Warming shifts the biomass distribution of soil microarthropod communities

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ABSTRACT

Climate warming is often more detrimental to large body sized organisms than small body sized organisms. Yet, how such differential effects of warming at organismal levels affect aggregate community properties, such as community biomass, remains little understood. Here, using geothermally warmed sub-Arctic grassland soils, we investigate how total biomass (product of density and individual body mass) of two major groups of soil microarthropods (Collembola and mites), which are composed of both large and small body sized species, shift in warmed soils when warmed by ~3–~6 °C. Our results show that total biomass of Collembola significantly decreased in warmed soils predominantly due to a decline in the density of large body sized species. In contrast, total mite biomass showed a unimodal response to warming. As a result, there was a shift towards mite biomass dominated microarthropod communities in warmed soils. Within Collembola, the deep soil living eu-edaphic functional group declined the most in total biomass, whereas the unimodal response in mites was most pronounced in oribatid mites. Our study highlights that warming induced shifts in total community biomass of soil microarthropods are likely due to greater detrimental effects of warming on several large body sized Collembola.

1. Introduction

Climate warming restructures ecological communities by altering the ecology and evolution of organisms (Ohlberger, 2013; Rangel et al., 2018; Urban et al., 2016). A large body of theoretical and empirical work suggests that climate warming usually favours small body sized ectotherms more than large body sized ones (Gardner et al., 2011; Sheridan and Bickford, 2011; Thakur et al., 2017; Tseng et al., 2018). Consequently, biomass distribution within animal communities can change in warmer environments, which can alter ecosystem stability (Pennekamp et al., 2018; Schwarz et al., 2017; Yvon-Durocher et al., 2015). Due to the temperature induced increase of the metabolic rate of organisms proportional to their body size (Brown et al., 2004), it is assumed that the energetic deficiency in large body sized organisms is reached faster than in small body sized organisms as the environment warms (Ohlberger, 2013; Thakur, 2020; Vucic-Pestic et al., 2011). Higher energetic deficiency at warmer temperatures lowers fitness and increases the mortality risk in organisms (Huey et al., 2012; Peralta-Maraver and Rezende, 2021). Yet, many studies also show that warming does not always favour small body sized organisms, and

ecological contexts, such as the availability of resources, and/or evolutionary contexts may consequently determine the net warming effects on an organism of a given body size (Huey and Kingsolver, 2019; Siepielski et al., 2019; Thakur et al., 2017). Moreover, how variable effects of warming on different body sized organisms scale to community biomass is still little known particularly in soil ecosystems.

Soils are among the most biodiverse terrestrial habitats containing organisms that vary by orders of magnitude in their body size, ranging from soil bacteria (few μm) to earthworms (thousands of μm) (Decaëns, 2010; Orgiazzi et al., 2016; Thakur et al., 2020). Several taxonomic groups in soils also overlap in body sizes (Decaëns, 2010). For instance, soil microarthropods, that are primarily composed of two taxonomic groups, mites and Collembola, exhibit both overlap and differences in their body sizes (Coleman et al., 2018; Decaëns, 2010). Mites and Collembola are usually in the range of 0.1 mm–3 mm in body length (Decaëns, 2010). These two microarthropods facilitate the decomposition of soil organic matter predominantly through fungal feeding (Orgiazzi et al., 2016; Seastedt, 1984; Soong and Nielsen, 2016). Despite some of their functional similarities, Collembola and mites exhibit numerous differences in their ecology (Coleman et al., 2018; Lindberg

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and Bengtsson, 2005). It is well known that many collembolan species differ in terms of their occupancy of various soil depths (Berg et al., 1998; Hopkin, 1997). For instance, some collembolans are surface-dwellers (epigeic or epi-edaphic), whereas some are found on the sub-surface (hemi-edaphic), and there are those that live deeper in the soil (eu-edaphic). While mite distribution in soils may also vary across soil depths, most soil mites are hemi-edaphic (Wallwork, 1967).

Soil mites are usually classified into four main groups primarily based on their feeding habits (Coleman et al., 2018): oribatid, prostigmatic, mesostigmatic, and astigmatic mites. Among many ecological differences in these four mite groups, a notable difference lies in their feeding behaviour: prostigmatic and mesostigmatic (or gamasid) mites are predatory and parasitic, whereas oribatid and astigmatic are microbial feeders, fungi being their main diet (Coleman et al., 2018; Wallwork, 1967). Recent advances in feeding assessment, such as through stable isotope techniques, also suggest that groups like astigmatic and prostigmatic mites can have omnivory feeding habits (Potapov et al., 2022). Among the four mite groups, oribatid mites are the most abundant ones, and they feed on a broad range of microbial diets when compared to astigmatic mites (Coleman et al., 2018; Walter and Proctor, 2013). Furthermore, given the vast diversity of oribatid mites, they can also be classified into various distinct feeding groups, such as lichen feeders as well as predators (Potapov et al., 2022). Predatory mites feed on other mites as well as on several Collembola and nematode species (Koehler, 1999). Collembola and microbial-feeding mites can further compete for fungal resources, particularly in frequently disturbed habitats (Maraun et al., 2003; Thakur and Geisen, 2019). Taken together, Collembola and mites represent a vast range of soil invertebrate biodiversity and exhibit a variety of biotic interactions, including predation and competition in the soil, while Collembola further showing variation in their spatial distribution. As such, the simultaneous responses of these two microarthropod groups to climate warming can provide important insights into how soil invertebrate biodiversity may change in a warmer world and further help provide insights into how co-occurring soil organisms of variable body sizes may respond to climate warming.

Warming-induced size-specific responses in Collembola and mites have been shown to vary in laboratory studies. For instance, the total biomass of Collembola decreased at higher temperatures when moisture was not a limiting factor, whereas mite biomass increased in warmed and moist conditions (Lang et al., 2014). Such a decline in total Collembola biomass in warmed environments was only true in the presence of predatory mites (Lang et al., 2014). An increase in relatively small body sized Collembola was also reported in a field study with several years of warming (Holmstrup et al., 2018). Interestingly, smaller body sized mites (body length less than 0.2 mm) were reported to increase in drier soil environments compared to larger mites (body length larger than 0.4 mm) in an open top-chamber experiment (Xu et al., 2012). Indeed, warming effects on soil invertebrates may very well depend on how warm temperature affects the soil water availability (Thakur et al., 2018; Vestergård et al., 2015), as soil water determines both microbial resource availability and their accessibility to Collembola and mites in soils (Chauvat et al., 2014; Thakur et al., 2020). Variation in soil water availability at different soil depths is therefore likely to differentially affect Collembola inhabiting different soil depths even by the same level of warming. Within Collembola, those living on the surface (epigeic) can have a greater capacity to acclimate to fluctuations in temperature and perhaps, therefore, may respond lesser to warming compared to those living deeper in the soil (eu-edaphic), given their habitats are thermally more stable (Holmstrup et al., 2018; van Dooremalen et al., 2013). Within mites, warmer environments can further negatively affect predatory groups (also occasionally larger in body size than their prey) as they are often more sensitive to disturbance, such as through direct physiological stress or indirectly through soil water deficiency in warmed soil environments (Thakur, 2020; Tsiafouli et al., 2015).

In this study, we investigate whether warming can restructure soil microarthropod communities by differentially affecting specific groups of Collembola and mites. We study Collembola responses for species residing at different soil depths (epigeic, hemi-edaphic, and eu-edaphic), whereas mite responses are studied for four major groups of mites (astigmatid, oribatid, gamasid and prostigmatid). By estimating the total biomass of these groups in warmed environments, we test the following hypotheses: 1) warming would decrease the total biomass of both Collembola and mites by reducing the density of large body sized organisms, presumably due to their higher metabolic demands and lower thermal tolerance than small body sized organisms, 2) the biomass of eu-edaphic Collembola (those living inside the soil) would decrease the most in warmed soil environments given their greater vulnerability to warming as they are least exposed to warming compared to epigeic and hemi-edaphic Collembola, and 3) Prostigmatic and gamasid mites would suffer the most from warming given their predatory behaviour.

2. Material & methods

2.1. Field site

The study was conducted at the ForHot research site (Sigurdsson et al., 2016), which is located in the Hengill geothermal area, 40 km east of Reykjavik, Iceland (64°00 N, 21°17 W; 100–225 m a.s.l.). The dominant soil type in this area is Silandic Andosols. The mean annual temperature between 2004 and 2017 in the nearby village of Eyrarbakki was 5.2 °C, and the mean temperature of the warmest and coldest months, July, and December were 12.2 °C and −0.1 °C, respectively. The mean annual precipitation during the same period was 1431 mm (Icelandic Meteorological Office). The main vegetation type at the ForHot research site is unmanaged grassland, dominated by *Agrostris capillaris*, *Ranunculus acris* and *Equisetum pratense*.

This grassland (Short term Warming Grassland, SWG) had been warmed since the May 29, 2008, when a large earthquake shifted geothermal systems to previously un-warmed soils (Sigurdsson et al., 2016). Within this site, two different heat sources (so-called "hotspots") were formed (see Fig. S1). Soil warming in the study plots was caused by heat conduction from the underlying bedrock that was warmed from within by hot groundwater. The soil warming increment remained relatively constant throughout the year as soil temperature at 10 cm depth (Ts) changed to a similar degree, with seasonal fluctuations of Ts at all warming levels. While geothermal warming is indeed a geographically limited phenomenon, it is also one of the only ways soil can be warmed naturally without using artificial heating methods (buried warming cables, infrared heating from above, passive night-time heating) (Sigurdsson et al., 2016). Further details of the study site have been described elsewhere (Holmstrup et al., 2018; Sigurdsson et al., 2016).

2.2. Experimental design

An overview of the study area is shown in Fig. S1. In October 2012, five replicate transects radiating from the hotspots were established. At the SWG site, transects 1–3 covered an area of about 40 m × 40 m, and approximately 500 m from transects 4–5 that covered an area of 50 m × 30 m (Fig. S1). At each transect, we selected three Ts levels consisting of un-warmed (or ambient) soil and two warming levels (intermediate and high warming). Plot-specific Ts (plot details are provided below) were recorded with HOBO TidbiT v2 Water Temperature Data Loggers (Onset Computer Corporation, USA) on an hourly basis at 10 cm soil depth for the entire period of soil sampling. The plot-specific temperature data for the two-year period of time (2017–2018) within which four soil samplings were performed revealed a gradient of soil warming: ambient, ambient +2.5 °C (intermediate warming) and ambient +5.7 °C (high warming) based on the mean of all hourly measurements (Fig. S2). Indeed, there were some variations in the monthly average temperatures in the months (see below for the exact dates) when soil samples were

taken (Fig. S2), but still, the gradient remained similar throughout the study with intermediate and high warming relative to ambient soil temperature (Fig. S2). A 2 m × 2 m permanent measurement plot was established within these warmer sites, accompanied by a 0.5 m × 0.5 m subplot for destructive measurements in which the soil cores for microarthropods were taken. The transects represented five similar temperature gradients running either uphill or downhill from the heat sources. Due to the small body size and relatively low mobility of microarthropods (Bengtsson et al., 1994), we judge the field plots to be sufficiently large to avoid noteworthy emi- or immigration and edge effects from neighbouring plots of different temperatures.

2.3. Sampling of microarthropods

Microarthropods were sampled on four occasions (August 28, 2017; November 29, 2017; April 17, 2018; June 19, 2018) using a cylindrical soil corer with an inner diameter of 6 cm and a depth of 10 cm. One soil core was sampled from each plot at each sampling time. Multiple sampling times allowed us to evaluate the robustness of warming effects across time points that have different ambient soil temperatures (Fig. S2). The cores were kept in closed plastic cylinders at 5 °C until extraction, which was initiated within one week after collection. Microarthropods were extracted in a high gradient extraction apparatus (MacFadyen type), where the temperature in the upper compartment increased stepwise from 25 °C to 50 °C within seven days while the temperature at the lower compartment remained constant at 3 °C (Krogh and Pedersen, 1997). If the soil cores had not dried after seven days, the extraction was continued until dryness was attained. The microarthropods were collected in benzoic acid and subsequently conserved and stored in glycerol until identification. Collembolans were identified and counted to species or genus level according to Fjellberg (Fjellberg, 1998, 2007), whereas mites were identified and counted to four major groups, i.e., Gamasida, Astigmata, Prostigmata and Oribatida. Within Oribatida, we were further able to identify specimens to three species and five different families (Supplementary Table S1). Collembola taxa were assigned to the life forms "eu-edaphic", hemi-edaphic", or "epedaphic or epigeic", as described in Holmstrup et al. (2018). For each species or taxonomic group, we measured the body length of 20 randomly chosen adult specimens using an eyepiece micrometre at 60 × magnification (to the nearest 0.1 mm), although this was only possible for species or groups for which more than ca. 40 individuals were found. We then estimated the taxon-specific mean body dry mass using published length-dry mass relationships (Mercer et al., 2001; Petersen, 1975). If such data did not exist, we used length-dry mass relationships of species with the same body shape and size, which were also done for species/groups that were rare (less than 40 individuals) in our samples. The list of all species and/or taxonomic groups, along with their respective functional groups, is provided in Supplementary Table S1. The total biomass of Collembola and mites and their respective functional group was calculated by multiplying their density by mean dry mass and is expressed as mg dry mass m^{-2} (i.e., using the multiplicative factor of the area of our soil cores: diameter 0.06 m; 0.00283 m^2).

2.4. Data analysis

Collembola and mite biomass responses were analysed using mixed-effects models with warming as a fixed effect (three levels) and the sampling period as a random intercept (four time points). Moreover, we examined warming effects on Collembola and mite biomass as a linear or as a quadratic regression. The use of quadratic regression allowed us to examine if there were any unimodal (or non-linear) biomass responses to warming. We report the results of both linear and quadratic models and provide log-likelihood information to illustrate the model fit. Models with a greater log-likelihood value were considered as a better model fit given the data. Some of the biomass responses were log-transformed (indicated in the result section) to meet the regression

assumptions - mainly the linear relationship (homoscedasticity) and the homogeneity of variance. We also report the density responses of Collembola and mites using the same modelling approach as for the biomass data. Since there was no overdispersion in any of the density responses, we ran mixed-effect models with Gaussian error terms and log-transformed some of the density data to meet the linearity and homogeneity of variance assumptions. All mixed-effects models were run with the lme4 package (Bates et al., 2015) in R statistical software version 4.1.0 (R Core Team, 2021). We estimated F- and p-values for each mixed-effect model using Satterthwaite's method with the lmerTest package (Kuznetsova et al., 2017). We also estimated the conditional R^2 for each mixed-effects model using the MuMIn package (Barton, 2020). All figures were drawn using the ggplot2 package (Wickham, 2016). Model assumptions were tested using the performance package (Lüdecke et al., 2021), whereas overdispersion in density data was tested using the DHARMa package (Hartig, 2021).

3. Results

Geothermal soil warming in our study sites significantly altered total biomass of both Collembola and mite communities. We found a strong decline in total biomass of Collembola with increasing temperature, whereas total mite biomass showed a unimodal pattern where the peak mite biomass occurred at the intermediately warmed soil (Fig. 1 A, Table 1). Similar to biomass responses, there was also a decline in Collembola density in the warmest soil, however, we found no significant change in total mite density as observed for total mite biomass (Supplementary Table S1). The relative biomass of Collembola (total biomass of Collembola divided by total biomass of mites and Collembola together) further seemed to decline with warming, whereas the relative biomass of mites (total biomass of mites divided by total biomass of mites and Collembola together) increased in warmer soils (Fig. 1 B, Table 1).

Among the three groups of Collembola, total biomass of deep-soil living eu-edaphic species decreased the most with warming (Fig. 2), which was also true for the density of eu-edaphic species (Supplementary Table S2). We further found a unimodal response both in biomass and density of sub-surface living (hemi-edaphic) Collembola species to warming (Fig. 2, Table 1, Supplementary Table S2). Warming effects on total biomass and total density of surface-dwelling (epigeic) Collembola were negligible (Fig. 2, Table 1). Among the four groups of mites, the only effect of geothermal warming was observed for oribatid mites, which also showed a unimodal response to geothermal warming in our study sites, which was true for both their density and total biomass (Fig. 3, Table 1, Supplementary Table S2).

4. Discussion

Effects of warmer temperatures have been shown to alter the biomass structure of ecological communities, and often these results have relied on aboveground and aquatic ecosystems (Tanentzap et al., 2020; Wu et al., 2019), and with focal species that vary by a large gradient in their body sizes (e.g., several folds) (Bideault et al., 2021; Junker et al., 2016). From naturally warmed soils in our study, we have shown that the biomass distribution may also change in soil communities comprised of two major taxonomic groups (Collembola and mites) that both overlap and vary in their body size. Notably, our first hypothesis that total microarthropod biomass would decrease in warmer soils could only be confirmed with Collembola, whereas mite biomass responses to warming were unimodal. That is, total mite biomass peaked at intermediately warmed soils and then declined in the warmest soils used in our study. This led to a relative increase in total mite biomass over Collembola biomass, suggesting that some soils, when warmed can become mite-dominated (at least in terms of biomass), which can have implications for soil food web stability and functions. The biomass response in Collembola was driven mainly by the dominant eu-edaphic species,
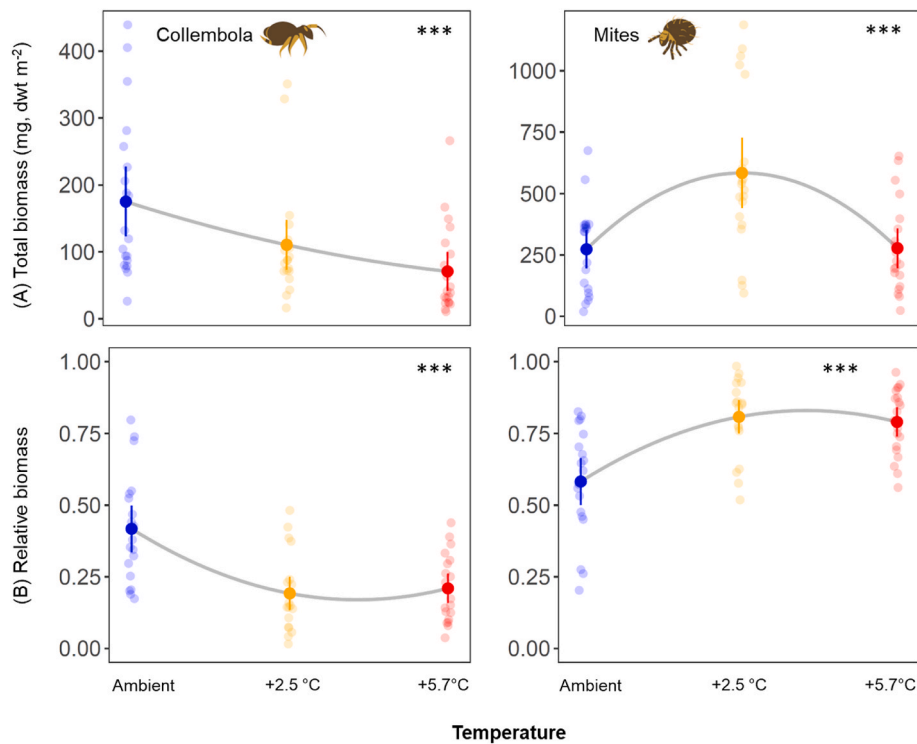
Fig. 1. (A): Warming effects on total Collembola and total mite biomass **(B):** Warming effects on relative Collembola and relative mite biomass. The raw data are shown through light-coloured dots, whereas dark-coloured dots represent mean values with a ($\pm$) standard error. The grey lines are smooth splines drawn using the ggplot2 package. *** sign indicates p-value<0.001.

Table 1

Linear and quadratic effects of geothermal warming on Collembola and mite biomass. The numbers in bold are statistically significant (p-value<0.05). The conditional R^2 is based on the combined warming (fixed) and sampling time (random intercept) effects. Model comparisons between linear and quadratic models are based on log-likelihood scores. Models with a higher log-likelihood score are considered a better model fit given the data.

Collembola	Warming (Linear)				Warming (Quadratic)				Better model
	F-value$_{df}$	p-value	R^2 conditional	log-likelihood	F-value$_{df}$	p-value	R^2 conditional	log-likelihood	
Total biomass	**18.27$_{1,55}$**	**<0.001**	**0.46**	−426.17	**18.27$_{2,54}$**	**<0.001**	**0.46**	−425.99	No difference
Relative biomass (to mite biomass)	**23.45$_{1,55}$**	**<0.001**	**0.45**	31.72	**20.84$_{1,54}$**	**<0.001**	**0.55**	37.77	Quadratic
Epigeic biomass	<0.01$_{1,55}$	0.96	0.27	−266.57	0.09$_{2,54}$	0.9	0.27	−266.47	No difference
Hemi-edaphic biomass (log-transformed)	3.59$_{1,55}$	0.06	0.33	−100.70	**7.75$_{2,54}$**	**<0.01**	**0.44**	−95.41	Quadratic
Eu-edaphic biomass	**25.63$_{1,55}$**	**<0.001**	**0.34**	−419.33	**15.03$_{2,54}$**	**<0.001**	**0.37**	−417.65	No difference
Mites									
Total biomass	<0.01$_{1,55}$	0.95	0.16	−497.35	**14.03$_{2,54}$**	**<0.001**	**0.44**	−408.78	Quadratic
Relative biomass (to Collembola biomass)	**23.45$_{1,55}$**	**<0.001**	**0.45**	31.72	**20.84$_{1,54}$**	**<0.001**	**0.55**	37.77	Quadratic
Astigmata biomass (log-transformed)	1.03$_{1,55}$	0.31	0.06	−71.38	3.00$_{2,54}$	0.05	0.13	−68.95	No difference
Gamasida biomass	2.30$_{1,55}$	0.13	0.24	−436.74	2.65$_{2,54}$	0.07	0.28	−435.27	No difference
Oribatida biomass	0.40$_{1,55}$	0.52	0.05	−487.41	**14.35$_{2,54}$**	**<0.001**	**0.37**	−475.68	Quadratic
Prostigmata biomass (log-transformed)	2.18$_{1,55}$	0.14	0.22	−78.11	1.10$_{2,54}$	0.33	0.22	−78.08	No difference

which confirms our second hypothesis. By contrast, we could not confirm the third hypothesis as we found no warming-induced vulnerability in predatory mite groups. Instead, the unimodal response in mites was driven by oribatid mites, which are predominantly fungal feeders.

Shifts in biomass distribution due to warming often depend on how the density of large and small body sized organisms change at higher temperatures (Brose et al., 2012; Yvon-Durocher et al., 2011). Indeed, this was the case for Collembola species in our study more so than in mite groups (Supplementary Figs. S3 and S4). Some of the large body sized Collembola species (e.g., *Anurida granaria*, an eu-edaphic species) in our study were lower in density in warmer soils (Supplementary Fig. S3), which could have contributed to an overall decline in total biomass of eu-edaphic Collembola group. Several previous studies

indicate that large body sized organisms, in general decrease in density given their greater vulnerability at a higher temperature, and in turn, communities become dominated by small body sized organisms (Daufresne et al., 2009; Holmstrup et al., 2018; Ohlberger, 2013; Yvon-Durocher et al., 2011). Moreover, several large body sized Collembola are susceptible to soil drying due to warming, as revealed by a field study (Yin et al., 2019a). Small body sized organisms can exploit warmer environments better owing to their faster developmental rates and higher rates of population growth when resource supply does not become limiting at higher temperatures (Brown et al., 2004; Thakur, 2020). However, recent studies also highlight that body size alone may not explain the thermal sensitivity of organisms, and it ultimately would depend on their thermal plasticity, which may not always be a function
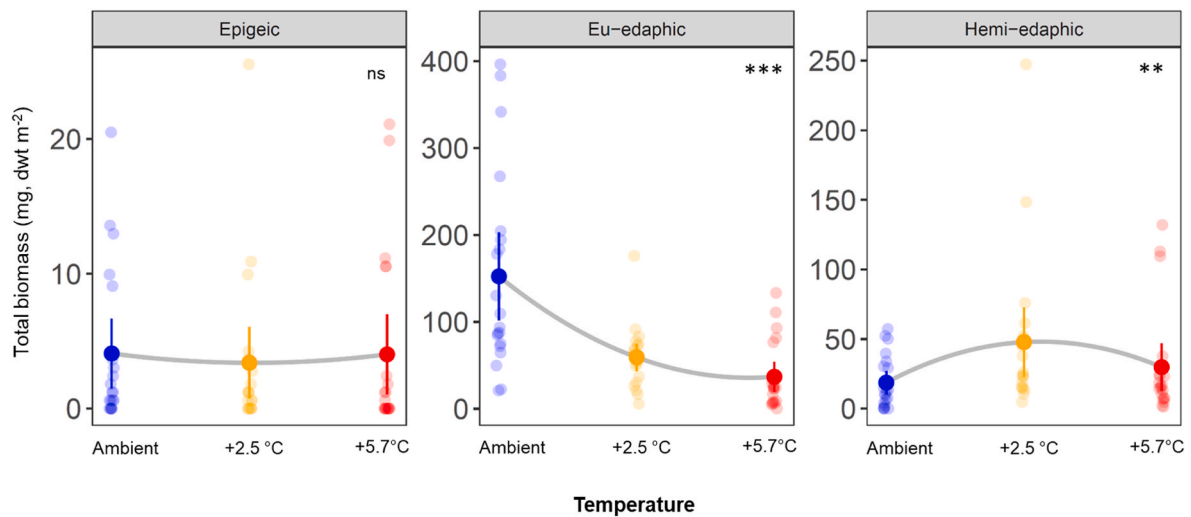
Fig. 2. Warming effects on three groups of Collembola. The raw data are shown through light-coloured dots, whereas dark-coloured dots represent mean values with a (±) standard error. The grey lines are smooth splines drawn using the ggplot2 package. ns stands for not significant (p-value<0.05), ** sign indicates p-value<0.01, *** sign indicates p-value<0.001.

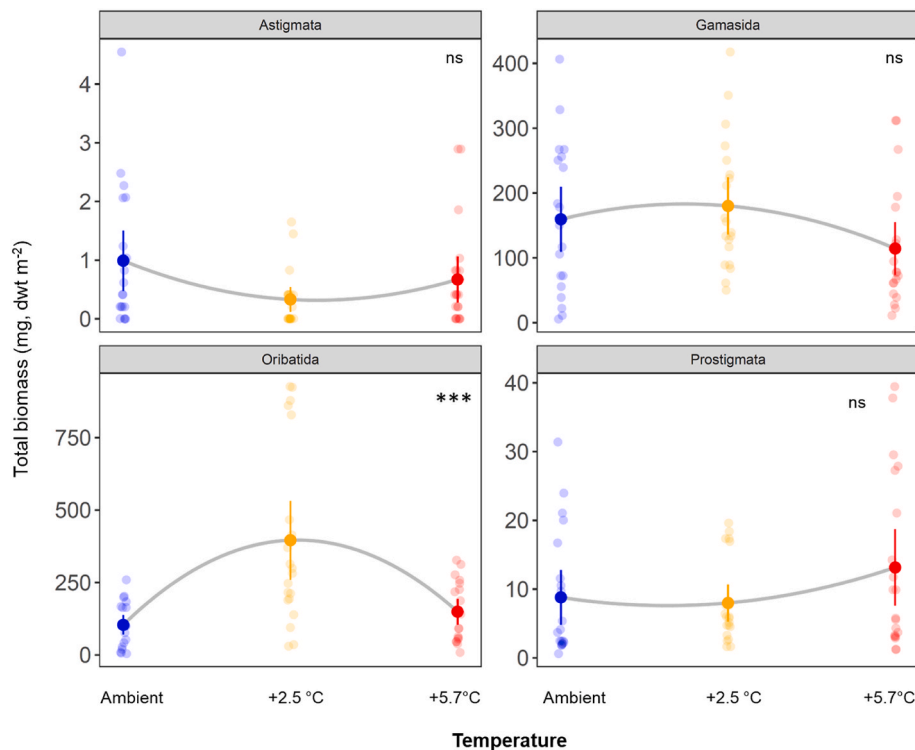**Fig. 3.** Warming effects on four groups of mites. The raw data are shown through light-coloured dots, whereas dark-coloured dots represent mean values with a (±) standard error. The grey lines are smooth splines drawn using the ggplot2 package. ns stands for not significant (p-value<0.05); *** sign indicates p-value<0.001.

of body size (Siepielski et al., 2019; Thakur et al., 2017; Thakur et al., 2021). For instance, a large body sized Collembola species was shown to be thermally more plastic than another Collembola species half its body size at a higher temperature in an experimental study (Thakur et al., 2017). While we did not examine thermal plasticity or acclimation in Collembola or mites in this study, shifts in microarthropod biomass due to responses in specific groups of Collembola and mites do indicate that warming effects on a given community could depend on their lifestyle, such as soil habitat of Collembola and feeding habit of mites. These findings are in line with studies advocating that further insights into the understanding of warming-induced shifts in ecological communities

require examining them through the ecological and evolutionary characteristics of organisms (Beever et al., 2017; Nogués-Bravo et al., 2018; Urban et al., 2016).

Deeper soil-living (eu-edaphic) collembolans are most likely to have the least adaptation to higher temperature compared to surface and subsurface living Collembola, which is perhaps the most plausible explanation for the decline in their biomass in warmed soils (van Dooremalen et al., 2013). These results slightly contradict with a previous study that only observed a marginal decrease in the density of eu-edaphic Collembola in geothermally warmed soils (Holmstrup et al., 2018), given that the density-level responses are often associated with total biomass

responses (Yin et al., 2020). However, the study of Holmstrup et al. (2018) was based on a single sampling in autumn, whereas the present study represents four sampling times representing both warm and cold seasons, therefore probably allowing for a more robust conclusion. Another study reported that the density of eu-edaphic Collembola was lower in warmed agricultural soils, but warming effects also occasionally increased them, such as in soils that are highly disturbed (Yin et al., 2019b). Eu-edaphic Collembola was also recently shown to be highly sensitive to shifts in resource quality (Kühn and Ruess, 2021), which could be influenced by warming (Poeplau et al., 2020) thereby triggering the overall negative biomass response in these groups of Collembola. Moreover, shifts in exposure to regular disturbance can change the tolerance in eu-edaphic Collembola, such as through their physiological adjustments along with resource quality and availability (Holmstrup et al., 2018; Thakur, 2020).

Among the various feeding groups of mites, the strong positive response of oribatid mites to moderate warming compared to other groups was surprising, as we expected predatory mites to be more sensitive to higher temperatures. The greater responsiveness of oribatid mites over the other mite groups to warming is consistent with a previous study that also showed a linear increase in the density of oribatid mites in warmer soils (Lindo, 2015). The same study speculated that the greater frequency of asexual reproduction in oribatid mites could be one of the plausible explanations for their increase in warmer environments compared to other mites (Lindo, 2015). Interestingly, warming also favoured an asexual Collembola species over a sexual Collembola species in an experimental study (Thakur et al., 2017). Whether asexual microarthropods gain an advantage over sexual ones in warmer environments remains speculation, however, studies do indicate higher tolerance and plasticity against stresses in organisms that have the asexual mode of reproduction (Browne et al., 1988; Dijkstra et al., 2017; Marty et al., 2022). Moreover, given their broader diet range, oribatid mites may further gain an advantage in warmer soils if warming alters their diet availability and quality through shifts in the microbial community. For instance, a previous study in the same site showed a shift towards mycorrhizal fungi over the free-living saprotrophic fungi due to warming (Radujković et al., 2018). While oribatid mites, in general, prefer saprotrophic fungi more than mycorrhizal fungi, they could potentially switch to other resources like mycorrhizal fungi (Schneider et al., 2004, 2005). The unimodal response of oribatid mites along the warming gradient confirms that warming effects on total biomass could also be non-linear, as often reported for physiological responses to warming, such as observed in thermal performance curves (Rezende and Bozinovic, 2019). Finally, the weak response of other mite groups in our study corresponds to another field study where in fact none of the feeding groups of mites responded to warming in terms of their density (Yin et al., 2019a), potentially due to their greater tolerance to warming-induced soil dryness than many collembolan species (Vestergård et al., 2015). Although given the lower taxonomic resolution of mites compared to Collembola in our study, we are unable to provide a more detailed comparison between mite and collembolan biomass responses based on the variation in their tolerance to warming and dryness.

Climate warming effects on soil ecosystems are gaining greater attention in recent years, given the increasing realization of the high importance of soil biodiversity in maintaining soil ecosystem functions (Bardgett and Van Der Putten, 2014). The current knowledge points out that climate warming can indeed restructure soil communities by often reducing the density of larger invertebrates and favouring the smaller ones (Lindo, 2015; Robinson et al., 2018; Yin et al., 2020), which can shift a balance in how soil organisms contribute to a range of ecosystem functions. Our study points out that such warming-driven shifts in aggregate community properties, such as total biomass, can even occur within soil organisms that are uniquely characterized by both differences and overlaps in body size. Moreover, we show that mites could become dominant in terms of biomass in warmed soils, the implications

for which remain to be examined in soil ecosystems. Our study also has some important limitations - one being that we did not have a direct measurement of the body mass of specimens collected, which could have provided a better insight into thermally plastic species within Collembola and mites. Furthermore, a mechanistic understanding of invertebrate biomass shifts in warmer environments could have been achieved by investigating how warming might have been shifting the resource availability and quality in our study system. Nevertheless, our results highlight that naturally warmed soil environments can have strong consequences for community shifts, mainly through biomass redistribution among the two most common and co-occurring soil invertebrate animal groups.

Data accessibility

All data used in this study can be downloaded from the following link: https://datadryad.org/stash/share/CtGkQs9hSvzaQ9TSCsr29bkOF1CdaBExCvdBSS44gWg

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.

Data availability

Link to access the data used in this study is provided in the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108894.

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