Hypogastruridae: *Hypogastrura intermedia* (36 Mya); Isotomidae: *Rhyniella praecursor* (409 Mya); Katiannidae: *Cretokatianna bucculenta* (103 Mya); Neanuridae: *Pseudoxenylla fovealis* (75 Mya); Tomoceridae: Tomoceridae indet. (96 Mya). These fossils were obtained from the Paleobiology database (<https://paleobiodb.org>, accessed in February 2022). We used 40 million generations of Markov chain Monte Carlo (MCMC) with a 10% burn-in to run the software Beast ver. 2.6.7 to generate our phylogenetic trees. The convergence of the chains was visualized in TRACER ver. 1.7 ([Rambaut et al. 2018](#)) considering a value of ESS > 200.

### Phylogenetic comparative methods

To analyze the level of phylogenetic signal during the evolution of the physiological traits under examination ( $CT_{max}$  and  $CT_{min}$ ), we used the  $K$ -statistic (also known as Blomberg's  $K$ , [Blomberg et al. 2003](#)). This index can quantify the similarity between species in a certain trait by comparing it with a Brownian motion model of trait evolution ([Blomberg et al. 2003](#)). In this way, when the  $K$ -statistic has values close to 0, trait evolution indicates a lower phylogenetic signal than expected by a Brownian motion model of trait evolution, whereas  $K$ -statistic values close to 1 indicate strong phylogenetic signal and  $K$ -statistic > 1 indicates that the similarity between species is higher than expected ([Blomberg et al. 2003](#)). We obtained values for the  $K$ -statistic with the 'geiger' package ([Harmon et al. 2008](#)) in R-Studio ver. 4.1.0 ([www.r-project.org](http://www.r-project.org)). After that, we performed a phylogenetic generalized least square (PGLS) analysis to evaluate whether CTL of polar species are different to those from other regions, while controlling the non-independence of species due to shared common ancestry ([Symonds and Blomberg 2014](#)). PGLS models were computed with the 'Caper' package ([Orme et al. 2013](#)) (lambda was adjusted by maximum likelihood) in R-Studio. We considered the intraspecific variation in  $CT_{max}$  and  $CT_{min}$  by adding the SD of the data, following the methodological approach of [Martinez et al. \(2015\)](#). As we are aware that our phylogeny is based on only one molecular marker, we conducted complementary analyses to control for phylogenetic uncertainty. To do this, we used the

100 trees derived for the Bayesian analyses and we calculated the mean of the  $p$  and  $K$ -statistic values, using the ‘Caper’ package. Additionally, as methodological variation may influence CTL values (Jørgensen et al. 2019, Rezende et al. 2020), we carried out additional analyses including acclimation time and duration trial (Supporting information). Based on the available data, acclimation time in each study was classified into three categories: ‘short’ (less than 48 h), ‘medium’ (one or two weeks), or ‘long’ (one month or two generations). The duration trial was calculated using the acclimation temperature (trial start temperature), the ramping rate and the CTL. Following Leiva et al. (2019), the logarithm of the duration trial was used to test the effect of this variable on CTL. We evaluated different models of these two variables following Terblanche et al. (2007):  $CT_{max}$  and  $CT_{min}$  affected by both variables (acclimation time and duration trial) together and separately. The best model was selected according to the AIC criteria with  $\Delta AIC < 2$  (Burnham and Anderson 2002) using the ‘Caper’ package. We also performed a phylogenetic correlation analysis (Revell 2012) to test if upper and lower limits are correlated across species, using the ‘phytools package’ (Revell 2012) in R-Studio. To evaluate whether physiological thermal range ( $CT_{range}$ ) is associated with invasiveness, we performed a PGLS with a logistic structure in the response variable, to accommodate the binary nature of the response variable (i.e. invasive/non-invasive) (Ives and Garland 2010), using the ‘phylolm’ package (Ho et al. 2020) in R-Studio. The ancestral reconstruction of the traits ( $CT_{max}$ ,  $CT_{min}$  and  $CT_{range}$ ) was performed with the ‘phytools package’.

## Results

Mean values of CTL vary among different families of springtails (Fig. 1). Hypogastruridae is the family with the highest

mean values for  $CT_{max}$ , differing by  $3.7^\circ\text{C}$  with Isotomidae, the family with the lowest mean values of  $CT_{max}$ . Similarly, Hypogastruridae displays the lowest mean values of  $CT_{min}$  and a difference of  $5.8^\circ\text{C}$  with Lepidocyrtidae, the family with the highest average values for  $CT_{min}$ . Furthermore, low  $CT_{min}$  values do not necessarily imply paired low  $CT_{max}$  values across the different springtail families studied (Fig. 1). Phylogenetic signal was not significant for  $CT_{max}$  ( $K$ -statistic=0.056,  $p=0.329$ ), but was significant for  $CT_{min}$  ( $K$ -statistic=0.229,  $p=0.005$ ). These results indicate that the CTL of springtails are labile, not showing strong phylogenetic structure. In addition to this, we found that upper and lower CTL are not correlated ( $p=0.380$ , CI low=0.347, CI high=0.413), suggesting that the traits are evolutionarily uncoupled. PGLS results showed that both  $CT_{min}$  ( $p < 0.001$ ) and  $CT_{max}$  ( $p=0.009$ ) were significantly lower for polar than non-polar species ( $3.1^\circ\text{C}$  of difference for  $CT_{max}$  and  $4.7^\circ\text{C}$  for  $CT_{min}$ ) (Table 1). These results indicate that the colonization of polar environments can promote a generalized significant decrease in both CTL, as expected from the Polar pressure hypothesis. Our analyses, albeit based on a single marker phylogeny, are robust to phylogenetic uncertainty since the means of  $p$  and  $K$ -statistic values from the 100 trees derived from Bayesian analyses are also in support of significant differences between polar and non-polar (Supporting information). Our analyses also identify the importance to incorporate methodological variation, as acclimation time and duration trial showed a significant effect on  $CT_{max}$  ( $p < 0.001$ , AIC=335.8; Supporting information), and only the acclimation time showed a significant effect on  $CT_{min}$  ( $p < 0.001$ , AIC=296.2; Supporting information). Yet, in agreement with the Polar pressure hypothesis, significant differences in CTL between polar and extra-polar springtails ( $CT_{max}$ :  $p=0.006$ ;  $CT_{min}$ :  $p < 0.001$ , Supporting information) remain when controlling for methodology (as measured by acclimation time and

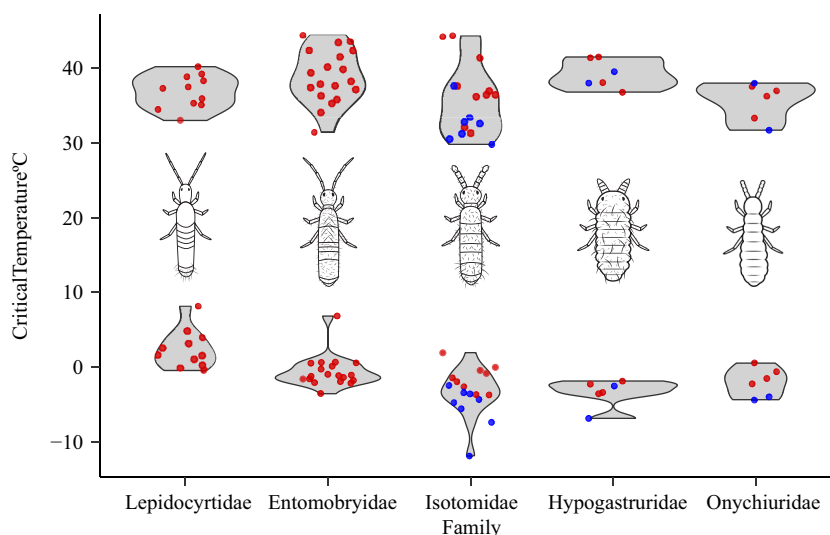


Figure 1. Medians, interquartile ranges, and minimum and maximum values of the critical thermal limits ( $CT_{max}$  and  $CT_{min}$ ) of the springtail species by families. Red points are non-polar species. Blue points are polar species. Families with less than three species are represented in the Supporting information.

Table 1. Results of the phylogenetic generalized least square (PGLS) by hypothesis. The 95% confidence interval (CI) is a result of the model estimates for 100 PGLS using different values of thermal tolerance in each species, to control for intraspecific variation (SD) of  $CT_{max}$  and  $CT_{min}$ . CI-l correspond to CI low, and CI-h correspond to CI high. The letters in parentheses indicate what each confidence interval correspond to: (i) correspond to intercept, (e) correspond to estimate and (p) correspond to p value.

Hypothesis	Response	Predictor	intercept	CI-l (i)	CI-h (i)	estimate	CI-l (e)	CI-h (e)	p	CI-l (p)	CI-h (p)
Polar pressure hypothesis	$CT_{max}$	Polar	37.46	37.44	37.47	-3.16	-3.21	-3.10	0.009	0.007	0.010
	$CT_{min}$	Polar	-0.75	-0.77	-0.73	-4.57	-4.61	-4.52	<0.001	0.000	0.000
Eurythermality hypothesis	$CT_{range}$	Invasive	-	-	-	-	-	-	0.255	-	-

duration trial). Regarding critical thermal range ( $CT_{range}$ ) for all species in our database, we did not detect a significant phylogenetic signal ( $K$ -statistic=0.027,  $p=0.502$ ). The lack of phylogenetic structure of these results shows that phylogenetically close species do not have to be similar in  $CT_{range}$ . Although differences of mean  $CT_{range}$  values are 1.6°C higher for invasive species, PGLS models showed no significant differences in  $CT_{range}$  between invasive and non-invasive species ( $p=0.255$ ). Hence, our results do not support the Eurythermality hypothesis. Although not the explicit focus of our analyses, we did not detect significant differences in  $CT_{range}$  for Polar and non-polar species ( $p=0.46$ ), neither for a comparison of  $CT_{max}$  ( $p=0.31$ ) and  $CT_{min}$  ( $p=0.73$ ) between invasive and non-invasive species.

## Discussion

Our study shows that thermal tolerance limits of springtails, both upper ( $CT_{max}$ ) and lower ( $CT_{min}$ ), are lower for polar than non-polar species (Fig. 2A–B). The existence of lower thermal limits for polar invertebrates had already been documented in the scientific literature (Everatt et al. 2013a, Holmstrup 2018), but here we use the most complete species-level dataset for Collembola and provide phylogenetically-informed analyses for this pattern. In polar regions, extremely cold temperatures are key selective pressures for lower thermal limits of species (Sinclair et al. 2003a), which tend to be more labile than thermal tolerance to heat (Muñoz et al. 2014). This selective pressure also supports the greater reduction in absolute terms of  $CT_{min}$  compared to  $CT_{max}$  of polar springtails that we found in our results. Although both polar regions are not similar in every climatic and ecological aspect and cannot be taken as exact equivalents (Sinclair et al. 2003a, Chown et al. 2004), our results do not differ when excluding the three polar species from the Northern Hemisphere. We also found differences in the means of  $CT_{min}$  and  $CT_{max}$  for the different families (Fig. 1). Although not all springtail families have representatives in polar environments, those that do (Isotomidae, Hypogastruridae and Onychiuridae) show lower mean  $CT_{min}$  values. Across the tree of life, it has been found that clades that originated under predominantly cold climates currently have better cold tolerances (Bennett et al. 2021).

Polar terrestrial species in general show higher warming tolerance (e.g. the difference between their upper thermal limits and maximum environmental temperatures they

experience) (Hodkinson et al. 1996, Deutsch et al. 2008, Everatt et al. 2013b). However, some notothenioid fishes and other marine invertebrates in Antarctica have lost the ability to withstand high temperatures (Peck et al. 2008, 2014, Beers and Jayasundara 2015), which limits their acclimation capacity and poses a disadvantage in the face of global warming events (Somero 2010). Indeed, it has been stressed that the physiological mechanisms to withstand high temperatures involve costs (Pörtner et al. 2007). Yet, terrestrial and marine environments are not entirely comparable in terms of organismal thermal tolerance patterns (due to the oxygen limitations that occur in aquatic environments, among others, Pörtner 2010). Also, some authors suggest that plasticity is not entirely lost, and species retain the ability to respond to high temperature stress (Bilyk et al. 2012), a feature which may vary between different Antarctic lineages (Bilyk et al. 2018). In non-polar terrestrial invertebrate species, that are adapted to less-extreme cold conditions, no tradeoff seems to exist between upper and lower thermal limits (Sørensen et al. 2016). Although our analyses are not designed to determine loss of plasticity or the extent to which upper limits (and their variance) are compromised by cold resistance, we do find evidence at a global level of a difference of  $CT_{max}$  between polar and non-polar species.

The modification of thermal limits in polar species could be explained by the adaptive hypothesis, under which some ecologically and physiologically relevant traits have a higher rate of evolution (Ho et al. 2017). This would lead to niche evolution (Losos et al. 2003), which would allow species to colonize new territories with novel environmental conditions different from those to which their ancestors were adapted (Wiens and Donoghue 2004). Our results show that phylogenetic signal was not significant for  $CT_{max}$  but was significant for  $CT_{min}$  with low values of the  $K$ -statistic. Previous studies with springtails, using Pagel's  $\lambda$  (Pagel 1999), found no phylogenetic signal for  $CT_{max}$  but a substantial signal for  $CT_{min}$  (Liu et al. 2020, Phillips et al. 2020). In insects and other ectotherms, the phylogenetic signal for upper thermal limits tends to be strong (Hoffmann et al. 2013, Leiva et al. 2019), contrary to our results. Some authors have also found a moderate signal for  $CT_{min}$  in *Drosophila* species (Kellermann et al. 2012), whereas others document a lack of phylogenetic signal for lower thermal limits (Bujan et al. 2020). As already indicated by some authors, more complete phylogenetic information based on a tree made with more genes could provide greater robustness in comparative approaches (the discussion by Liu et al. 2020).

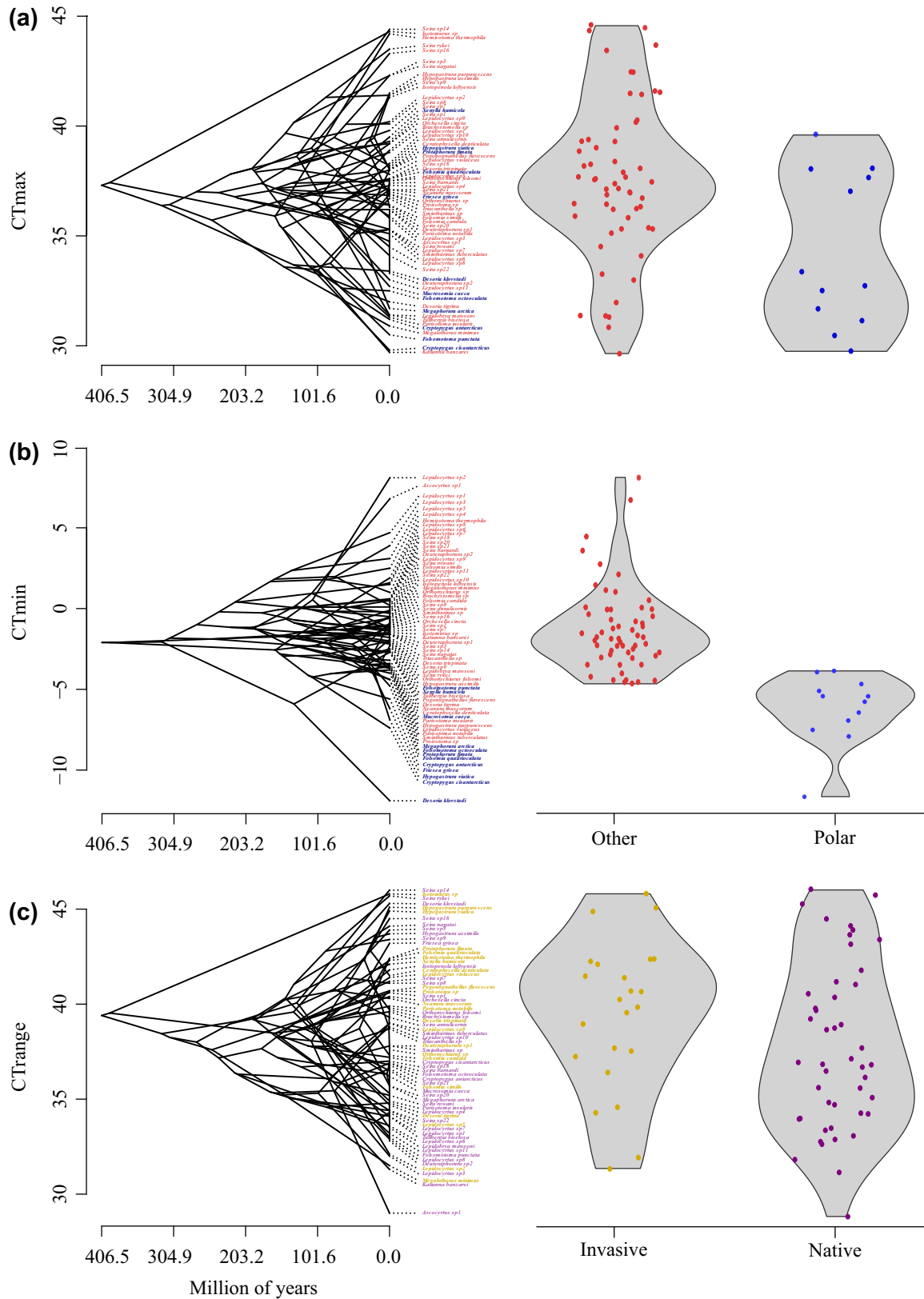


Figure 2. Ancestral reconstruction of the mean values for thermal limits and violin plots of critical thermal data. (A) Critical thermal maxima ( $CT_{max}$ ). Red names and points correspond to non-polar species. Blue names and points correspond to polar species. (B) Critical thermal minima ( $CT_{min}$ ). Red names correspond to non-polar species. Blue names correspond to polar species. (C) Critical thermal range ( $CT_{range}$ ). Yellow names and points correspond to invasive species. Purple names and points correspond to non-invasive species.

We observe a decoupling of  $CT_{\max}$  and  $CT_{\min}$  across species so that increases in cold tolerance limits does not immediately entail increasing heat tolerance ( $p=0.380$ ). This decoupling of upper and lower thermal limits has already been mentioned in the literature (Chen et al. 1990, Chown 2001), and may be associated with the different physiological mechanisms to withstand extreme high and low temperatures (Araújo et al. 2013). While mechanisms to avoid damage by high temperatures involves molecular chaperones (Feder and Hofmann 1999) or the release of some hormones (e.g. octopamine) (Armstrong and Robertson 2006), those to resist low temperatures include the accumulation of cryoprotectants (e.g. trehalose or glycerol) in dehydration processes (Holmstrup and Sømme 1998), the synthesis of antifreeze proteins or the removal of ice nucleator proteins (Duman 2001). Although it should be noted that according to a recent study by Scholl et al. (2023), antifreeze proteins are widespread among springtail species from polar and temperate regions, emerging around 400 million years ago. In this context, plastic changes to modify both thermal limits may not involve the same molecular and cellular pathways. For example, it has been postulated that more drastic biochemical changes are needed to increase heat tolerance in order to result in an effective adaptation (Hoffmann et al. 2013). Furthermore, across evolutionary scales, the time needed for these changes in the upper limits to occur is also considered slower (Sørensen et al. 2016). Perhaps this can also explain the smaller decrease in  $CT_{\max}$  of polar springtails compared to  $CT_{\min}$ .

Considering the importance of temperature in the distribution of ectotherms (Sunday et al. 2012), the amplitude of the range between both thermal limits (eurythermality), can offer greater flexibility for species to establish in new regions (Rejmánek 2000, Kelley 2014). This becomes especially important in a context of increasing human-mediated transport of species around the world (Hulme 2009). In our study we cannot support Kelley's (2014) Eurythermality hypothesis, although we can see that the general trend seems to be for invasive species to have higher  $CT_{\text{range}}$  (Fig. 2C). The inability of our study to detect significant differences in thermal tolerance breadth between native and invasive species may be related to the number of analysed species, since previous findings for plants (Rejmánek and Richardson 1996), epibenthic marine species (Zerebecki and Sorte 2011) and tropical and sub-Antarctic springtails (Janion-Scheepers et al. 2018, Phillips et al. 2020) have supported the Eurythermality hypothesis. However, published studies for other ectotherms such as amphibians and insects, have also found opposite results (Barahona-Segovia et al. 2016, Cortes et al. 2016). In the latter case, authors have made a call for caution when interpreting their results, as the trait they measured (locomotion) is produced by complex biochemical and metabolic mechanisms (the discussion by Cortes et al. 2016). Even so, thermal tolerance breadth ( $CT_{\text{range}}$ ) is not the only characteristic that confers an advantage for invasive species to establish in new regions (Kleunen et al. 2010, Kelley 2014). Some studies have found that desiccation resistance (Phillips et al.

2020, da Silva et al. 2021), the expression of chaperon proteins (Kelley 2014), or hatching success at high temperatures (Janion et al. 2010), can also be higher for invasive species, a benefit for them under global change scenarios (Chown et al. 2007).

When comparing different thermal tolerance studies with different protocols, it is important to consider the effects of methodological variation on the results (Jørgensen et al. 2019, Rezende et al. 2020). One of the methodological variables that may affect CTL values is ramping rate (Terblanche et al. 2007) but in our study we can observe that the ramping rate remains the same across studies, with the exception of four species (Supporting information). Another methodological variable that may affect the estimation of CT values would be exposure time (Jørgensen et al. 2019), here tested as duration trial (Supporting information). Interestingly, we have found that acclimation time and duration trial does have a significant effect on our results ( $CT_{\max}$  affected by acclimation time and duration trial and  $CT_{\min}$  affected only by acclimation time). Although analyses that control for acclimation time are still in support of the Polar pressure, these results reinforce the importance of incorporating methodological variation in comparative studies of thermal tolerance (Rezende et al. 2020). Plasticity in thermal limits could also be affecting critical values of the species (Weaving et al. 2022), but in this study we did not find enough data of acclimation response ratio (ARR) for the set of analysed species (Supporting information). Even so, studies with springtails have not found an effect of ARR between alien and indigenous species in  $CT_{\min}$  and only a weak effect for  $CT_{\max}$  (Janion-Scheepers et al. 2018, Phillips et al. 2020). It would be interesting to compare ARR between polar and non-polar species in future studies.

Another important consideration to bear in mind when discussing thermal tolerance limits at a macroscale, and especially when dealing with soil organisms, is microclimate (Duffy et al. 2015). Springtails can live at different depth in the soil (Rusek 1998, Potapov et al. 2020), which can provide a buffer effect against changes in temperature (Montejo-Kovacevich et al. 2020). On the one hand, and according to the climatic variability hypothesis (Stevens 1989), species that live in more stable environments will have lower thermal tolerance breadth (Addo-Bediako et al. 2000, Kellermann et al. 2009). Studies from springtails suggest that species that live deeper in the soil, and therefore with greater thermal stability, differ in their thermal tolerance limits with those species that live on the surface (van Dooremalen et al. 2013, Raschmanová et al. 2018, Pallarés et al. 2019, 2021). In addition to this, the possibility of moving through avoidance behaviours can help then find more suitable microclimates to survive (Hayward et al. 2004, Boiteau and Mackinley 2012, 2013). Even so, the buffering effect of the deeper layers of the soil and the thermoregulatory behaviours are limited in coping with increases in temperature and desiccation caused by climate change (Huey et al. 2012).

Although the effects of climate change may be different for native species between polar regions in both hemispheres (Nielsen and Wall 2013), invasive species do have a negative

effect on the diversity and abundance of native species, at least in Antarctica (Chown et al. 2022). The number of non-native Collembola detected in Antarctica in recent years is alarmingly high against other groups (Enríquez et al. 2019). Moreover, the risk of establishment of new non-native species in Antarctica is high (Hughes et al. 2020), especially in the Antarctic Peninsula where predictive models indicate that the climate will be suitable for species that are already invasive worldwide (Duffy et al. 2017). Recent review studies postulate the main mechanisms that would play a role in the success of alien springtail species in reaching and establishing in Antarctica (Pertierra et al. 2022). The proximity of the South American continent, together with the movement of people between both continents, increases the possibilities of inadvertently transporting non-native species (Chown et al. 2012). This situation becomes more serious for small invertebrates such as springtails, since invasion events are likely to occur with a single arrival (Myburgh et al. 2007). Considering that invasive springtails will have an advantage under increasing temperatures (Slabber et al. 2007), and that polar springtail communities recover very slowly from disturbances (Beet et al. 2022), future studies should focus on understanding how springtails interact with other groups of edaphic fauna, due to the importance of these biotic interactions for ecosystem health (Coyle et al. 2017).

## Conclusions

Polar dwelling springtail species have adapted to the extremely low temperatures of their environment, which may have indirectly caused a parallel decrease in their upper tolerance limits as a tradeoff. The decoupling between  $CT_{\min}$  and  $CT_{\max}$  support the assumption that the limits are caused by different physiological mechanisms. The lack of phylogenetic signal for  $CT_{\max}$  and the low values for  $CT_{\min}$  indicates that these traits are not conserved. It would be interesting to test in depth, as suggested by Bennett et al. (2021), whether polar species have ancestors that evolved in cold climates, as suggested by the recent study of Scholl et al. (2023). Regarding thermal tolerance breadth, we cannot confirm that eurythermality is a trait that differentiates invasive springtails from non-invasive ones. While invasive species have a higher  $CT_{\text{range}}$  than native species, differences are not statistically significant. This finding cannot confirm previous findings for sub-Antarctic species (Phillips et al. 2020). Considering that there are other environmental factors associated with climate change that affect springtail communities, it would be stimulating to study how these variables have affected them over long evolutionary time periods.

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**Pablo Escribano-Álvarez:** Data curation (equal), Formal analysis (equal), Visualization (equal), Writing – Original draft (lead), Writing – review and editing (equal). **Pablo A. Martínez:** Conceptualization (equal), Data curation (equal), Formal analysis (lead), Visualization (equal), Writing – review and editing (equal). **Charlene Janion-Scheepers:** Conceptualization (equal), Data curation (equal), Writing – review and editing (equal). **Luis R. Pertierra:** Conceptualization (equal), Visualization (equal), Writing – review and editing (equal). **Miguel Á. Olalla-Tárraga:** Conceptualization (lead), Formal analysis (equal), Funding acquisition (lead), Project administration (lead), Supervision (lead), Writing – review and editing (equal).

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## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4j0zpc8gb> (Escribano-Álvarez et al. 2023).

## Supporting information

The Supporting information associated with this article is available with the online version.

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