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Population resistance and recovery after an extreme heat event are explained by thermal effects on life-history traits

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Extreme heat events lower the fitness of organisms by inducing physiological stress and increasing metabolic costs. Yet, little is known about the role of life-history traits in elucidating population responses to extreme heat events. Here, we used a trait-based approach to understand population resistance and recovery using four closely related species of soil-dwelling Collembola. We measured thermal reaction norms of life-history traits (survival and reproductive traits) and used this information to identify ecological mechanisms linked to population responses after an extreme heat event (i.e. one week at 26–30°C, representing + 10°C above ambient conditions). Furthermore, we investigated potential shifts in the body size distribution of recovering populations to better understand if extreme heat events can restructure body size spectra within populations. While resistance remained unaltered across species in our study, the recovery response of the most heat-sensitive species (*Protaphorura pseudovanderdrifti*, predominantly a boreal species) was strongly affected by the extreme heat event (−54% population change compared to ambient conditions). Given that the fecundity (linked to recovery) of *P. pseudovanderdrifti* was more sensitive to heat than their survival (linked to resistance), we detected a decoupling between population resistance and recovery to an extreme heat event in this species. In addition, the detrimental effects of heat on fecundity were largely responsible for a drop in the proportion of small-sized (juvenile) individuals in the recovering populations of *P. pseudovanderdrifti*. Thermally insensitive resistance and recovery in the other three species (*P. armata*, *P. fimata*, *P. tricampata*; predominantly temperate species) can be explained by their high survival and fecundity at warmer temperatures. We highlight that life-history trait responses to warming can help explain population resistance and recovery after extreme heat events.

Keywords: body size, climate change, fecundity, functional traits, survival

Introduction

Climate extremes are getting more frequent as a result of anthropogenic global warming, with detrimental consequences for biodiversity (Meehl and Tebaldi 2004, Christidis et al. 2015, Buckley and Huey 2016, IPCC 2021). Extreme heat events,

in particular, compromise the fitness of organisms as a result of severe physiological stress (Harvey et al. 2020, Ma et al. 2020, Thakur et al. 2022) and increased metabolic costs (Gillooly et al. 2001, Dillon et al. 2010). Ectothermic animals are especially vulnerable to extreme heat events as their body temperatures get pushed towards their upper critical thermal limits (Deutsch et al. 2008, Buckley and Huey 2016), potentially triggering large ecological responses (Harris et al. 2018). These responses are composed of both the magnitude of the impact on a species, reflected in an initial reduction of its population size (also known as resistance) and the ability of that species to return to a reference state – such as the population size in absence of disturbance (also known as recovery; Hillebrand et al. 2018). While recent syntheses have shown that several species usually return close to their reference population levels after pulse disturbances, including extreme heat events, we still know little about when and how do species recover (Hillebrand and Kunze 2020, Neilson et al. 2020), and whether population resistance can predict recovery (Isbell et al. 2015, Capdevila et al. 2022, Thakur et al. 2022). Establishing links between resistance and recovery can provide a comprehensive picture of how organisms respond to climate extremes, as even if populations may not show an immediate response (i.e. greater resistance), there could be a cost in the longer run, which would be reflected only through studying their recovery over a period of time (Harris et al. 2018, Ma et al. 2020). To this end, we here aim to apply trait-based approaches to better understand population resistance and recovery of various species exposed to extreme heat events (Neilson et al. 2020, Thakur 2020).

Among the suite of traits potentially affected by temperature, life-history traits deserve particular attention since they could directly relate to population-level responses (McLean et al. 2016, Sinclair et al. 2016, Capdevila et al. 2022). These comprise all traits influencing the schedule of the life cycle of an individual ranging from reproduction, growth, and maturation to survival. During extreme heat events, physiological responses to warming can trigger shifts in life-history traits that, in turn, might scale up to higher levels of ecological organization (Harvey et al. 2020). For instance, regular periods of extreme or moderate warming induce small effects on mortality that accumulate over time, thereby triggering population crashes even below critical temperatures (Rezende et al. 2020). Negative impacts at the population level may also emerge from declines in the reproductive output of surviving individuals (Harvey et al. 2020, Ma et al. 2015), as a result of tradeoffs between stress tolerance or avoidance and reproduction (Klockmann et al. 2017, Walsh et al. 2019). Predicting population-level responses to extreme heat events may therefore require the consideration of warming impacts on reproductive traits, given that the thermal ranges of these traits are narrower than those of survival (Rezende and Bozinovic 2019, Walsh et al. 2019, Ma et al. 2020). Indeed, heat-induced shifts in reproductive strategies can arise as a result of altering the number of offspring in each reproductive event (i.e. brood/clutch size), a delay or altered frequency of reproductive events

(e.g. skipping reproduction), or simultaneously affecting both (Forsman 2001). Such effects of heat on reproductive traits will only translate into changes in the population size after a time period necessary for recruitment, which underscores the need to consider this time lag in assessing population recovery (Neilson et al. 2020).

In addition to life-history traits, relationships between population size and trait variation within populations in changing environments can be further linked to functional traits like body size. Warming can trigger changes in the relative abundances of distinct life stages in a population when thermal tolerance differs across stages (Ohlberger 2013), which can be linked to variation in their body sizes (Franken et al. 2018, Peralta-Maraver and Rezende 2021). Across species, it has been shown that smaller organisms could be more tolerant to short periods of extreme heat (e.g. hours or days), whereas larger organisms can endure longer periods of moderate warming (e.g. weeks; Peralta-Maraver and Rezende 2021). Population size structures might also shift in response to warming as a result of altered life-history traits (Gårdmark and Huss 2020). For instance, extreme heat events could induce lowered proportions of small-sized (juvenile) individuals in a population because of detrimental impacts of heat on fecundity. As opposed to the general pattern of body size reductions at higher temperatures (Gardner et al. 2011, Sheridan and Bickford 2011), this mechanism could actually produce greater average body sizes in the short-term response to warming, making it further challenging to predict how heat events affect population size structures.

Population responses to extreme heat events might also be shaped by their biotic environments (Stoks et al. 2017, Boukal et al. 2019). One such biotic environment is predation, which itself is temperature sensitive and a key determinant of prey population dynamics (Rall et al. 2010, Brose et al. 2012, Thakur 2020). Predation can shape prey responses to heat events in various ways, which obscure predictions of resistance and recovery purely on prey traits. For instance, because trophic interactions are often strong when prey are smaller than their predators (Brose et al. 2006, Rall et al. 2012), prey population recovery after extreme heat might be constrained if their body sizes put them at risk of predation, regardless of their thermal sensitivity (Thakur 2020). However, predators could also be more vulnerable to extreme heat than their prey as they often have higher metabolic demands and could easily reach the risk of starvation if prey availability at higher temperatures is low (Fussmann et al. 2014, Huey and Kingsolver 2019). Altogether, how predation can modulate trait-based predictions of prey population responses to extreme heat events remains unclear.

Here, by using two complementary experiments, we aim to apply information obtained from life-history responses to warming to predict population level responses to an extreme heat event. We first measured thermal reaction norms (i.e. phenotypic changes as a function of temperature) of life-history (survival and reproductive traits) and physiological traits (lipid concentration and dry body mass) for one week in four closely related species of Collembola (from the genus

Protaphorura). Collembola are among the largest groups of terrestrial invertebrates (in terms of density and diversity) living in soils (Potapov et al. 2023). This first experiment allows us to build testable hypotheses to predict population-level responses to an extreme heat event (simulating a one-week heat wave) in our second experiment, using the same four study species together with a predator in soil microcosms. We expect that the distinct climatic niches of our four study species (details in Methods section) will underlie differences in their thermal performance, which will then affect their resistance and recovery after the extreme heat event. Specifically, we predict that the population resistance response will reflect thermal effects on survival, whereas the population recovery response will depend on thermal effects on fecundity (i.e. reproductive output). Given that warming induces higher metabolic rates and may therefore reduce organisms' energy reserves (e.g. storage lipids; Meehan et al. 2022), we predict that the lipid concentration of collembolans will decline at higher temperatures, thereafter limiting their population's ability to recover after the extreme heat event. Moreover, since changes in life-history traits affect particular life stages and could subsequently alter the population size structure, we expect that the body size distribution (as a measure of functional trait in our study) will shift in response to extreme heat. More precisely, we predict that changes in the body size distribution in the resistance response will depict size-specific effects on survival, as a result of distinct thermal tolerances across body sizes (e.g. a lower proportion of small-sized individuals will indicate lower survival of juveniles compared to other size stages). In turn, the body size distribution in the recovery response will depict thermal effects on fecundity (e.g. a lower proportion of small-sized individuals will indicate negative impacts on fecundity during the week of extreme heat). Finally, we hypothesize that predation will constrain prey recovery, particularly for prey of smaller size (e.g. juvenile individuals) as they might be more susceptible to predation. Our study offers potential links among life-history, population size and functional trait responses to extreme heat events to help improve our predictions on climate change effects on population resistance and recovery.

Material and methods

Study species

We used four species of the genus *Protaphorura* (Collembola: Onychiuridae): *P. armata*, *P. fimata*, *P. pseudovanderdrifti* and *P. tricampata* (Supporting information). These are sexually reproducing, euedaphic invertebrates (i.e. permanently living in the soil) commonly found in various habitats across Europe (Gisin 1960, Fjellberg 1998). These four closely related species differ markedly in their geographic distributions, which in turn reflect their distinct climatic niches (Supporting information). Specifically, *P. armata* is typically a warm-temperate species; *P. fimata* and *P. tricampata* are cold-temperate

species; and *P. pseudovanderdrifti* is found in boreal and arctic regions at high latitudes (Gisin 1960, Fjellberg 1998). These species further differ in body size (potentially related to predation risk as well as to thermal tolerance; Rall et al. 2012, Franken et al. 2018), with *P. fimata* (mean ± SD body length at the start of the life-history experiment: 1829 ± 233 μm; n = 180) and *P. pseudovanderdrifti* (1698 ± 198 μm; n = 180) being larger species than *P. tricampata* (1487 ± 158 μm; n = 181) and *P. armata* (1373 ± 166 μm; n = 181). Hence, using these four closely related species not only offers a conservative experimental design due to their evolutionary relatedness, but their ecological differences further help to capture important organismal variation to offer some level of generality to understand what underlies the relationship between population resistance and recovery. Therefore, we aimed to capture variation in their population responses when each of the four species are exposed to the same extreme heat event, and link these population responses to their distinct thermal performances.

The origin of the animals that initiated the cultures as well as their local climatic conditions are provided in Table 1 in Xie et al. (2023). All species were reared for several generations (since the time of their collection in the field) in incubators at 20°C and fed with dry yeast before we used them for the experiments (Supporting information). We therefore adopted 20°C as the ambient temperature in our experiments. To recreate typically dark conditions experienced by soil-dwelling collembolans, as those used in our study (Hopkin 1997), we kept all cultures and experiments under constant darkness. Additionally, we measured egg development time (i.e. time from egg laying to hatching) of all four species at the ambient temperature (20°C) of our experiments (Supporting information). Egg development time at 20°C was shorter in *P. fimata* (estimated mean ± SE: 12.7 ± 0.7 days; n = 96), followed by *P. armata* (13.9 ± 0.6 days; n = 145) and *P. pseudovanderdrifti* (14.8 ± 0.7 days; n = 35), and was longest in *P. tricampata* (15.8 ± 0.5 days; n = 55). Based on our own observations as well as developmental times from other Collembola species (Siepel 1994), we estimate that the generation time of the study species at 20°C is around 4–5 weeks.

Experiment 1. Life-history responses to warming

We established experimental units by adding 20 adult individuals into 60 mm petri dishes with a moist substrate of plaster of Paris and activated charcoal (9:1), and measured the body length of ten individuals at 5×. Petri dishes were then exposed to three different temperatures separately: 20, 25 and 30°C. This temperature range spans +10°C from the control conditions, which aims to simulate an extreme heat event as predicted in temperate regions for the next 100 years (CH2018 2018, IPCC 2021). Furthermore, the highest experimental temperature is considerably above the warmest soil temperatures experienced by the four species in their collection sites (Lembrechts et al. 2022, Xie et al. 2023), demonstrating the thermal extremity of our treatments. We

established a total of 72 experimental units: 4 Collembola species × 3 temperature regimes × 6 replicates. Every day for the entire duration of the experiment (i.e. one week), we counted the number of dead animals (i.e. individuals not responding to a tactile stimulus), clutches (i.e. discrete groups made of at least three eggs; further details in Supporting information), and the number of eggs in each clutch. All dead individuals and eggs were removed daily, and food (dry yeast) was provided ad libitum and replaced once during the experimental period to prevent any excessive fungal growth. At the end of the experiment, all living animals (12–20 individuals per plate) were collected and stored in the freezer at −20°C for ten days, before the lipid analysis. Lipid concentration, an indicator for stored energy reserves, was determined with the gravimetric method, adapted from Williams et al. (2011). After being dried at 60°C, animals were transferred to glass vials with 1 ml of analytical chloroform. The chloroform containing dissolved lipids was withdrawn daily and replaced three times to ensure the complete extraction of lipids. Later, the animals were dried again in the oven and weighed to obtain lipid-free dry mass, which was used as a measure of body mass at the end of the experiment. The lipid concentration was then calculated as the weight difference between total dry body mass (with lipids) and lipid-free dry mass, and afterwards divided by total dry body mass. All weight measurements were determined to the nearest 0.001 mg.

Experiment 2. Population response to extreme heat event

We established soil microcosms with monocultures of the same four *Protaphorura* species used above in the life-history experiment, and this time further with a generalist predatory mite, *Stratiolaelaps scimitus* (formerly known as *Hypoaspis miles*), which is known to prey on Collembola (Koehler 1999), even those of similar or greater size as the predator itself (Thakur et al. 2017, 2018). Predatory mites were purchased from Andermatt Biocontrol Suisse AG and acclimated at 20°C for ten days before they were added to the microcosms.

Soil microcosms consisted of polypropylene pots (height: 7.5 cm and diameter: 8 cm) filled with 100 g of commercial soil (3:1 mixture of garden soil and sand; pH = 6.8, C:N ratio = 10.1, organic matter = 10.5%) and 500 mg of hay litter on the surface to provide habitat structure and resources for the soil animals (Klironomos and Kendrick 1995, Kalinkat et al. 2013). Both substrates were sterilized at 121°C (autoclaved), and hay litter was then dried at 50°C for 72 h. To further promote fungal colonization, 20 mg of baker's yeast was added on top of the substrates (the same yeast used in culturing of the four Collembola species), and then incubated for five days at 20°C. After this period, we added 20 adult Collembola individuals of similar body size (based on the measurement of body size for experiment 1) in every microcosm, and those with the predation treatment received six individuals of *S. scimitus* one week later to allow some time for collembolan (prey) populations to establish.

To prevent animal escape from the microcosms, we installed a 90 µm mesh at the bottom and a 5 cm high plastic fence from the top of the microcosm (Supporting information) coated with olive oil around the upper edge of the pots. The experimental populations were thus established and incubated at control conditions from week 1 until week 5, exposed to an extreme heat event on week 6, and were allowed to recover at control conditions from week 7 until week 12, i.e. until the end of the experiment. The length of the recovery period was chosen according to the estimated generation time of the study species at 20°C, as suggested by Neilson et al. (2020). Even though the generation times might differ to some extent across species and temperature regimes (Siepel 1994), our five-week recovery period encompasses at least one full generation time for all four species, and thus manages to capture possible effects of the extreme heat event on their reproduction and recruitment. Further, to add more realism to our temperature regimes in the population dynamics experiment, we adopted a diel temperature cycle (8:00:16:00 h, constant darkness) set at 16–20°C for control conditions, and 26–30°C for the extreme heat treatment. The extreme heat event (+10°C above control conditions) was chosen to simulate a heat wave scenario as described for the life-history experiment. Air temperature and relative humidity were monitored at 30 min intervals throughout the experiment, and soil temperature at 5 cm depth was recorded twice every day during the extreme heat phase to capture the night (measurement at 08.00–10.00 h) and day (measurement at 14.00–18.00 h) soil temperatures. The realised air temperatures during extreme heat were +9.4°C compared to control conditions (mean ± SD, extreme heat: 27.5 ± 2.2°C; control: 18.1 ± 2.2°C), while in the soil this difference reached +8.4°C (extreme heat: 25.4 ± 1.5°C; control: 17.0 ± 1.4°C; Supporting information). As a result of the buffering effect of the soil, the temperature conditions experienced by the animals during extreme heat closely resembled those of the 25°C regime from the life-history experiment.

We measured Collembola densities and body size at three time points: before the extreme heat event (harvest 1, week 5), after the extreme heat event (harvest 2, week 6), and at the end of the experiment (harvest 3, week 12). All treatment combinations and harvests were replicated five times except for the first harvest of *P. pseudovanderdrifti*, which had only four replicates because of the low numbers of animals of this species in our stock cultures. This resulted in a total of 236 experimental units: 4 Collembola species treatments × 2 temperature treatments × 2 predation treatments × 3 harvests × 5 replicates. In each harvest, soil animals were sampled using heat extraction with gradual heating from 25°C up to 55°C for 7 days following the Macfayden extraction method (Macfadyen 1961). All animals were collected in glycol water solution (1:1) and later transferred to 70% ethanol. Counts of Collembola and predatory mites as well as body size measurements of Collembola were performed under a stereomicroscope with high performance camera. For each sample, we measured body length from 20% of the animals

at 20×, with a minimum number of 20 individuals when available. We took measurements at random (i.e. adults and juveniles indiscriminately) with the aim of detecting shifts in the body size distribution triggered by the experimental treatments. This yielded a total of 9480 body size measurements from 42 039 collected Collembola individuals.

Statistical analyses

In the life-history experiment, we tested the effect of temperature, species, and their interaction on survival by means of Cox proportional hazards (R package 'survival', ver. 3.2-13; https://CRAN.R-project.org/package=survival, Therneau, 2021). Given that mortality was negligible at 20°C, we restricted this analysis to the 25 and 30°C temperature regimes. Furthermore, we fitted linear regressions to investigate the effect of the experimental treatments on reproduction (i.e. fecundity, clutch size and egg laying frequency) and physiological variables (i.e. lipid concentration and dry body mass). We did not include the 30°C treatment in the linear models including reproduction-related variables since this temperature regime induced a complete infertility in nearly all study species. Fecundity (i.e. total number of eggs laid over the study period) was analysed with zero-inflated negative binomial models to account for overdispersed and zero-inflated counts (R package 'glmmTMB', ver. 1.1.2.3; https://cran.r-project.org/web/packages/glmmTMB, Brooks et al. 2017). Clutch size (i.e. number of eggs per clutch) and egg-laying frequency (i.e. number of clutches per day) were tested using generalized linear mixed models with negative binomial and Poisson distribution, respectively. In these mixed models, sample ID was added as a random intercept to account for repeated observations during the experimental period. For the physiological variables, we used linear models to analyse lipid concentration, as well as generalized linear models for lipid-free dry body mass (R package 'lme4', ver. 1.1-26; https://cran.r-project.org/web/packages/lme4, Bates et al. 2015). The Gamma distribution was adopted for the latter, given that this variable can only take positive values (Zuur et al. 2009), and because linear models with Gaussian distribution provided higher AIC values and linearity assumptions (e.g. homogeneity of variance) were not met. An overview of all models fitted for the life-history experiment and their structure is provided in the Supporting information.

In the population response experiment, Collembola densities were examined using generalized linear models with negative binomial distribution (R package 'MASS', ver. 7.3-54; https://cran.r-project.org/web/packages/MASS, Venables and Ripley 2002). Fixed effects were species, extreme heat, predation, and the interaction between species and extreme heat. Interactions with predation lacked statistical support and always resulted in higher AIC values, so they were not retained in the final models (Supporting information). In order to examine population responses to extreme heat, we decomposed population responses into two components: resistance and recovery (e.g. Hillebrand et al.

2018). First, we fitted separate models for each sampling time: baseline (harvest 1), resistance (i.e. harvest 2, at the end of the extreme heat), and recovery (i.e. harvest 3, after five weeks, equivalent to the estimated species generation time). We then obtained Cohen's d standardised effect sizes with 95% confidence intervals (CI) using the function eff_size (R package 'emmeans', ver. 1.7.0; https://cran.r-project.org/web/packages/emmeans, Lenth 2021). Cohen's d effect sizes were calculated using differences of estimates between control and extreme heat treatments, divided by the pooled standard deviation (Lenth 2021). This method allowed us to compare means between treatments while adjusting for differences in scale among species (Koricheva et al. 2013). Therefore, Cohen's d immediately after the week of extreme heat (i.e. harvest 2) is considered as resistance in our study, and Cohen's d obtained five weeks after extreme heat (i.e. harvest 3) is a measure of recovery. In addition, we visually explored relationships between population responses to extreme heat by plotting standardised effect sizes of resistance against recovery across the four study species. Finally, we examined the effects of the experimental treatments on the body size distribution with quantile regressions (R package 'lqmm', ver. 1.5.6; https://cran.r-project.org/web/packages/lqmm, Geraci 2014), using sample ID as a random intercept to account for non-independent measurements from individuals of the same population. This method allows estimatation of conditional quantiles of the response distribution (Cade and Noon 2003), enabling us to explore how our treatments might have particular effects across the body size distribution within populations. More specifically, we assessed the response on the 0.1, 0.5, and 0.9 quantiles, which represent small (juveniles), medium (young adults), and large (old adults) individuals of the population (Jørgensen et al. 2008). Linearity assumptions for all linear models from both life-history and population response experiments were tested and visually inspected with the 'DHARMa' package (ver. 0.4.1; https://cran.r-project.org/web/packages/DHARMa, Hartig 2021). We performed post hoc tests to obtain all p-values, using the function $emmeans$ from the package 'emmeans' (Lenth 2023). All statistical analyses were carried out in R statistical software (ver. 4.0.2; www.r-project.org).

Results

Life-history responses to warming

After exposing our study species for one week to one of the three temperature regimes (20, 25 and 30°C), we found that warming affected life-history traits differently across the four species. Survival declined strongly in *Protaphorura pseudovanderdrifti* from 25 to 30°C, with no individuals remaining alive after five days of exposure at 30°C. We detected effects on survival of a moderate magnitude in *P. tricampata* (hazard ratio ± SE: 8.40 ± 5.36; p < 0.001), while no differences in survival between 25 and 30°C were found in *P.

armata and *P. fimata* (Fig. 1). In contrast, the 30°C treatment drastically affected reproduction in all species as barely any eggs were found in this temperature regime, thereby causing a complete infertility across study species (Fig. 2). Focusing on the response of fecundity from 20 to 25°C (Fig. 2), this again depended on the species considered: egg production in *P. pseudovanderdrifti* dropped by 71.9% as a result of a lower frequency of reproductive events, whereas *P. armata* produced 76.6% more eggs at the higher temperature because of an increase in clutch size (Supporting information). Clutch size declined in *P. tricampata* at 25°C (Supporting information), but this did not cause any detectable change in the fecundity of this species (Fig. 2). All reproductive traits remained unaltered in *P. fimata* between 20 and 25°C (Supporting information). Regarding the physiological traits, the lipid concentration in living animals at the end of the one-week study period did not differ across temperature regimes in any of the species, but lipid-free dry body mass declined in all species from 25 to 30°C (Supporting information). Overall, our results suggest that *P. pseudovanderdrifti* is the most heat-sensitive species among the four Collembola species due to its lowest survival at 30°C and fecundity at 25°C, whereas the other three Collembola only ceased their reproduction at 30°C with little effects on their survival. All detailed model outputs are provided in Supporting information.

Population response to an extreme heat event

Population growth was generally slower at the start of the experiment (from H0 to H1), but later increased by the end of the experiment (from H2 to H3), especially in *Protaphorura armata* and *P. fimata* (Fig. 3). One week of an extreme heat event did not affect population resistance responses in any of the four study species (Fig. 3, 4, Supporting information). Later, after a recovery period of one generation time, we detected an incomplete recovery in the most heat-sensitive species, *P. pseudovanderdrifti*, showing a −54% population change in the extreme heat treatment compared to the control

(Fig. 3, Supporting information). We did not detect any significant impacts of extreme heat on the recovery responses of the other three species (Fig. 4, Supporting information). Note that even in the species with the strongest warming-driven decline in fecundity (*P. pseudovanderdrifti*), population growth was positive from H2 to H3 in the extreme heat treatment, but with a much shallower population increase compared to the control treatment.

The body size distribution within the *P. pseudovanderdrifti* population was also not affected during its resistance response, but it shifted during the recovery response (Fig. 5). More specifically, the individuals at the lower end of the distribution (quantile 0.1) were larger in size in the extreme heat treatment within *P. pseudovanderdrifti*, while the sizes at the median (quantile 0.5) and higher end of the distribution (quantile 0.9) were little affected (Fig. 5, Supporting information). The body size distribution did not change for any of the other three Collembola species during both resistance and recovery phases.

Predation did not have any detectable effect on Collembola densities but altered their body size distribution at the baseline harvest, by reducing the number of the largest individuals in the populations for all Collembola species (quantile 0.9; Supporting information). Nonetheless, the effect of predation faded out in subsequent harvests, as predatory mites did not manage to reproduce and persist until the end of the study period (Supporting information). All model outputs are provided in the Supporting information.

Discussion

Our results from two complementary experiments highlight that population responses (i.e. resistance and recovery) to an extreme heat event can to some extent be explained by depicting how life-history traits, namely survival and fecundity, respond to warming. We found that although population resistance was not affected across four species, the recovery
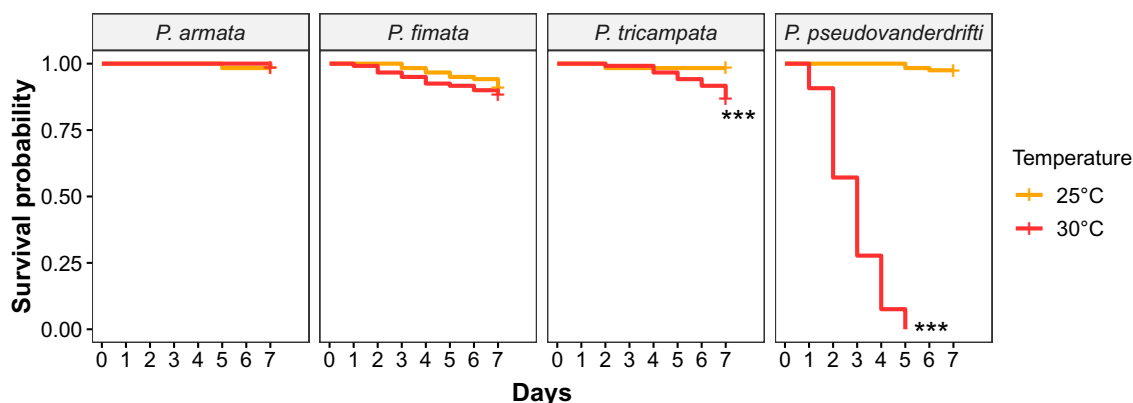

Figure 1. Survival probability as a function of temperature across four study species of *Protaphorura* in the life-history experiment. Survival curves were plotted with the package 'survminer' (ver. 0.4.9; Kassambara et al. 2021). Species are displayed by ranking of heat tolerance, from higher (left side) to lower (right side) tolerance, based on their survival. We present the same order of species in all following figures. Symbols show significant differences between temperature treatments: n.s. p > 0.05, ***p < 0.001.
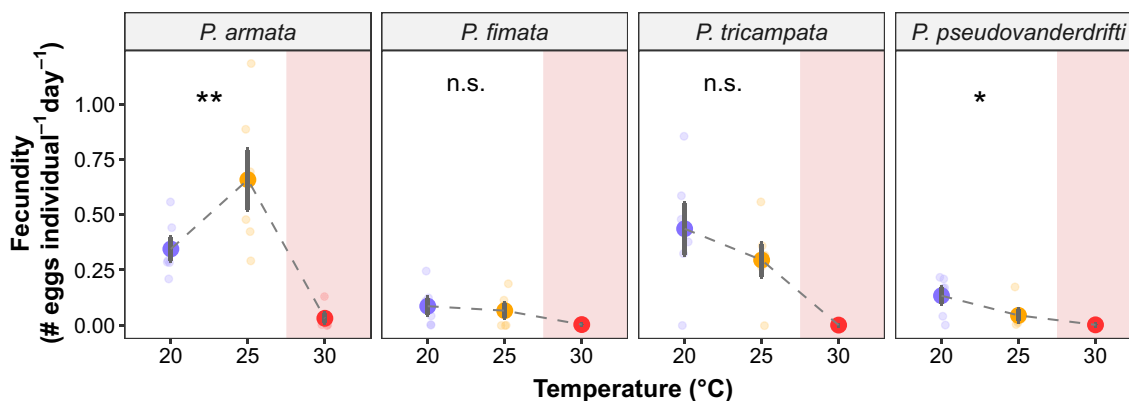
Figure 2. Fecundity as a function of temperature across four study species of *Protaphorura* in the life-history experiment. Solid points represent means, dark solid bars represent standard errors, and faded points are raw data. The red faded area indicates that the 30°C temperature regime was not included in the models because this treatment induced nearly complete infertility across four species. Symbols show significant differences between temperature treatments: n.s. $p > 0.05$, *$p < 0.05$, **$p < 0.01$.

response was negatively affected in the most heat-sensitive species. In contrast, the other three species did not have any detectable recovery response to extreme heat, implying a coupling between their population resistance and recovery after an extreme heat event. The decoupling between population resistance and recovery responses in one of the species, *P. pseudovanderdrifti*, could be linked to thermal effects on its fecundity, which also affected the body size distribution of its recovering populations. More specifically, the detrimental effects of heat on fecundity were most likely responsible for a decline in the number of small (juvenile) individuals within recovering populations of *P. pseudovanderdrifti*. Taken together, our study provides a novel insight by demonstrating trait-based explanations (both life-history and functional traits) for how temperature extremes could impact populations during their recovery.

We found that reproductive traits were consistently more heat sensitive than survival. Indeed, the highest temperature regime of 30°C induced a substantial mortality in *P. pseudovanderdrifti*, whereas in the other three species there were minor or no effects on their survival, which could have contributed to negligible resistance responses to extreme heat. In contrast, the 30°C temperature regime caused near complete infertility across four species, while all species managed to lay eggs at 25°C. Quantitative differences in fecundity across species at 25°C might underlie distinct adaptations to the thermal conditions in their distribution ranges. The species that showed the lowest survival at 30°C, *P. pseudovanderdrifti*, was also the only one that reduced egg production (~70%) from 20 to 25°C, whereas the change in fecundity in the species *P. armata* was of similar magnitude but in the opposite direction (Fig. 2). Remarkably, warming affected fecundity in these two species by altering their reproductive strategies in different ways: egg laying frequency declined in *P. pseudovanderdrifti*, whereas clutch size increased in *P. armata* (Supporting information). In the case of *P. tricampata*
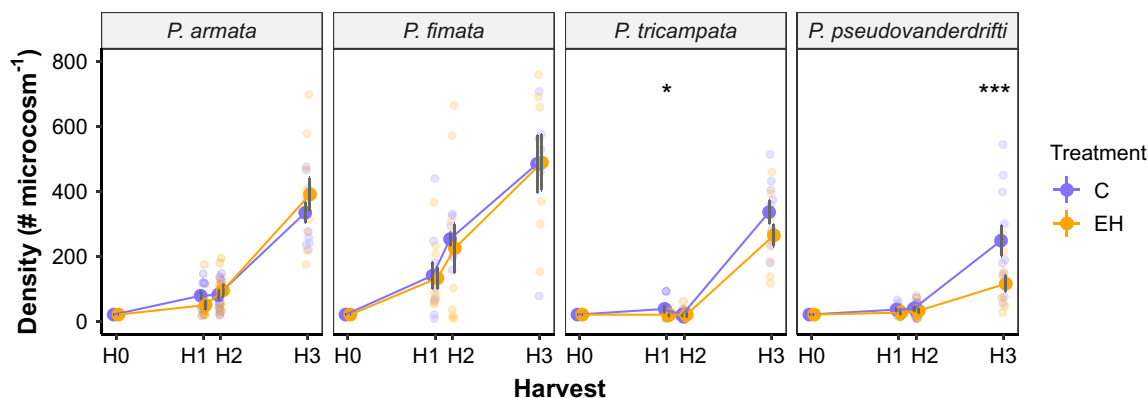

Figure 3. Temporal dynamics of the densities across four study species of *Protaphorura* in the population response experiment. 'Harvest' specifies the different time points in which Collembola densities were assessed during the experiment: H0: start of the experiment; H1: baseline; H2: resistance; H3: recovery. Solid points represent means, dark bars represent standard errors, and faded points are raw data. Note that raw data points for densities above 800 individuals are not displayed for visualisation purposes. Colours indicate different experimental treatments: blue: control (C); orange: extreme heat (EH; +10°C on ambient temperature). Stars show significant differences between treatments: *$p < 0.05$, ***$p < 0.001$.
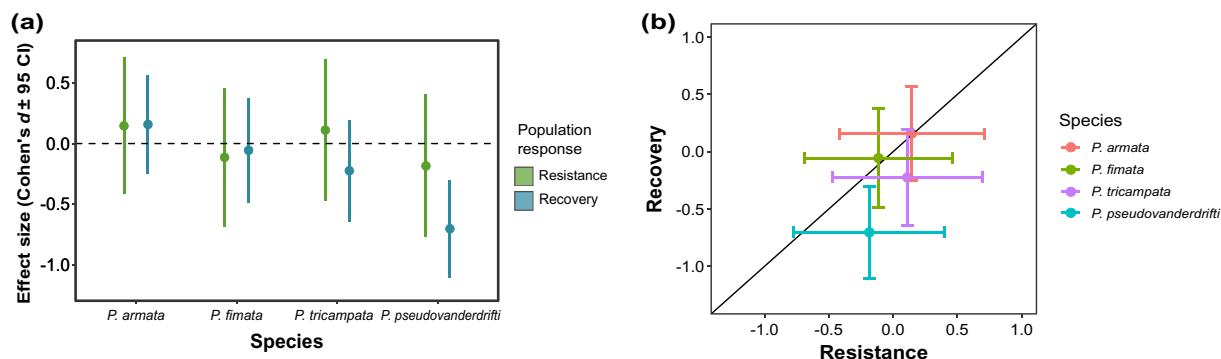
Figure 4. (a) Standardised effect sizes (Cohen's *d*) with 95% confidence intervals (CI) showing the population responses (resistance and resilience) to a one-week extreme heat event in the population response experiment. Confidence intervals crossing zero values (dotted line) are statistically indifferent to zero. Negative values indicate a population decline in response to extreme heat, compared to the control treatment. Colours indicate different population responses: green: resistance; turquoise: recovery. (b) Resistance against recovery response, using standardised effect sizes with 95% CI. The solid diagonal line shows the 1:1 relationship between resistance and recovery. Collembola species are indicated with different colours: red: *Protaphorura armata*; green: *P. fimata*; purple: *P. tricampata*; blue: *P. pseudovanderdrifti*.

and *P. fimata*, our results suggest that their thermal optimum for fecundity might lie between 20 and 25°C, which would explain the apparent lack of fecundity responses in these two species. It has been shown that acute thermal limits vary substantially across the four Collembola species, given the variation in their geographic range, and are related to the warmest soil temperatures found in their natural habitats (Xie et al. 2023). Our results also confirm that variation in thermal performance of ectotherms could depend on their latitudinal origin (Sunday et al. 2011, Sengupta et al. 2017), as species collected from temperate regions (*P. armata*, *P. fimata*, *P. tricampata*) maintained a more constant performance across experimental temperatures than boreal species (*P. pseudovanderdrifti*). It is worth noting that dry body mass declined only at 30°C across species, which indicates that animals were experiencing significant heat stress at this temperature, hindering their growth and development (Mallard et al. 2020). Although collembolans attained lower body masses at 30°C, their lipid concentration remained constant across species in all temperature regimes. We speculate that the organisms' energy reserves in terms of lipid concentration were possibly maintained as a result of downregulating their metabolism (e.g. reduced physiological and/or behavioural activities) at 30°C to avoid further heat stress (Ehnes et al. 2011) or, alternatively, that lipid concentration may be responsive to warming only over longer exposure times (Meehan et al. 2022). Altogether, these findings allowed us to predict that *P. pseudovanderdrifti* would show the lowest population resistance due to high mortality, and the lowest recovery after an extreme heat event due to cessation of reproduction – hence a coupling between its population resistance and recovery. In contrast, we expected that the other three species would display a decoupling between resistance (high survival) and recovery (low reproduction) after the week of extreme heat event.

Agreeing with our expectations based on the results from the life-history experiment, we found that the most heat-sensitive species, *P. pseudovanderdrifti*, was also showing the lowest population recovery after an extreme heat event (+10°C above ambient conditions). However, no effects on population resistance were detected in *P. pseudovanderdrifti* nor in the other three species. Such strong resistance to extreme heat can potentially be explained by the buffering effect of the soil in the moist conditions of our experiment, which produced conditions on average 2°C cooler and with more dampened thermal fluctuations than in the air (Lembrechts et al. 2022). Indeed, the average temperatures reached in the soil during the week of extreme heat remained just above 25°C, and the population responses nearly mirrored our results of the life-history experiment at this temperature regime. For instance, survival in *P. pseudovanderdrifti* was hardly affected but fecundity dropped by 72% at 25°C, which can be linked to the strong resistance (demonstrating high survival) and a 54% population decline at recovery (demonstrating the legacy of thermal impacts on fecundity). By contrast, a 77% increase in fecundity in *P. armata* at 25°C was surprisingly not reflected in the population recovery response, which did not differ from control conditions. It is possible that such warming-driven increase in fecundity came at the cost of compromising egg viability, although this merits further investigation. Alternatively, differences in daily temperature fluctuations between the life-history experiment (constant temperature) and the population experiment (daily fluctuation of 4°C) could further explain quantitative discrepancies between both, given that temperature cycles provide greater population growth, as shown by Liefting et al. (2017) in the collembolan *Orchesella cincta*. One limitation from the temperature buffering in the soil at the 30°C treatment in the population experiment is that it prevents comparison between the corresponding population responses and life-history responses at 30°C. Nevertheless, we interpret that the coupling between population resistance and recovery in *P. armata*, *P. fimata*, and *P. tricampata* (i.e. strong resistance and recovery) can be explained by the high survival and lack of thermal impact on fecundity for these species in
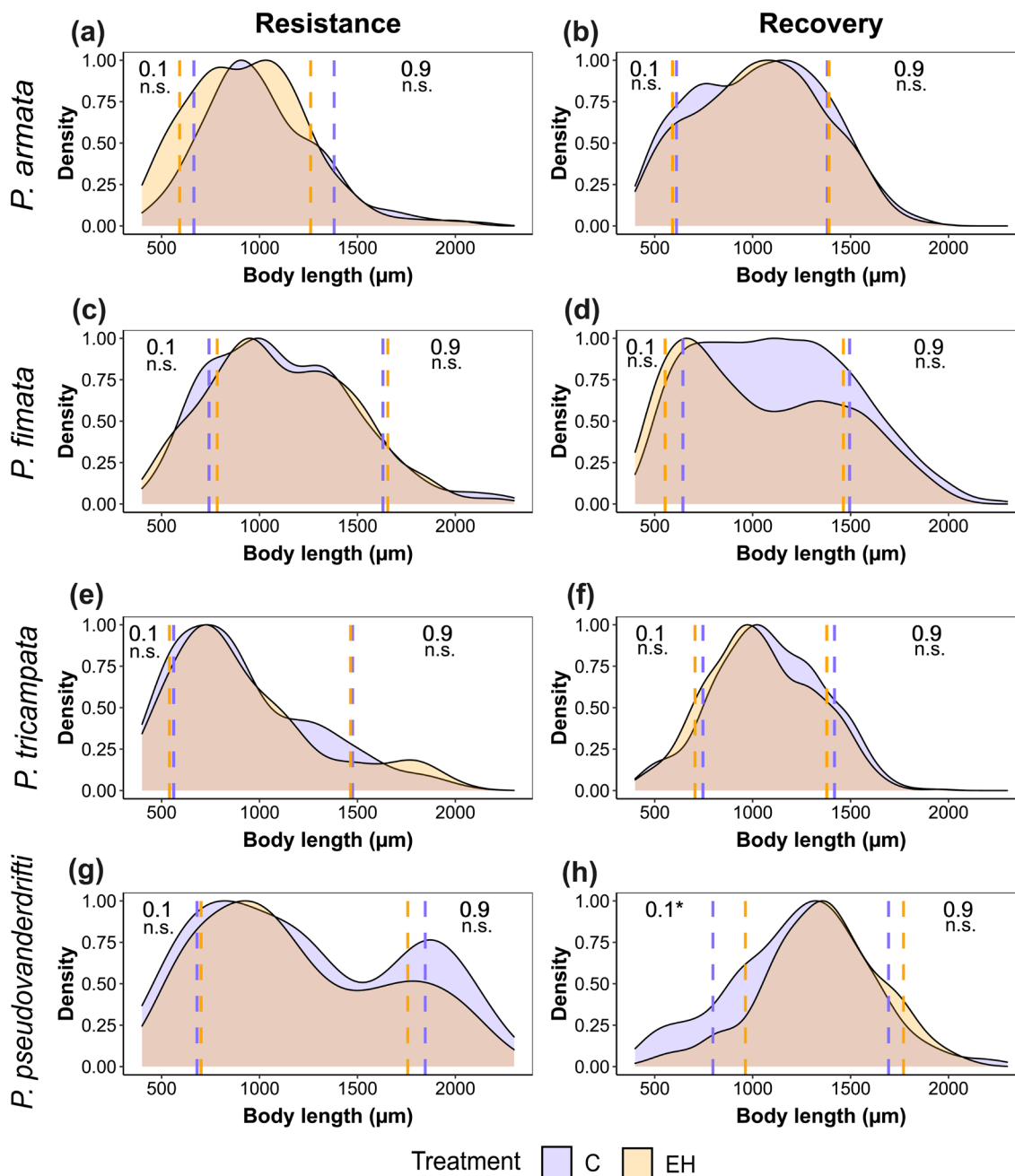
Figure 5. Pooled body size distribution of the four *Protaphorura* species during the resistance phase (a, c, e, g; left column) and the recovery phase (b, d, f, h; right column) of the population response experiment. The number of body size measurements in each species is provided for the resistance and recovery responses, respectively: *P. armata* (n = 487 and n = 1407), *P. fimata* (n = 977 and n = 2402), *P. tricampata* (n = 245 and n = 1142) and *P. pseudovanderdrifti* (n = 336 and n = 841). Dashed lines display the estimates of quantile regressions at the 0.1 and 0.9 quantiles with sample ID as a random intercept. Colours indicate different experimental treatments: blue: control (C); orange: extreme heat (EH). Symbols show significant differences between temperature treatments: n.s. p > 0.05, *p < 0.05.

the temperature conditions of our experiment. Our findings are consistent with theoretical and empirical evidence showing lower thermal tolerances at higher levels of organisation (Rezende and Bozinovic 2019, Bozinovic et al. 2020), since recovery (mostly affected by fecundity) was more heat-sensitive than resistance (mostly affected by individual survival), particularly in *P. pseudovanderdrifti*.

Our results show that the extreme heat event triggered shifts in the population body size distribution in *P. pseudovanderdrifti* that were detectable only during the recovery period, mirroring the responses of recovering populations. By measuring the body size from a large set of individuals (minimum 20% of the population), and through the use of quantile regression, we provide a mechanistic link between

warming effects on life-history traits and population level responses. An extreme heat event reduced the number of small individuals (juveniles) in the population of the most heat-sensitive species *P. pseudovanderdrifti* during the recovery response, while no such body size-specific shifts were found during the resistance phase. In this species, reproduction was disrupted during the week of extreme heat, thus the individuals that should have recruited in the population failed to do so during the recovery period. Importantly, the body size distribution of the other three species remained unaltered, where a strong coupling between resistance and recovery was also observed in response to extreme heat. In contrast to our findings, Lindo (2015) and Holmstrup et al. (2018) showed that positive effects of warming on fecundity contributed to a greater representation of smaller invertebrate species in natural soil communities, therefore causing an overall decline in body size at the community level. The occurrence of heat-tolerant species in these communities might thus explain the discrepancy in our results related to the shifts in the body size distribution of *P. pseudovanderdrifti*.

Predation had a negligible role on the population responses of their prey to the extreme heat event in our study. We argue that although predators initially removed prey individuals, as detected by shifts in the body size distribution, their top-down control became weak as prey populations outpaced predators by several fold. In fact, predators also did not manage to effectively reproduce, perhaps due to the excretion of deleterious defence substances by prey species in our study system (Jensen et al. 2019).

We conclude that distinct effects of warming on life-history traits can scale up to population level responses after pulse disturbances like extreme heat events, and can be effectively linked through shifts in the body size distribution of recovering populations. Our findings related to the (de)coupling between population resistance and recovery responses to an extreme heat event have important implications for a better understanding of both the short- and long-term responses of species exposed to climate extremes. Without an appropriate consideration of recovery periods tailored according to the species generation time, one might risk overlooking the shifts in life-history traits, such as fecundity, that subsequently could shape population recovery responses. We demonstrated this even with one generation time of our study species, which essentially resembles a shorter recovery period. Our study is a step towards establishing relationships between thermal effects on life-history traits and population responses to climate warming, and we call for future studies exploring these relationships by incorporating trait-based approaches (e.g. life-history and functional traits) to predict both population- and community-level resistance and recovery in a changing world.

Author contributions

Gerard Martínez-De León: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (equal); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Arianne Marty**: Investigation (supporting); Writing – review and editing (supporting). **Martin Holmstrup**: Methodology (supporting); Resources (equal); Writing – review and editing (equal). **Madhav P. Thakur**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (equal); Resources (lead); Supervision (lead); Validation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the figshare Repository: https://doi.org/10.6084/m9.figshare.19494665.v4 (Martínez-De León et al. 2023).

Supporting information

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

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