



Contents lists available at ScienceDirect

Current Research in Insect Science

journal homepage: www.elsevier.com/locate/cris

Half a century of thermal tolerance studies in springtails (Collembola): A review of metrics, spatial and temporal trends

Pablo Escribano-Álvarez^{1,*}, Luis R. Pertierra¹, Brezo Martínez¹, Steven L. Chown², Miguel Á. Olalla-Tárraga¹

¹ Dpto. Biología, Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, 28933, Móstoles, Spain

² Securing Antarctica's Environmental Future, School of Biological Sciences, Monash University, Melbourne, VIC, 3800, Australia

ARTICLE INFO

Keywords:

Collembola
thermal tolerance
critical thermal limits
supercooling point
lethal temperature

ABSTRACT

Global changes in soil surface temperatures are altering the abundances and distribution ranges of invertebrate species worldwide, including effects on soil microarthropods such as springtails (Collembola), which are vital for maintaining soil health and providing ecosystem services. Studies of thermal tolerance limits in soil invertebrates have the potential to provide information on demographic responses to climate change and guide assessments of possible impacts on the structure and functioning of ecosystems. Here, we review the state of knowledge of thermal tolerance limits in Collembola. Thermal tolerance metrics have diversified over time, which should be taken into account when conducting large-scale comparative studies. A temporal trend shows that the estimation of 'Critical Thermal Limits' (CTL) is becoming more common than investigations of 'Supercooling Point' (SCP), despite the latter being the most widely used metric. Indeed, most studies (66%) in Collembola have focused on cold tolerance; fewer have assessed heat tolerance. The majority of thermal tolerance data are from temperate and polar regions, with fewer assessments from tropical and subtropical latitudes. While the hemiedaphic life form represents the majority of records at low latitudes, euedaphic and epedaphic groups remain largely unsampled in these regions compared to the situation in temperate and high latitude regions, where sampling records show a more balanced distribution among the different life forms. Most CTL data are obtained during the warmest period of the year, whereas SCP and 'Lethal Temperature' (LT) show more variation in terms of the season when the data were collected. We conclude that more attention should be given to understudied zoogeographical regions across the tropics, as well as certain less-studied clades such as the family Neanuridae, to identify the role of thermal tolerance limits in the redistribution of species under changing climates.

INTRODUCTION

The environmental conditions that enable the survival and development of a species define its fundamental niche, whilst the realized niche is affected by geographic barriers and interspecific competition, among other factors (Hutchinson, 1957; Soberón, 2007). The projection of the niche on geographic space is used for delimiting the actual or potential geographic distribution of species (Colwell and Rangel, 2009). On a global scale, climatic conditions are the main driver of the geographic distributions of species, which become more important than biotic interactions over large spatial scales (Pearson and Dawson, 2003). Hence, physiological tolerance ranges of species to climatic conditions can provide an accurate estimation of their distribution in space (i.e., an approximation to the fundamental niche (Kearney and Porter, 2004)). Together with the role of human-assisted movements of species that make natural dispersal barriers more permeable (Banks et al., 2015), ther-

mal tolerance is key to understand the ongoing global redistribution of species under climate change (Hughes, 2000; Walther et al., 2002; Sunday et al., 2012). Ectotherms are particularly vulnerable to thermal variations in the environment (Kingsolver et al., 2013; Paaijmans et al., 2013) as ambient temperatures have a direct effect on both their physiological activity processes (Kingsolver and Woods, 1997; Mondal and Rai, 2001; Jonsson et al., 2013) and behaviour [e.g. (Amarasekare and Coutinho, 2014)].

To explain the observed breadth of thermal tolerance in ectothermic animals, Huey and Stevenson (Huey and Stevenson, 1979) proposed a bell-like curve response, where the optimum temperature range represents the body temperature at which the relative performance of the organism is close to its maximum. Thermal tolerance breadth, as delimited by both ends of the bell curve, varies with latitude in ectotherms, thus reflecting adaptive mechanisms of species to withstand the climate where they live (Sunday et al., 2011). However, up-

* Corresponding author.

E-mail address: pablo.escribano@urjc.es (P. Escribano-Álvarez).

<https://doi.org/10.1016/j.cris.2021.100023>

Received 19 July 2021; Received in revised form 17 November 2021; Accepted 23 November 2021

2666-5158/© 2021 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>)

per tolerance limits do not vary as much with latitude as lower limits (Araújo et al., 2013, Sunday et al., 2019) in an asymmetric pattern that has been referred to as Brett's rule (Brett, 1956; Gaston et al., 2009), although this may be due to a bias in the amount of data for some regions [see (Addo-Bediako et al., 2000)]. To better understand organismal responses within their thermal tolerance breadth, Vannier (Vannier, 1994) defined a thermo-biological scale fit for insects. Vannier's (Vannier, 1994) scale identifies several point steps that go from an optimum temperature point to lethal temperatures, defining intermediate points such as 'heat/cold stupor', 'heat/chill coma', and 'critical thermal limits'. These physiological points used as thermal limits can, in turn, be used to measure the responses of ectothermic animals to changes in climate (Sinclair et al., 2016). Examination of multi-species thermal tolerance datasets worldwide can be very useful to better understand patterns and processes in the field of macrophysiology (Addo-Bediako et al., 2000; Bennett et al., 2018; Bennett et al., 2021), provided that the methodological variations between different studies are addressed (Rezende et al., 2014; Jørgensen et al., 2021). Indeed, the need to disentangle environmental signal from experimental noise when documenting large-scale interspecific patterns in physiological variation and understanding its causes, has long been an issue in macrophysiology (Chown et al., 2003).

The methodology used to identify temperature extremes of the response curve can be implemented either through a 'lethal temperature' (LT), or a 'Critical thermal limits' (CTL) approach (Lutterschmidt and Hutchison, 1997). LT methods, also categorized as 'static', measure the 'lethal time' or time necessary to cause a percentage of mortality (MacMillan and Sinclair, 2011), and the 'lethal temperature' or temperature necessary to cause a percentage of mortality to the exposed population (Addo-Bediako et al., 2000). The CTL approach, on the other hand, is considered a 'dynamic' method since it consists of a progressive increase or decrease in temperature marked by a rate (Lutterschmidt and Hutchison, 1997; Cowles and Bogert, 1944). Even so, these metrics may be related since variation in temperature and exposure time cause cumulative effects on organisms (Jørgensen et al., 2021; Rezende et al., 2020). Lower limit measurements have an additional complication, as animal responses may be different when facing freezing (Sinclair et al., 2003). Freezing can cause mechanical damage to both cells and tissues due to cellular dehydration or metabolic limitations, in addition to other factors [see (Toxopeus and Sinclair, 2018)]. In order to prevent such damages, some freeze avoiding insects and other ectotherms can survive by lowering the freezing point of their body fluids (supercooled fluids), to the supercooling point (the temperature at which body fluids freeze) (Sinclair et al., 2003, Cannon and Block, 1988). On the other hand, other freezing tolerant species are able to withstand the formation of extracellular ice (Sinclair et al., 2003; Zachariassen, 1985). Although Bale (1993) usefully proposed up to five types of responses to freezing (freeze-tolerant, freeze-avoiding, chill-tolerant, chill-susceptible and opportunistic survival), mainly freeze avoiding and freezing tolerant can be considered parallel alternative strategies for surviving extremely low temperatures, though with considerable diversity associated with each of these major categories (Sinclair, 1999), and with cryoprotective dehydration adding an apparently less common third (Holmstrup et al., 2002; Sørensen and Holmstrup, 2011).

The potential effects of climate change on soil arthropods is an understudied issue [see (Meehan et al., 2020)], despite the fact that these animals play a key role in maintaining soil health (Van der Putten, 2012; Bardgett and Van der Putten, 2014; Coyle et al., 2017) and affect aboveground ecosystem functioning (Wardle et al., 2004). Collembola (Hexapoda: Entognatha) contribute to the structuring of the soil by decomposing organic matter and excrements (Cragg and Bardgett, 2001; Potapov et al., 2020; Rusek, 1998). These wingless and ametabolous animals help soil particle aggregation (Maaß et al., 2015), modifying organic matter that directly influences soil nutrient flux (Lussenhop and BassiriRad, 2005; Kaneda and Kaneko, 2008). For this reason, an increasing number of publications have used them as

sentinels of anthropogenic-driven changes in ecosystems or as bioindicators of ecological stress (Convey et al., 2003; Cassagne et al., 2006; Greenslade, 2007; Zeppelini et al., 2009; Roithmeier et al., 2018). Both global warming and land use changes can have a significant impact on the processes of decomposition of organic matter (Jucevica and Meleci, 2006; Yin et al., 2019), which reinforces the importance of deepening the biology and ecophysiology of Collembola as a key group to understand the effects of global change on soil functioning. However, large spatial biases still exist in the field of thermal biology, which impairs understanding and limits mitigation strategies, including those of conservation (White et al., 2021). Both the vertical stratification along the soil column of springtail communities and the micro-habitat introduce an additional spatial dimension in the relationship between temperature and geographic distribution in this taxonomic group that should be considered. Based on the soil layer or part of the vegetation they occupy, Potapov et al. (2016) defined four different life forms in Collembola (eu-edaphic, hemiedaphic, epedaphic and atmibiotic). These distinctions are important in a climate-change response setting because of variation in soil thermal regimes with depth (Rosenberg et al., 1983).

The aim of this work is to review the current state of scientific knowledge on thermal tolerance limits in Collembola, given their significance in the soil fauna, their global distribution, and the apparent differences in thermal tolerance traits between indigenous and introduced species in local assemblages and at broader spatial scales (Janion-Schepers et al., 2018; Phillips et al., 2020). Thermal tolerance data become of great help to manage those areas that species may or may not occupy under changing climates (Evans et al., 2015). To articulate our review, we have used the conceptual framework proposed by Hortal et al. (Hortal et al., 2015) about knowledge shortfalls in the biodiversity literature. Specifically, our findings are expected to contribute to filling existing knowledge gaps around the Hutchinsonian shortfall on the physiological limits related to extreme temperatures for this taxonomic group [see also (Cardoso et al., 2011)]. Moreover, considering that springtails are one of the invertebrate groups that are present in all continents, including polar regions (Potapov et al., 2020), we aim to detect spatial gaps in thermal tolerance studies by examining if some zoogeographic regions of the planet are better sampled than others [see (White et al., 2021)]. We also describe the degree of representativeness at the taxonomic level, deconstruct the analyses based on ecological characteristics (i.e. life forms), and characterize thermal tolerance metrics according to sampling season. To answer all these questions, we systematically compile and review the scientific literature published over the past fifty years and discuss existing challenges ahead that should be highlighted to further consolidate research approaches on the ecophysiology of springtails.

MATERIAL and METHODS

Literature review and network analysis in the terminology of thermal tolerance

To generate our database about thermal tolerance limits in Collembola, we searched peer-reviewed articles using the scientific database 'Web of Science', since it is considered an appropriate scientific citation search platform for natural sciences (Li et al., 2018). We prepared this review in accordance with the recommendations of the PRISMA-EcoEvo method (O'Dea et al., 2021), with some modifications (see Supplementary Information). A first search query was implemented with general keywords for thermal tolerance in Collembola (see Supplementary Information). This search produced 856 results, ranging from some that actually focused on other animal groups to those that, despite focusing on Collembola, dealt with molecular biology, genetic, toxicity or reproduction related to thermal tolerance without giving information on thermal limits. Such studies were all discarded. From the initial search (856 results), 50 articles were selected for this review. After this first screening, more specific terms were selected, and a second refined search was performed (see Supplementary Information). This produced 145 results,

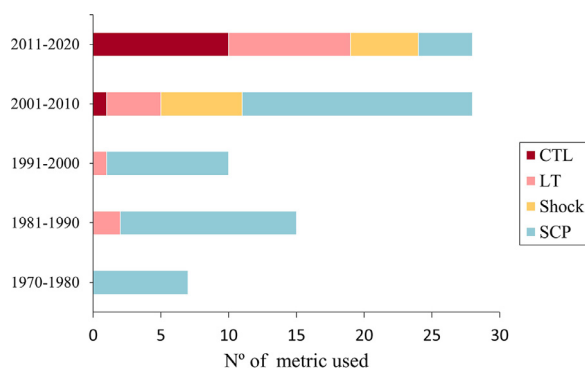


Figure 1. Usage of thermal tolerance metrics through time. Number of works published in the scientific literature for each decade using each of the following thermal tolerance metrics: Critical Thermal Limits (CTL), Supercooling Point (SCP), Lethal Temperature (LT) and Cold or heat shock, as a brief exposure of sub-lethal temperature (Shock). Some publications use more than one metric, so the total number of publications in this figure exceeds with the total number of publications of this review.

and the same selection procedure was used. From this second search, 24 additional articles were selected for this review. The results of each search were combined, obtaining a total of 83 articles (nine publications were added during the manuscript review process) from which the following data were obtained: type of metric used (Figure 1), rate, information about the maintenance of the animals and type of study (Table A1 Supplementary Material).

To visualize the network of terms on this topic in the scientific literature (i.e. thermal physiology in Collembola), we undertook a social network analysis (Van Eck and Waltman, 2010) (VOSviewer software version 1.6.15) of the list of publications retrieved from the first raw search (856 results; Figure 2S Supplementary Material) and from the refined list of selected works (83 results; Figure 2). This analysis was done with a binary counting method for title and abstract and a minimum number of occurrences of three (plotted 60% of the most relevant terms). The approach enabled us to detect dominant terms used by the scientific community around the topic of thermal tolerance in Collembola and the strength of the interactions between them (how frequently they are used together).

Each species for which data were extracted from the 83 publications finally used was assigned to the climatic region from which the individuals representing that species had been sampled, based on the world temperature domains defined by Sayre et al. (Sayre et al., 2020) (Table A4 Supplementary Material). This includes four climatic regions: Polar region (90° - 60°), Cold Temperate region (60° - 45°), Warm Temperate region (45° - 30°) and Tropical Subtropical region (30° - 0°). Thermal tolerance data for CTL, SCP or LT were assigned depending on the season in which the individuals had been sampled, into three categories: Warmest, Intermediate or Coldest period (Table A5 Supplementary Material). In most cases, each original source reported the period in which the time of year when the data had been collected. In cases where information was only available on the sampling months, we assigned the category 'coldest period', 'warmest period' or 'intermediate period' of the year according to Haylock et al. (Haylock et al., 2008) for Europe, Leihy et al. (Leihy et al., 2018) for the sub-Antarctic Islands and Vega et al. (Vega et al., 2017) for Antarctica. Species were also divided according to their life form as epedaphic, hemiedaphic, euedaphic or atmobiotic [see (Potapov et al., 2016)] to incorporate local-scale conditions in the examination of general broad-scale spatial patterns. These categories were taken directly from the studies of our database or from an additional search, if the information was not provided in the original source (Table A4 Suppl. Mat.).

Thermal tolerance data and spatial distribution of studies

The thermal tolerance outcomes generated from each publication are detailed in Table A1 (Suppl. Mat.). Among the publications examined, several ones incorporated different ramping rates in dynamic measures of thermal tolerance. To address this variation in ramping rates, which can significantly influence thermal tolerance limit estimations in springtails (Allen et al., 2016), we selected the slowest ramping rates used in each work. To evaluate whether the number of publications (response variable) increases over the years (predictor) we performed a linear regression model analysis using R-Studio version 4.1.0 (Core Team, 2021). We generated another database (Table A2 Suppl. Mat.) of presence / absence in each zoogeographic region (as defined by Bellinger et al. (Bellinger et al., 2020)), for all springtail species with available thermal tolerance data. Each individual species for which thermal tolerance data exists was assigned to a zooregion based on the sampling point location where specimens were collected. We generated a map (Fig. 3) with ESRI's ArcMap Software 9.1 (licensed by Universidad Rey Juan Carlos).

Data Availability Statement

Data is provided in excel files as supplementary material.

RESULTS AND DISCUSSION

Diversity of metrics used in thermal tolerance studies

The number of publications per year on this topic appears not to be increasing significantly according to our statistical analyses ($\beta=0.004$, confidence intervals 95%: 0.05, -0.04, $p>0.05$). In contrast the general trend for the ecological discipline as a whole [see (Borthakur and Singh, 2018)], shows a significant increase of scientific production ($\beta=2.73$, confidence intervals 95%: 3.01, 2.46, $p<0.001$). Even though some publications are not restricted to a single methodology for the estimation of thermal tolerance, a total of 50 publications (57%) have reported SCPs for Collembolans. Lethal Temperatures ('LT') (18%), Critical Thermal Limits ('CTL') (12.5%) and 'shock' (12.5%) rank similarly in terms of frequency of use (Fig. 1). Only two publications have evaluated 'knock-down time' in Collembola. The metrics that have been most commonly adopted to evaluate thermal tolerance in springtails have changed over the last two decades. CTL and LT have risen in frequency as a metric of interest over the past ten years relative to SCP, that was the main method used in thermal tolerance studies in Collembola from 1970 to 2010 (Fig. 1). Initially, an emphasis was given to documenting *supercooling points* ('SCP'), the method most used historically. SCP is a metric based on the physical process of freezing body water (Wilson et al., 2003), and can be measured in several different ways, from the relatively simple, involving a thermocouple to detect the point of release of heat produced by the crystallization of fluids (Sinclair et al., 2015), to the more complex, using a differential scanning calorimeter to achieve similar ends (Worland et al., 1998). Although SCP does not necessarily indicate the death of the individual (Sinclair et al., 2003), it can be considered a useful method to measure minimum lethal temperature in freeze avoiding species (Renault et al., 2002), or at least for species that do not inhabit tropical areas (Chen et al., 1990). In addition, it can also be used to obtain other parameters as the melting point, the fractions of osmotically active water and osmotically inactive water (Holmstrup, 2018). On the other hand, CTL is a metric based on the temperature at which the animal loses the righting response (Allen et al., 2016) and may include estimates of both the upper and lower limits. Although the estimation of CTLs in springtails seems to have been more used in the last decade, it had been widely used in other animal groups before (Bennett et al., 2018).

The ramping rate used in dynamics methods has also changed over the years. For SCP, 66% of publications adopted a cooling rate of

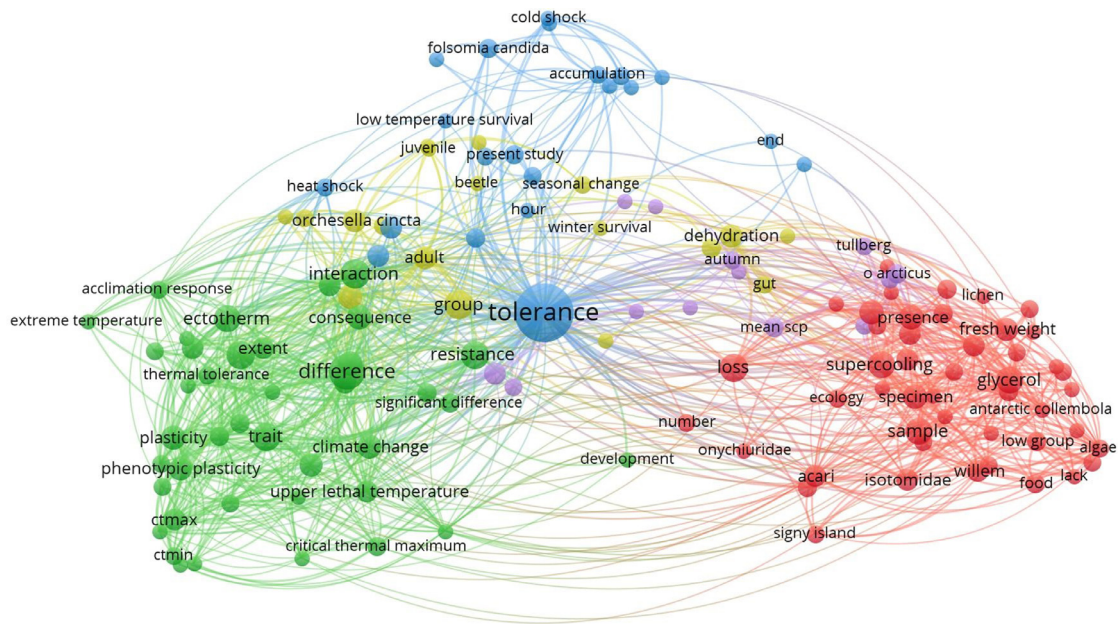


Figure 2. Network of terms of the titles and abstracts of the 83 publications reviewed on this work. The different clusters are represented by colours and the font size of the terms represents their importance.

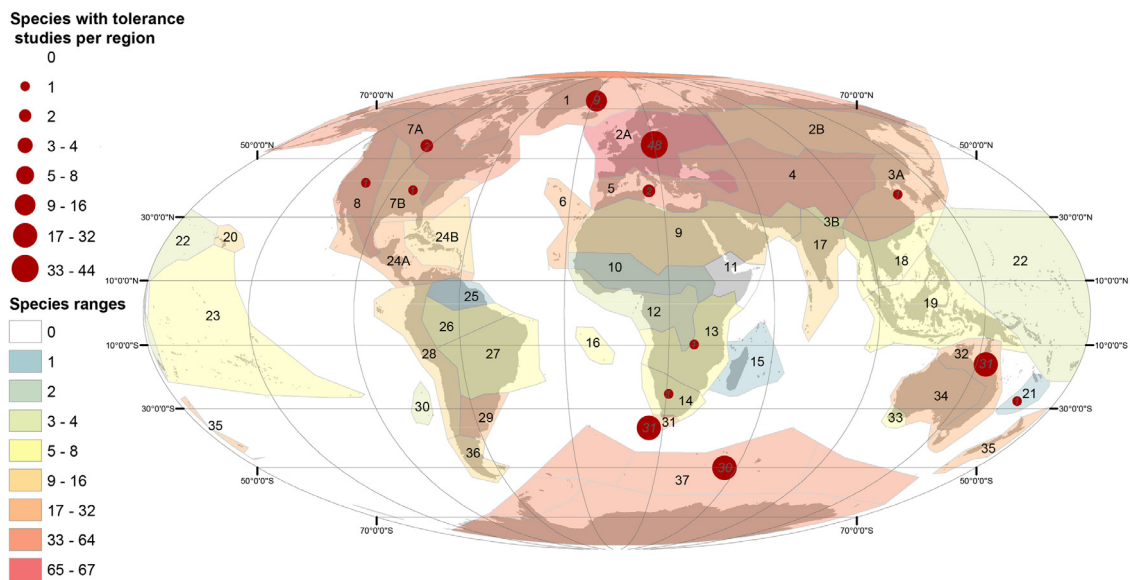


Figure 3. Number of species sampled in each zooregion with thermal tolerance data are represented by red circles of variable size (each species was assigned to a zoogeographic region depending on the sampling point location). Numbers on the map correspond to the zooregions assigned by Bellinger et al. (Bellinger et al., 2020) on the website collembola.org. Since all species in this review have sampling point location information, pseudo-species not formally named (genus + sp.) are included in the circles. The colours on the map represent the distributional range of the species formally named of this review, according to Bellinger et al. (Bellinger et al., 2020). Pseudo-species not formally named (genus + sp.) are not included because there is no data on their distribution.

$\geq 1^{\circ}\text{C}/\text{min}$, following the thermal gradient suggested by seminal studies of Salt (Salt, 1966) and Cannon (Cannon, 1983). However, authors interested in CTL have typically used slower rates ($< 0.5^{\circ}\text{C}/\text{min}$) (Table A1). The use of slow rates could make more ecological sense, since it is assumed that in nature temperature changes do not occur so abruptly [see (Kelty and Lee, 1999; Terblanche et al., 2007; Terblanche et al., 2011)], although some authors also suggest that a very low cooling rate ($< 0.1^{\circ}\text{C}/\text{h}$) could vary the results due to a ‘hardening’ process (Worland, 2005). In studies that use CTL published in the last ten years, there is no consensus on the rate to use, but there seems to be a range between 0.2 and $0.05^{\circ}\text{C}/\text{min}$ (Table A1).

Finally, two methodological issues that deserve attention if we are to approach a certain degree of standardization in experimental methodologies are the conditions of the animals in the laboratory and the living generation that are used (i.e., if workers have directly used field-collected individuals or individuals raised in the laboratory). In our review, only $\sim 23\%$ of publications provide information about the generation used in the experiments (Table A1), thus we can only assume that for the rest they are the original, field-collected specimens. Recent studies have observed no significant differences in thermal tolerance or another type of stress-tolerance metric between field-collected and second-generation individuals (Phillips et al., 2020; Maclean et al., 2018), but

this is not always the case as investigations of laboratory adaptation and intergenerational effects have demonstrated (Sgrò and Partridge, 2000; Hoffmann et al., 2017). First, the rearing of animals in the laboratory enables control of certain factors than can affect thermal tolerance, such as the age of individuals (Alemu et al., 2017) or their feeding status (Nyamukondiwa and Terblanche, 2009). Second, the method used to extract soil organisms (Berlese-Tullgren funnels) (Bano and Roy, 2016), usually applies a heat source that could have an effect on the thermal tolerance of the individuals [see (Waagner et al., 2010)], which also could be controlled by stabilizing populations in the laboratory. In addition, studies with field collected individuals can offer information on local acclimation of certain populations due to temperatures of the microhabitat (Jensen et al., 2019), which would provide very valuable information when combined with laboratory studies. Thus, scientific reporting of results in future publications would benefit from the inclusion of the generation or origin of the individuals that has been examined.

Regarding acclimation, debate is ongoing about where to place the boundaries between acclimation and hardening (Bowler, 2005; Loeschcke and Sørensen, 2005). Our review indicates that acclimation temperature points are consistent with the temperature range of the region of collection, except in those publications that explicitly aim to use acclimation temperature as a variable (Table A1). The time of acclimation in the examined publications varies widely, and for 50% of the publications revised we could not find any information about acclimation time (Table A1). Overall, thermal tolerance publications in springtails throughout the last five decades present methodological differences that could affect future large-scale comparative studies. Future research effort should focus, as far as possible, on choosing a standard methodology that can be used in a general way for a large number of organisms or taxa.

Overview of thermal tolerances in Collembola

The scientific literature published over the years on the thermal tolerance of springtails is notably rich, including 83 papers published in a total of 30 journals (Figure 1S Suppl. Mat.). An important proportion of these papers has been published in the *Journal of Insect Physiology* and *Functional Ecology* that have jointly published ~31% of the total number of publications on this topic (see Fig. 1S). Springtails are typically considered freeze avoiding species (Sinclair et al., 2003; Cannon and Block, 1988) and the examined literature on their thermal profiles shows a predominance towards the examination of cold tolerances. It is noted that 66% of the papers exclusively focused on cold tolerance, whereas only ~10 % explored heat tolerance and the remaining 24% documented both heat and cold tolerance. The accumulated number of species studied per zooregion is shown in Fig. 3 as red circles. This mapping includes experimental results for 144 species, including those pseudo-species that were not formally named (genus + sp.), since we have the sampling point locations. In addition, Fig. 3 also shows the global-scale spatial aggregation of distributional ranges for those species for which thermal tolerance data are available (i.e. species richness variation across the regions in Bellinger et al. (Bellinger et al., 2020) following a colour scale, see also Table A3 Suppl. Mat.). The species richness map does not include pseudo-species that are not formally named due to the impossibility in assigning their global zoogeographic distribution (leaving out 97 species for display). In this map (Fig. 3) we can see a clear geographical pattern in the distribution of species whose thermal limits have been studied, with most of them occurring in cold and temperate regions of the planet. This is in stark contrast with other taxa, which in general tend to show a more homogenous distribution of records on a global scale (Bennett et al., 2018). Heat and cold tolerances of springtails from tropical and subtropical latitudes are less documented. The strong relationship between cold tolerance and latitudinal distribution has been widely documented in insects (Addo-Bediako et al., 2000; Kimura, 2004; Calosi et al., 2010). In the same

way, similar publications have reported this pattern for Collembola as a study group [see (Janion-Scheepers et al., 2018; Holmstrup, 2018; Hawes et al., 2006; Bahrndorff et al., 2009)]. Yet, a few regions of the planet (Europe, north and southeast coast of Australia, South Africa, and Antarctica and the Southern Ocean) harbour most of the localities that have been sampled to conduct experiments on the thermal tolerance of springtails (Fig. 3). Interestingly, a limited number of studies exist from the Americas and Asia. It must be noted that such result may be partly affected by the search engine primary focus on English language publications and so it may underestimate those published in other languages. Despite this, we believe that the works published in English language can give a sufficiently good notion of the current state of the topic.

Network analysis of scientific terms used in the literature

In the network of scientific terms from the initial search on general ecophysiological studies (356 results) three emergent clusters are detected (Fig. 2S). A first cluster (green) shows 'reproduction' and 'toxicity' as dominant topics, thus inferring the interest to assess their interaction. This group of publications correspond to ecotoxicological studies that use Collembola as a study model for other groups and human health (Filser et al., 2014). Another cluster (blue) seems not to have a predominant topic, but the words that stand out the most are 'strategy' and 'summer' suggesting some attention to life histories around phenological processes under macroclimatic conditions. This cluster could be considered the closest aggregation to our review topic because we also find related terms like 'cold tolerance', 'cold hardiness', '*Cryptopygus antarcticus*' (an Antarctic Collembola superspecies, (Stevens et al., 2006)), and 'lethal temperature', among others. On the other hand, a red cluster, highlights the topics 'abundance' and 'richness' as dominant, in turn suggesting the relevance of thermal tolerance limits to account for community level patterns and the geographic distribution of species. Finally, we can see a more dispersed cluster, (yellow), which is in the centre with words as 'diet', 'prey' and 'spider' that may focus on trophic interactions (Fig. 2S).

When the network of terms is examined for the publications specifically selected (83 results) as relevant for this review on the thermal tolerances of springtails (Fig. 2), we can see two dominant clusters linked by the term 'tolerance' (blue cluster). Tolerance as a central term is associated with key terms in this review such as 'heat shock', 'cold shock' and '*Folsomia candida*'. The species *F. candida* could appear due to its prominent use as model organism in laboratory research (Fountain and Hopkin, 2005). One of the clusters (red), highlights terms like 'supercooling', 'loss', 'glycerol' or 'fresh weight', encompassing those publications that relate thermal tolerance to dehydration processes. The other cluster (green) identifies 'difference', 'climate change', 'ectotherm', 'upper lethal temperature'. It seems that these two clusters differentiate between supercooling process and thermal tolerance limits. From the 83 publications examined for this review, we find that 25 of them are involved in the study of 'hardening'. Works focused on 'hardening' typically consist of an exposure of one or several hours to a certain temperature, while monitoring the increase or reduction of thermal tolerance in species. This set of 'hardening' publications often adopt more than one metric to measure various ecological aspects but this term does not emerge explicitly in this network. Overall, we can conclude that the literature on ecophysiological works in springtails has three main lines, one related to reproduction and toxicity, another one related to thermal tolerance strategies and a last one related to abundance and richness (Fig. 2S), whereas studies specifically focused on thermal tolerance differentiate clearly between supercooling examinations and thermal tolerance in general (Fig. 2). The literature on ecophysiological studies of springtails is very extensive and it can be laborious to make systematic searches. The use of the terms that refer to the metrics used help refine the searches.

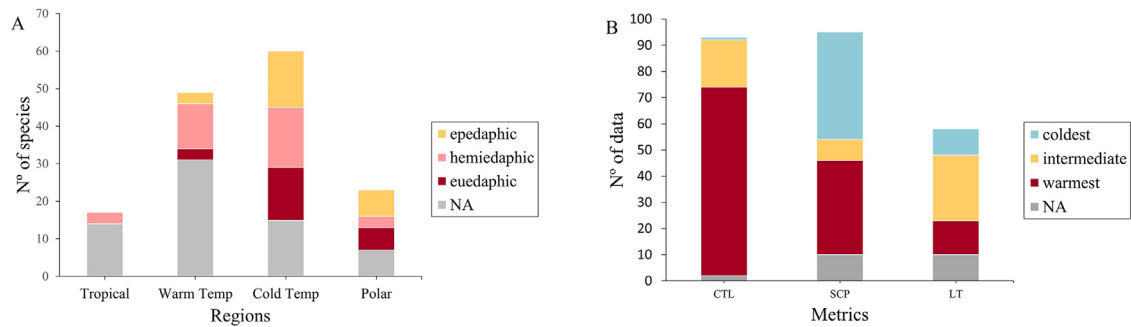


Figure 4. A: Number of species differentiated by their life form in four different climatic regions. Tropical-Subtropical region (0° – 30°), Warm-Temperate region (30° – 45°), Cold-Temperate region (45° – 60°) and Polar region (60° – 90°). The number of species in this graph does not coincide with the total number of individuals in the study because there are species for which thermal tolerance data have been obtained in different climatic regions. The species for which no information was found were classified as NA (not available). No information was found for the atmobiotic species. B: Number of thermal tolerance data of the different metrics according to whether the study species were collected in the warmest, intermediate or coldest period of the year. The data for which no information was found were classified as NA (not available).

Taxonomic coverage of species in the estimation of thermal tolerance limits

Taxonomic biases can limit predictive models of species distributions (Hortal et al., 2008) and can be a problem in conservation research (Clark and May, 2002). For this reason, it is also relevant to examine the relative attention given to different subclades among Collembola. The taxonomic order with the greatest number of species registered so far in Collembola is Entomobryomorpha (4328 species; 47.1% of the total described species), followed by Poduromorpha (3539 species; 38.5%), Symphypleona (1257 species; 13.7%) and Neelipleona (60 species; 0.7%) (Bellinger et al., 2020); though acknowledging a Linnean shortfall in the group – (Potapov et al., 2020)). The proportion of springtail species for which thermal tolerance data exist coincides in proportion to the number of known species with each group (see Fig. S3 Suppl. Mat.). We found that Entomobryomorpha is by far the most studied order of springtails in terms of thermal tolerance (almost two thirds of the total studied species in this work belong to this taxonomic group). Neelipleona, instead, has a very low representation, although this may be because its diversity is underestimated (Schneider et al., 2011). At the family level, Entomobryidae is the family containing the largest number of species described (1725; 18.8% of the total described species) (Bellinger et al., 2020), although this does not correspond with the highest number of thermal tolerance data (36 species; 25% of the studied species). This family ranks second after Isotomidae, to which 15.9% of the total described species belong (Bellinger et al., 2020), but which dominates in the literature focused on thermal tolerance assessments (41 species; 28.5% of the studied species). In contrast, the family Neanuridae shows a great disparity between described species and species studied in thermal tolerance publications. With 1567 described species (17% of the total diversity) (Bellinger et al., 2020), thermal tolerances have been studied for only three species belonging to this family. No apparent explanation exists to account for such a paucity of thermal tolerance data in this family, especially bearing in mind that species continue to be described in this group (Benito and Palacios-Vargas, 2008; Weiner et al., 2009; Deharveng et al., 2015). One explanation might be, however, that the group has proven difficult to maintain or culture in the laboratory, with a recent breakthrough demonstrating that they tend to be slime-mould feeders and can be maintained and cultured on such a diet (Hoskins et al., 2015). In this review, we have only found thermal tolerance data for 1% of the species described to date. Although not strictly comparable, this percentage is roughly similar to those obtained for other groups (Bennett et al., 2018; Lancaster and Humphreys, 2020). The lack of data for many species makes it difficult to predict biological effects of climate change if responses are species dependent.

Ecological characteristics of thermal tolerance data

Springtails can be differentiated according to the position they occupy in or above the soil column as epedaphic, hemiedaphic, euedaphic or atmobiotic [see (Potapov et al., 2016)]. This information is not only a taxonomically relevant characteristic (Hopkin, 1997), but an appropriate descriptor of the trophic niche (Potapov et al., 2016) and thermal fluctuations of the habitat (Willmer, 1982). Of the 144 species of this review, we have not found information in the scientific literature on their life form for almost half of the data (47%) (Table A4 Suppl. Mat.). For the remaining half, life forms are 21.5% hemiedaphic, 15.6% euedaphic and 16% epedaphic. Cold-Temperate region shows a balanced distribution of the three life forms (Fig. 4a). In contrast, hemiedaphic species have a greater representation in the Warm-Temperate region and are the only life form represented in the Tropical-Subtropical region (Fig. 4a). This information is important when measuring thermal tolerance data because some authors have found that surface living species have greater heat tolerance than soil living species (Van Dooremalen et al., 2013; Pallarés et al., 2019). Local microclimate and other microhabitat conditions are also key factors that can modify thermal tolerance between different populations (Kutcherov et al., 2020; Liefting and Ellers, 2008), affecting spatial patterns on a large scale (Sengupta et al., 2016; Sengupta et al., 2017). In this way, some recent works on the effects of global warming on hexapod populations have emphasized its importance, including data on Collembola (Tüzün and Stoks, 2018; Verheyen et al., 2019). Comparison of thermal tolerance between species that inhabit more stable environments (deeper soil) and those that inhabit more fluctuating environments (soil surface), should be done taking this factor into account. For instance, in polar regions, snow cover can act as insulator (Convey et al., 2015), generating a decoupling between ground and air temperatures (Convey et al., 2018). In terms of seasonal activity, 79% of the CTL records were obtained in the warmest period, whereas only 1% of the data have a sampling period during the coldest part of the year (Fig. 4b). However, for SCP and LT data, the season of sampling varies more. For SCP, 43% of the data are from the coldest period and for LT records the predominant period is the intermediate (spring/autumn) with 43% of the data in this group (Fig. 4b). Depending on whether the species are summer or winter active, physiological adjustments to tolerate limit temperatures may be different (Saeidi et al., 2021), for this reason, thermal tolerance values can vary depending on the season in which specimens are sampled (Heiman and Knight, 1972; David and Vannier, 1996; Hopkin et al., 2006). The variability shown by SCP and LT could bias large-scale comparative studies, which suggests the need to incorporate this variation when analysing multi-species data.

CONCLUSIONS

Research on thermal tolerance in Collembola has accumulated at a slower rate than in other biological disciplines such as ecology. As in other organisms, there are strong Hutchinsonian knowledge gaps that remain to be addressed for this taxonomic group. Thermal tolerance limits for around 99% of the currently described species in the group are waiting to be characterized. Moreover, those species for which thermal tolerance data exist have been sampled in a few geographical areas of the planet, thus indicative of a spatial bias in the aggregation of knowledge around these physiologically relevant traits. In the context of global warming, precise knowledge of physiological mechanisms is essential for predicting the functional responses of organisms to climate (Pörtner and Farrell, 2008). Rapid climate changes have placed ectotherms, especially those inhabiting tropical environments, at high risk of extinction [(Deutsch et al., 2008; Sinclair et al., 2003), among others]. Our findings suggest that a more complete characterization of thermal tolerances in Collembola should pay attention to largely underrepresented tropical and subtropical regions of the planet if we are to better forecast biotic responses to climate change and assess extinction risk [see discussions for example in (Deutsch et al., 2008; Diamond et al., 2012; Duffy et al., 2015; Kingsolver and Buckley, 2017; Lembrechts et al., 2020)]. On the other hand, both the diversity of methods identified in this review, either in the type of metrics or differences in the use of rates, as well as differences in the maintenance of animals (or lack of information in this case), should be considered when addressing comparative studies. New methods of doing so are becoming increasingly available [e.g. (Jørgensen et al., 2021; Rezende et al., 2020)]. The potential to integrate different methods of assessment of thermal tolerances brings renewed value for understanding intrinsic thermal limits and their ecological significance. This is especially critical for springtails due to their contribution to the importance of soil fauna in shaping ecosystems (Potapov et al., 2020) and the current trend of substantially changing thermal regimes of soils globally (Lembrechts et al., 2020).

FUTURE DIRECTIONS

Our review brings to light a number of knowledge gaps around the thermal tolerance of springtails that should be taken into account in future studies. First, we have found 47 pseudo-species with thermal tolerance data for which the species-level taxonomy is not resolved. Future phylogenetic comparisons would benefit from molecular analyses [e.g. (Liu et al., 2020)] that name and place in the tree of life these unresolved species. Second, thermal tolerance studies could be increased for those families that are less represented in order to reach a representative balance the knowledge in this group of edaphic animals. Third, it is important to incorporate local microclimatic effects to characterize the true exposure levels that different populations experience in the field and relate them to thermal tolerances obtained under laboratory experiments [see (Kutcherov et al., 2020; Liefing and Ellers, 2008)].

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Pablo Escribano-Álvarez: Data curation, Writing – original draft, Formal analysis, Writing – review & editing. **Luis R. Pertierra:** Conceptualization, Formal analysis, Writing – review & editing. **Brezo Martínez:** Writing – review & editing. **Steven L. Chown:** Conceptualization, Writing – review & editing. **Miguel Á. Olalla-Tárraga:** Conceptualization, Funding acquisition, Formal analysis, Writing – review & editing.

ACKNOWLEDGEMENTS

This study was supported by CGL2017-89820-P research grant to M.A.O.T. funded by the Ministry of Science & Innovation. P.E.A. is funded by a FPI contract PRE2018-085903; S.L.C. is funded by Australian Research Council SRIEAS Grant SR200100005 Securing Antarctica's Environmental Future.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cris.2021.100023.

REFERENCES

- Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2000. Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. B Biol. Sci.* 267, 739–745. doi:10.1098/rspb.2000.1065.
- Alemu, T., Alemneh, T., Pertoldi, C., Ambelu, A., Bahrndorff, S., 2017. Costs and benefits of heat and cold hardening in a soil arthropod. *Biol. J. Linn. Soc.* 20, 1–9. doi:10.1093/biolinnean/blx092.
- Allen, J.L., Chown, S.L., Janion-Scheepers, C., Clusella-Trullas, S., 2016. Interactions between rates of temperature change and acclimation affect latitudinal patterns of warming tolerance. *Conserv. Physiol.* 4, 1–14. doi:10.1093/conphys/cow053.
- Amarasekare, P., Coutinho, R.M., 2014. Effects of temperature on intraspecific competition in ectotherms. *Am. Nat.* 184, E50–E65. doi:10.1086/677386.
- Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F., Chown, S.L., 2013. Heat freezes niche evolution. *Ecol. Lett.* 16, 1206–1219. doi:10.1111/ele.12155.
- Bahrndorff, S., Loeschcke, V., Pertoldi, C., Beier, C., Holmstrup, M., 2009. The rapid cold hardening response of Collembola is influenced by thermal variability of the habitat. *Funct. Ecol.* 23, 340–347. doi:10.1111/j.1365-2435.2008.01503.x.
- Bale, J.S., 1993. Classes of Insect Cold Hardiness. *Funct. Ecol.* 7, 751–753. <http://www.jstor.org/stable/2390198>.
- Banks, N.C., Paini, D.R., Bayliss, K.L., Hodda, M., 2015. The role of global trade and transport network topology in the human-mediated dispersal of alien species. *Ecol. Lett.* 18, 188–199. doi:10.1111/ele.12397.
- Bano, R., Roy, S., 2016. Extraction of Soil Microarthropods: A low cost BerleseTullgren funnels extractor. *Int. J. Fauna Biol. Stud.* 3, 14–17.
- Bardgett, R.D., Van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. *Nature* 515, 505–511. doi:10.1038/nature13855.
- Bellinger, P.F., Christiansen, K.A., Janssens, F., 2020. Checklist of the Collembola of the world. Available from: <http://www.collembola.org>
- Benito, J.C.S., Palacios-Vargas, J.G., 2008. Two new species of Paranura (Collembola: Neanuridae) from southeastern Mexico. *Ann. Entomol. Soc. Am.* 101, 683–688. doi:10.1603/0013-8746(2008)101[683:TNSOPC]2.0.CO;2.
- Bennett, J.M., Calosi, P., Clusella-Trullas, S., Martínez, B., Sunday, J., Algar, A.C., Araújo, M.B., Hawkins, B.A., Keith, S., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Villalobos, F., Olalla-Tárraga, M.A., Morales-Castilla, I., 2018. GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci. Data* 5, 180022. doi:10.1038/sdata.2018.22.
- Bennett, J.M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., Araújo, M.B., Algar, A.C., Clusella-Trullas, S., Hawkins, B.A., Keith, S., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Morales-Castilla, I., Olalla-Tárraga, M.A., 2021. The evolution of critical thermal limits of life on Earth. *Nat. Commun.* doi:10.1038/s41467-021-21263-8.
- Borthakur, A., Singh, P., 2018. Global research trends in 'Ecology: A scientometric analysis. *Trop. Ecol.* 59, 431–443.
- Bowler, K., 2005. Acclimation, heat shock and hardening. *J. Therm. Biol.* 30, 125–130.
- Brett, J., 1956. Some principles in thermal requirements of fishes. *Q. Rev. Biol.* 31, 75–87. doi:10.1086/401257.
- Calosi, P., Bilton, D.T., Spicer, J.I., Votier, S.C., Atfield, A., 2010. What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). *J. Anim. Ecol.* 79, 194–204. doi:10.1111/j.1365-2656.2009.01611.x.
- Cannon, R.J.C., 1983. Experimental studies on supercooling in two Antarctic microarthropods. *J. Insect Physiol.* 8, 617–624. doi:10.1016/0022-1910(83)90013-6.
- Cannon, R.J.C., Block, W., 1988. Cold tolerance of microarthropods. *Biol. Rev. - Cambridge Philos. Soc.* 63, 23–77. doi:10.1111/j.1469-185X.1988.tb00468.x.
- Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R., 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biol. Conserv.* 144, 2647–2655. doi:10.1016/j.biocon.2011.07.024.
- Cassagne, N., Gauquelin, T., Bal-Serin, M.C., Gers, C., 2006. Endemic Collembola, privileged bioindicators of forest management. *Pedobiologia (Jena)* 50, 127–134. doi:10.1016/j.pedobi.2005.10.002.
- Chen, C.P., Lee Jr, R.E., Delinger, D.L., 1990. A comparison of the responses of tropical and temperate flies (Diptera: Sarcophagidae) to cold and heat stress. *J. Comp. Physiol.* B 160, 543–547. doi:10.1007/BF00258982.
- Chown, S.L., Addo-Bediako, A., Gaston, K.J., 2003. Physiological diversity: listening to the large-scale signal. *Funct. Ecol.* 17, 568–572. doi:10.1046/j.1365-2435.2003.07622.x.
- Clark, J.A., May, R.M., 2002. Taxonomic bias in conservation research. *Science* 297, 191–192. doi:10.1126/science.297.5579.191b.

- Colwell, R.K., Rangel, T.F., 2009. Hutchinson's duality: The once and future niche. *Proc. Natl. Acad. Sci. U.S.A.* 106 (2), 19651–19658. doi:10.1073/pnas.0901650106.
- Convey, P., Abbandonato, H., Bergan, F., Beumer, L.T., Biersma, E.M., Brathen, V.S., D'Imperio, L., Jensen, C.K., Nilsen, S., Paquin, K., Stenkevit, U., Svonen, M.E., Winkler, J., Müller, E., Coulson, S.J., 2015. Survival of rapidly fluctuating natural low winter temperatures by High Arctic soil invertebrates. *J. Therm. Biol.* 54, 111–117. doi:10.1016/j.jtherbio.2014.07.009.
- Convey, P., Block, W., Peat, H.J., 2003. Soil arthropods as indicators of water stress in Antarctic terrestrial habitats? *Glob. Chang. Biol.* 9, 1718–1730. doi:10.1046/j.1365-2486.2003.00691.x.
- Convey, P., Coulson, S.J., Worland, M.R., Sjöblom, A., 2018. The importance of understanding annual and shorter-term temperature patterns and variation in the surface levels of polar soils for terrestrial biota. *Pol. Biol.* 41, 1587–1605. doi:10.1007/s00300-018-2299-0.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>.
- Cowles, R.B., Bogert, C.M., 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the AMNH* ; v. 83, article 5. *Bull. Am. Museum Nat. Hist.* 83, 261–296.
- Coyle, D.R., Nagendra, U.J., Taylor, M.K., Campbell, J.H., Cunard, C.E., Joslin, A.H., Mundepi, A., Phillips, C.A., Callahan Jr., M.A., 2017. Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biol. Biochem.* 110, 116–133. doi:10.1016/j.soilbio.2017.03.008.
- Cragg, R.G., Bardgett, R.D., 2001. How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. *Soil Biol. Biochem.* 33, 2073–2081. doi:10.1016/S0038-0717(01)00138-9.
- David, J.F., Vannier, G., 1996. Changes in supercooling with body size, sex, and season in the long-lived millipede *Polyzoniium germanicum* (Diplopoda, Polyzoniidae). *J. Zool. Lond.* 240, 599–608. doi:10.1111/j.1469-7998.1996.tb05310.x.
- Deharveng, L., Zoughailech, A., Hamra-Kroua, S., Porco, D., 2015. A new species of Deutoneura (Collembola: Neanuridae) from north-eastern Algeria, and characterisation of two intraspecific lineages by their barcodes. *Zootaxa* 3920, 281–290. doi:10.11646/zootaxa.3920.2.4.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* 105, 6668–6672. doi:10.1073/pnas.0709472105.
- Diamond, S.E., Sorger, D.M., Hulcr, J., Pelini, S.L., Toro, I.D., Hirsch, C., Oberg, E., Dunn, R.R., 2012. Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Glob. Chang. Biol.* 18, 448–456. doi:10.1111/j.1365-2486.2011.02542.x.
- Duffy, G.A., Coetzee, B.W., Janion-Scheepers, C., Chown, S.L., 2015. Microclimate-based macrophysiology: implications for insects in a warming world. *Curr. Opin. Insect Sci.* 11, 84–89. doi:10.1016/j.cois.2015.09.013.
- Evans, T.G., Diamond, S.E., Kelly, M.W., 2015. Mechanistic species distribution modelling as a link between physiology and conservation. *Conserv. Physiol.* 3, 1–16. doi:10.1093/conphys/cov056.
- Filser, J., Wiegmann, S., Schröder, B., 2014. Collembola in ecotoxicology - Any news or just boring routine? *Appl. Soil Ecol.* 83, 193–199. doi:10.1016/j.apsoil.2013.07.007.
- Fountain, M.T., Hopkin, S.P., 2005. *Folsomia candida* (Collembola): A 'standard' soil arthropod. *Annu. Rev. Entomol.* 50, 201–222. doi:10.1146/annurev.ento.50.071803.130331.
- Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., Clusella-Trullas, S., Ghalambor, C.K., Konarzewski, M., Peck, L.S., Porter, W.P., Pörtner, H.O., Rezende, E.L., Schulte, P.M., Spicer, J.I., Stillman, J.H., Terblanche, J.S., Kleunen, M., 2009. Macrophysiology: A conceptual unification. *Am. Nat.* 174, 595–612. doi:10.1086/605982.
- Greenslade, P., 2007. The potential of Collembola to act as indicators of landscape stress in Australia. *Aust. J. Exp. Agric.* 47, 424–434. doi:10.1071/EA05264.
- Hawes, T.C., Couldridge, C.E., Bale, J.S., Worland, M.R., 2006. Habitat temperature and the temporal scaling of cold hardening in the high Arctic collembolan, *Hypogastrura tullbergi* (Schäffer). *Ecol. Entomol.* 31, 450–459. doi:10.1111/j.1365-2311.2006.00796.x.
- Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *J. Geophys. Res. Atmos.* 113, 1–12. doi:10.1029/2008JD010201.
- Heiman, D.R., Knight, A.W., 1972. Upper-Lethal-Temperature Relations of the Nymphs of the Stonefly, *Paragnetina media*. *Hydrobiologie* 39, 479–493. doi:10.1007/BF00046741.
- Hoffmann, A.A., Sgrò, C.M., Kristensen, T.M., 2017. Revisiting Adaptive Potential, Population Size, and Conservation. *Trends Ecol. Evol.* 32, 506–517. doi:10.1016/j.tree.2017.03.012.
- Holmström, M., 2018. Screening of cold tolerance in fifteen springtail species. *J. Therm. Biol.* 77, 1–6. doi:10.1016/j.jtherbio.2018.07.017.
- Holmström, M., Bayley, M., Ramlöv, H., 2002. Supercool or dehydrate? An experimental analysis of overwintering strategies in small permeable arctic invertebrates. *PNAS* 99, 5716–5720. doi:10.1073/pnas.082580699.
- Hopkin, R.S., Qari, S., Bowler, K., Hyde, D., Cuculescu, M., 2006. Seasonal thermal tolerance in marine Crustacea. *J. Exp. Mar. Biol. Ecol.* 331, 74–81. doi:10.1016/j.jembe.2005.10.007.
- Hopkin, S.P., 1997. *Biology of the springtails*. Oxford University Press, Oxford, UK.
- Hortal, J., De Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annu. Rev. Ecol. Syst.* 46, 523–549. doi:10.1146/annurev-ecolsys-112414-054400.
- Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M., Baselga, A., 2008. Historical bias in biodiversity inventories affects the observed environmental niche of species. *Oikos* 117, 847–858. doi:10.1111/j.0030-1299.2008.16434.x.
- Hoskins, J.L., Janion-Scheepers, C., Chown, S.L., Duffy, G.A., 2015. Growth and reproduction of laboratory-reared nearurban Collembola using a novel slime mould diet. *Sci. Rep.* 5, 11957. doi:10.1038/srep11957.
- Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Amer. Zool.* 19, 357–366. doi:10.1093/icb/19.1.357.
- Hughes, L., 2000. Biological consequences of global warming: Is the signal already apparent? *Trends Ecol. Evol.* 15, 56–61. doi:10.1016/S0169-5347(99)01764-4.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Symposium on Quantitative Biology* 22, 415–427.
- Janion-Scheepers, C., Phillips, L., Sgrò, C.M., Duffy, G.A., Hallas, R., Chown, S.L., 2018. Basal resistance enhances warming tolerance of alien over indigenous species across latitude. *PNAS* 115, 145–150. doi:10.1073/pnas.1715598115.
- Jensen, A., Alemu, T., Alemneh, T., Pertoldi, C., Bahrndorff, S., 2019. Thermal acclimation and adaptation across populations in a broadly distributed soil arthropod. *Funct. Ecol.* 33, 833–845. doi:10.1111/1365-2435.13291.
- Jonsson, B., Jonsson, N., Finstad, A.G., 2013. Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. *J. Anim. Ecol.* 82, 201–210. doi:10.1111/j.1365-2656.2012.02022.x.
- Jørgensen, L.B., Malte, H., Ørsted, M., Klahn, N.A., Overgaard, J., 2021. A unifying model to estimate thermal tolerance limits in ectotherms across static, dynamic and fluctuating exposures to thermal stress. *Sci. Rep.* 11, 12840. doi:10.1038/s41598-021-92004-6.
- Jucevica, E., Meleci, V., 2006. Global warming affect Collembola community: A long-term study. *Pedobiologia (Jena)* 50, 177–184. doi:10.1016/j.pedobi.2005.10.006.
- Kaneda, S., Kaneko, N., 2008. Collembolans feeding on soil affect carbon and nitrogen mineralization by their influence on microbial and nematode activities. *Biol. Fertil. Soils* 44, 435–442. doi:10.1007/s00374-007-0222-x.
- Kearney, M., Porter, W., 2004. Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85 (11), 3119–3131. doi:10.1890/03-0820.
- Kelty, J.D., Lee Jr, R.E., 1999. Induction of rapid cold hardening by cooling at ecologically relevant rates in *Drosophila melanogaster*. *J. Insect Physiol.* 45, 719–726. doi:10.1016/S0022-1910(99)00040-2.
- Kimura, M.T., 2004. Cold and heat tolerance of drosophilid flies with reference to their latitudinal distributions. *Oecologia* 140, 442–449. doi:10.1007/s00442-004-1605-4.
- Kingsolver, J.G., Buckley, L.B., 2017. Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. *Philos. Trans. R. Soc. B* 372, 20160147. doi:10.1098/rstb.2016.0147.
- Kingsolver, J.G., Diamond, S.E., Buckley, L.B., 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct. Ecol.* 27, 1415–1423. doi:10.1111/1365-2435.12145.
- Kingsolver, J.G., Woods, H.A., 1997. Thermal sensitivity of growth and feeding in *Manduca sexta* caterpillars. *Physiol. Biochem. Zool.* 70, 631–638.
- Kutcherov, D., Slotsbo, S., Sigurdsson, B.D., Leblans, N.I.W., Berg, M.P., Ellers, J., Marién, J., Holmström, M., 2020. Temperature responses in a subarctic springtail from two geothermally warmed habitats. *Pedobiologia* 78, 150606. doi:10.1016/j.pedobi.2019.150606.
- Lancaster, L.T., Humphreys, A.M., 2020. Global variation in the thermal tolerances of plants. *PNAS* 117, 13580–13587. doi:10.1073/pnas.1918162117.
- Leihy, R.L., Duffy, G.A., Nortje, E., Chown, S.L., 2018. High resolution temperature data for ecological research and management on the Southern Ocean Islands. *Sci. Data* 5, 180177. doi:10.1038/sdata.2018.177.
- Lembrechts, J.L., Aalto, J., Ashcroft, M.B., et al., 2020. SoilTemp: A global database of near-surface temperature. *Glob. Change Biol.* 26, 6616–6629. doi:10.1111/gcb.15123.
- Li, K., Rollins, J., Yan, E., 2018. Web of Science use in published research and review papers 1997–2017: a selective, dynamic, cross-domain, content-based analysis. *Scientometrics* 115, 1–20. doi:10.1007/s11192-017-2622-5.
- Liefting, M., Ellers, J., 2008. Habitat-specific differences in thermal plasticity in natural populations of a soil arthropod. *Biol. J. Linn. Soc. Lond.* 94, 265–271. doi:10.1111/j.1095-8312.2008.00969.x.
- Liu, W.P.A., Phillips, L.M., Terblanche, J.S., Janion-Scheepers, C., Chown, S.L., 2020. Strangers in a strange land: Globally unusual thermal tolerance in Collembola from the Cape Floristic Region. *Funct. Ecol.* 34, 1601–1612. doi:10.1111/1365-2435.13584.
- Loeschke, V., Sørensen, J.G., 2005. Acclimation, heat shock and hardening - A response from evolutionary biology. *J. Therm. Biol.* 30, 255–257. doi:10.1016/j.jtherbio.2004.12.005.
- Lussenhop, J., BassiriRad, H., 2005. Collembola effects on plant mass and nitrogen acquisition by ash seedlings (*Fraxinus pennsylvanica*). *Soil Biol. Biochem.* 37, 645–650. doi:10.1016/j.soilbio.2004.08.021.
- Lutterschmidt, W.I., Hutchison, V.H., 1997. The critical thermal maximum: History and critique. *Can. J. Zool.* 75, 1561–1574. doi:10.1139/z97-783.
- Maaf, S., Caruso, T., Rillig, M.C., 2015. Functional role of microarthropods in soil aggregation. *Pedobiologia (Jena)* 58, 59–63. doi:10.1016/j.pedobi.2015.03.001.
- Maclean, H.J., Kristensen, T.N., Sørensen, J.G., Overgaard, J., 2018. Laboratory maintenance does not alter ecological and physiological patterns among species: a *Drosophila* case study. *J. Evol. Biol.* 31, 530–542. doi:10.1111/jeb.13241.
- MacMillan, H.A., Sinclair, B.J., 2011. Mechanisms underlying insect chill-coma. *J. Insect Physiol.* 57, 12–20. doi:10.1016/j.jinsphys.2010.10.004.
- Meehan, M.L., Barreto, C., Turnbull, M.S., Bradley, R.L., Bellenger, J.P., Darnajoux, R., Lindo, Z., 2020. Response of soil fauna to simulated global change factors depends on ambient climate conditions. *Pedobiologia* 83, 150672. doi:10.1016/j.pedobi.2020.150672.

- Mondal, S., Rai, U., 2001. In vitro effects of temperature on phagocytic and cytotoxic activities of splenic phagocytes of the wall lizard, *Hemidactylus flaviviridis*. *Comp. Biochem. Physiol. Part A* 129, 391–398. doi:10.1016/S1095-6433(00)00356-1.
- Nyamukondiwa, C., Terblanche, J.S., 2009. Thermal tolerance in adult Mediterranean and Natal fruit flies (*Ceratitis capitata* and *Ceratitis rosa*): Effects of age, gender and feeding status. *J. Therm. Biol.* 34, 406–414. doi:10.1016/j.jtherbio.2009.09.002.
- O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H., Gurevitch, J., Page, M.J., Stewart, G., Moher, D., Nakagawa, S., 2021. Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biol. Rev.* 1–28. doi:10.1111/brv.12721.
- Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C., Thomas, M.B., 2013. Temperature variation makes ectotherms more sensitive to climate change. *Glob. Chang. Biol.* 19, 2373–2380. doi:10.1111/gcb.12240.
- Pallarés, S., Colado, R., Pérez-Fernández, T., Wesener, T., Ribera, I., Sánchez-Fernández, D., 2019. Heat tolerance and acclimation capacity in subterranean arthropods living under common and stable thermal conditions. *Ecol. Evol.* 9, 13731–13739. doi:10.1002/ece3.5782.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371. doi:10.1046/j.1466-822X.2003.00042.x.
- Phillips, L.M., Aitkenhead, I., Janion-Scheepers, C., King, C.K., McGeoch, M.A., Nielsen, U.N., Terauds, A., Liu, W.P.A., Chown, S.L., 2020. Basal tolerance but not plasticity gives invasive springtails the advantage in an assemblage setting. *Conserv. Physiol.* 8, 1–18. doi:10.1093/conphys/coaa049.
- Pörtner, H.O., Farrell, A.P., 2008. Physiology and Climate Change. *Science* 322, 690–692. <https://www.jstor.org/stable/20145158>.
- Potapov, A., Bellini, B.C., Chown, S.L., Deharveng, L., Janssens, F., Kováč, L., Kuznetsova, N., Ponge, J.F., Potapov, M., Querner, P., Russell, D., Sun, X., Zhang, F., Berg, M.P., 2020. Towards a global synthesis of Collembola knowledge: challenges and potential solutions. *Soil Org* 92, 161–188. doi:10.25674/so92iss3pp161.
- Potapov, A.A., Semenina, E.E., Korotkevich, A.Y., Kuznetsova, N.A., Tiunov, A.V., 2016. Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic identity and life forms. *Soil Biol. Biochem.* 101, 20–31. doi:10.1016/j.soilbio.2016.07.002.
- Renault, D., Salin, C., Vannier, G., Vernon, P., 2002. Survival at low temperatures in insects: What is the ecological significance of the supercooling point? *Cryo-Letters* 23, 217–228.
- Rezende, E.L., Bozinovic, F., Szilágyi, A., Santos, M., 2020. Predicting temperature mortality and selection in natural *Drosophila* populations. *Science* 369, 1242–1245. doi:10.1126/science.aba9287.
- Rezende, E.L., Castañeda, L.E., Santos, M., 2014. Tolerance landscapes in thermal ecology. *Funct. Ecol.* 28, 799–809. doi:10.1111/1365-2435.12268.
- Roithmeier, O., Burkhardt, U., Daghghi, E., Filser, J., 2018. *Desoria trispinata* (MacGillivray, 1896), a promising model Collembola species to study biological invasions in soil communities. *Pedobiologia (Jena)* 67, 45–56. doi:10.1016/j.pedobi.2017.11.003.
- Rosenberg, N.J., Blad, B.L., Verma, S.B., 1983. *Microclimate. The biological environment*, Second edn John Wiley & Sons, New York.
- Rusek, J., 1998. Biodiversity of Collembola and their functional role in the ecosystem. *Biodivers. Conserv.* 7, 1207–1219. doi:10.1023/A:1008887817883.
- Saeidi, F., Mikani, A., Moharrampour, S., 2021. Thermal tolerance variations and physiological adjustments in a winter active and a summer active aphid species. *J. Therm. Biol.* 98, 102950. doi:10.1016/j.jtherbio.2021.102950.
- Salt, R.W., 1966. Effect of cooling rate on the freezing temperatures of supercooled insects. *Can. J. Zool.* 44, 655–659. doi:10.1139/z66-064.
- Sayre, R., Karagulle, D., Frye, C., Boucher, T., Wolff, N.H., Breyer, S., Wright, D., Martin, M., Butler, K., Van Graafeiland, K., Touval, J., Sotomayor, L., McGowan, J., Game, E.T., Possingham, H., 2020. An assessment of the representation of ecosystem in global protected areas using new maps of world climate regions and world ecosystem. *Glob. Ecol. Conserv.* 21, 1–21. doi:10.1016/j.gecco.2019.e00860.
- Schneider, C., Cruaud, C., D'Haese, C.A., 2011. Unexpected diversity in Neelipleona revealed by molecular phylogeny approach (Hexapoda, Collembola). *Soil Org* 83, 383–398.
- Sengupta, S., Ergon, T., Leinaas, H.P., 2016. Genotypic differences in embryonic life history traits of *Folsomia quadrioculata* (Collembola: Isotomidae) across a wide geographical range. *Ecol. Entomol.* 41, 72–84. doi:10.1111/een.12270.
- Sengupta, S., Ergon, T., Leinaas, H.P., 2017. Thermal plasticity in postembryonic life history traits of a widely distributed Collembola: Effects of macroclimate and microhabitat on genotypic differences. *Ecol. Evol.* 7, 8100–8112. doi:10.1002/ece3.3333.
- Sgrò, C.M., Partridge, L., 2000. Evolutionary Responses of the Life History of Neel-Caught *Drosophila melanogaster* to Two Standard Methods of Laboratory Culture. *Am. Nat.* 156, 341–353. doi:10.1086/303394.
- Sinclair, B.J., 1999. Insect cold tolerance: How many kinds of frozen? *Eur. J. Entomol.* 96, 157–164.
- Sinclair, B.J., Coello Alvarado, L.E., Ferguson, L.V., 2015. An invitation to measure insect cold tolerance: Methods, approaches, and workflow. *J. Therm. Biol.* 53, 180–197. doi:10.1016/j.jtherbio.2015.11.003.
- Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slosbo, S., Dong, Y., Harley, C.D.G., Marshall, D.J., Helmhuth, B.S., Huey, R.B., 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol. Lett.* 19, 1372–1385. doi:10.1111/ele.12686.
- Sinclair, B.J., Vernon, P., Klok, C.J., Chown, S.L., 2003. Insects at low temperatures: An ecological perspective. *Trends Ecol. Evol.* 18, 257–262. doi:10.1016/S0169-5347(03)00014-4.
- Soberón, J., 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* 10, 1115–1123. doi:10.1111/j.1461-0248.2007.01107.x.
- Sørensen, J.G., Holmstrup, M., 2011. Cryoprotective dehydration is widespread in Arctic springtails. *J. Insect Physiol.* 57, 1147–1153. doi:10.1016/j.jinsphys.2011.03.001.
- Stevens, M.I., Greenslade, P., Hogg, I.D., Sunnucks, P., 2006. Southern Hemisphere springtails: could any have survived glaciation of Antarctica? *Mol. Biol.* 23, 874–882. doi:10.1093/molbev/msj073.
- Sunday, J.M., Bates, A.E., Dulvy, N.K., 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* 278, 1823–1830. doi:10.1098/rspb.2010.1295.
- Sunday, J.M., Bates, A.E., Dulvy, N.K., 2012. Thermal tolerance and the global redistribution of animals. *Nat. Clim. Chang.* 2, 686–690. doi:10.1038/nclimate1539.
- Sunday, J.M., Bennett, J.M., Calosi, P., Clusella-Trullas, S., Gravel, S., Hargreaves, A.L., Leiva, F.P., Verberk, W.C.E.P., Olalla-Tárraga, M.A., Morales-Castilla, I., 2019. Thermal tolerance patterns across latitude and elevation. *Phil. Trans. R. Soc. B* 374, 20190036. doi:10.1098/rstb.2019.0036.
- Terblanche, J.S., Deere, J.A., Clusella-Trullas, S., Janion, C., Chown, S.L., 2007. Critical thermal limits depend on methodological context. *Proc. R. Soc. B Biol. Sci.* 274, 2935–2942. doi:10.1098/rspb.2007.0985.
- Terblanche, J.S., Hoffmann, A.A., Mitchell, K.A., Rako, L., Le Roux, P.C., Chown, S.L., 2011. Ecologically relevant measures of tolerance to potentially lethal temperatures. *J. Exp. Biol.* 214, 3713–3725. doi:10.1242/jeb.061283.
- Toxopeus, J., Sinclair, B.J., 2018. Mechanisms underlying insect freeze tolerance. *Biol. Rev.* 93, 000. doi:10.1111/brv.12425.
- Tüzün, N., Stoks, R., 2018. Evolution of geographic variation in thermal performance curves in the face of climate change and implications for biotic interactions. *Curr. Opin. Insect Sci.* 29, 78–84. doi:10.1016/j.cois.2018.07.004.
- Van der Putten, W.H., 2012. Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts. *Annu. Rev. Ecol. Syst.* 43, 365–383. doi:10.1146/annurev-ecolsys-110411-160423.
- Van Dooremalen, C., Berg, M.P., Eilers, J., 2013. Acclimation responses to temperature vary with vertical stratification: implications for vulnerability of soil-dwelling species to extreme temperature events. *Glob. Chang. Biol.* 19, 975–984. doi:10.1111/gcb.12081.
- Van Eck, N.J., Waltman, L., 2010. Software survey: VOSviewer, a computer program for bibliometric mapping. *Scientometrics* 84, 523–538. doi:10.1007/s11192-009-0146-3.
- Vannier, G., 1994. The thermobiological limits of some freezing tolerant insects: the supercooling and thermotupor points. *Acta Oecol* 15, 31–52.
- Vega, G.C., Pertierra, L.R., Olalla-Tárraga, M.A., 2017. MERRAclim, a high-resolution global dataset of remotely sensed bioclimatic variables for ecological modelling. *Sci. Data*, 1700787 doi:10.1038/sdata.2017.78.
- Verheyen, J., Tüzün, N., Stoks, R., 2019. Using natural laboratories to study evolution to global warming: contrasting altitudinal, latitudinal and urbanization gradients. *Curr. Opin. Insect Sci.* 35, 10–19. doi:10.1016/j.cois.2019.06.001.
- Waagner, D., Heckmann, L.H., Malmendal, A., Nielsen, N.C., Holmstrup, M., Bayley, M., 2010. Hsp70 expression and metabolite composition in response to short-term thermal changes in *Folsomia candida* (Collembola). *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 157, 177–183.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395. doi:10.1038/416389a.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van der Putten, W.H., Wall, D.H., 2004. Ecological Linkages Between Aboveground and Belowground Biota. *Science* 304, 1629–1633. doi:10.1126/science.1094875.
- Weiner, W.M., Bedos, A., Deharveng, L., 2009. Espèces du genre *Friezea* (Collembola, Neanuridae) de Nouvelle-Calédonie et du Vanuatu. *Zoosystema* 31, 507–518. doi:10.5252/z2009n3a8.
- White, C.R., Marshall, D.J., Chown, S.L., Clusella-Trullas, S., Portugal, S.J., Franklin, C.E., Seebacher, F., 2021. Geographical bias in physiological data limits predictions of global change impacts. *Funct. Ecol.* 00, 1–7. doi:10.1111/1365-2435.13807.
- Willmer, P.G., 1982. Microclimate and the environmental physiology of insects. *Adv. Insect Physiol.* 16, 1–57. doi:10.1016/S0065-2806(08)60151-4.
- Wilson, P.W., Heneghan, A.F., Haymet, A.D.J., 2003. Ice nucleation in nature: Supercooling point (SCP) measurements and the role of heterogeneous nucleation. *Cryobiology* 46, 88–98. doi:10.1016/S0011-2240(02)00182-7.
- Worland, M.R., 2005. Factors that influence freezing in the sub-Antarctic springtail *Tullbergia antarctica*. *J. Insect Physiol.* 51, 881–894. doi:10.1016/j.jinsphys.2005.04.004.
- Worland, M.R., Grubor-Lajsic, G., Montiel, P.O., 1998. Partial desiccation induced by sub-zero temperatures as a component of the survival strategy of the Arctic collembolan *Onychiurus arcticus* (Tullberg). *J. Insect Physiol.* 44, 211–219. doi:10.1016/S0022-1910(97)00166-2.
- Yin, R., Gruss, I., Eisenhauer, N., Kardol, P., Thakur, M.P., Schmidt, A., Xu, Z., Siebert, J., Zhang, C., Wu, G.L., Schädler, M., 2019. Land use modulates the effects of climate change on density but not community composition of Collembola. *Soil Biol. Biochem.* 138, 107598. doi:10.1016/j.soilbio.2019.107598.
- Zachariassen, K.E., 1985. Physiology of cold tolerance in insects. *Am. J. Physiol.* 65, 799–832. doi:10.1152/physrev.1985.65.4.799.
- Zeppelini, D., Bellini, B.C., Creão-Duarte, A.J., Hernández, M.I.M., 2009. Collembola as bioindicators of restoration in mined sand dunes of Northeastern Brazil. *Biodivers. Conserv.* 18, 1161–1170. doi:10.1007/s10531-008-9505-2.