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Experimental Impacts of Temperature and Predator Diversity on Collembola Communities and Decomposition Rates

Leipzig, 2023

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Einreichung:
Leipzig, 11. Juni 2023

<u>Bibliographic Description</u>:

Jahn, Susanne: Experimental Impacts of Temperature and Predator Diversity on Collembola Communities and Decomposition Rates. - 2023. – 3, 31, 0. Leipzig, Hochschule Mittweida, Fakultät Angewandte Computer- und Biowissenschaften, Masterarbeit, 2023

<u>Abstract:</u>

To investigate the effects of climate change on interactions within ecosystems, a microcosm experiment was conducted. The effects of temperature increase and predator diversity on Collembola communities and their decomposition rate were investigated. The predators used were mites and Chilopods, whose predation effects on several response variables were analysed. This data included Collembola abundance, biomass and body mass as well as basal respiration and microbial biomass carbon. These response variables were tested against the predictors in several models. Temperature showed high significance in interaction with mite abundance in almost all models. Furthermore, the results of the basal respiration and microbial biomass carbon support the suggestion of a trophic cascade within the animal interaction.

<u>Acknowledgements</u>

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1 Introduction

The climate crisis is one of humanity's biggest current challenges. News articles reporting rising temperatures and mass extinction, movies and especially demonstrations are putting the issue into focus and draw attention to this important topic and to what has been known since the 1970s [1]. Climate change will have a lasting impact on our lives as well as the lives of plants and animals. Not only will this change cause forced adaptation to changing environmental conditions, but also the death of people and the loss of habitat and biodiversity. According to the IPCC report of 2014, the first effects of climate change should be noticeable now [2]. Considerintg the disasters that have taken place globally, this can be confirmed. Furthermore, it can be confirmed that the climate target of 1.5°C of the "Parisian Agreement" cannot be reached and the risks are devastating [4]. In order to implement the plan of reaching the 1.5°C target, strategies had to be prioritised, which resulted in a limitation of options [1,5]. The sixth report of the IPCC from 2022 summarises the impacts of climate change [6]. In this report, different risks and coping strategies can be found, which are specified regarding the continents and their geography. For Europe, various risks of climate change are identified in this report which the population will have to face if the 3°C global warming level (GWL) is reached. Human mortality and morbidity will be greatly influenced due to heat waves Assuming that a 3°C GWL is reached, there is a risk of a two- to threefold increase in human deaths. In addition to the direct impact of heat waves on humans (an example of this would be the heat wave in England - the hottest summer in London since the instrumental recording of temperature (1659) [4,7,8]), there is the risk of crop failure due to drought. Furthermore, water scarcity will play a significant role especially in the area of West-Central Europe and Southern Europe. But this crisis will not only have an impact on human life. Given that temperature is one of the most important abiotic factors influencing dynamics in ecosystems, the warming will have a significant impact on ecosystems, their interactions and biodiversity. Based on the information of the sixth report of the IPCC, this change will be accompanied by species loss and mass extinctions of animals and plants. Not only climate-related conditions are influential factors, but human behaviour also contributes significantly to the reduction of biodiversity through hunting, fishing, environmental pollution, nutrient enrichment, water abstraction, etc.

These effects are particularly noticeable with regard to biodiversity hotspots (i.e., regions that are globally located in the area of the equator and are characterised by a particular richness of species and whose existence is severely threatened [9,10]), but also lower-diversity, e.g. temperate ecosystems will be subjected to change. Biodiversity seems to be particularly threatened with regard to terrestrial ecosystems (shown in Figure 1) [6].
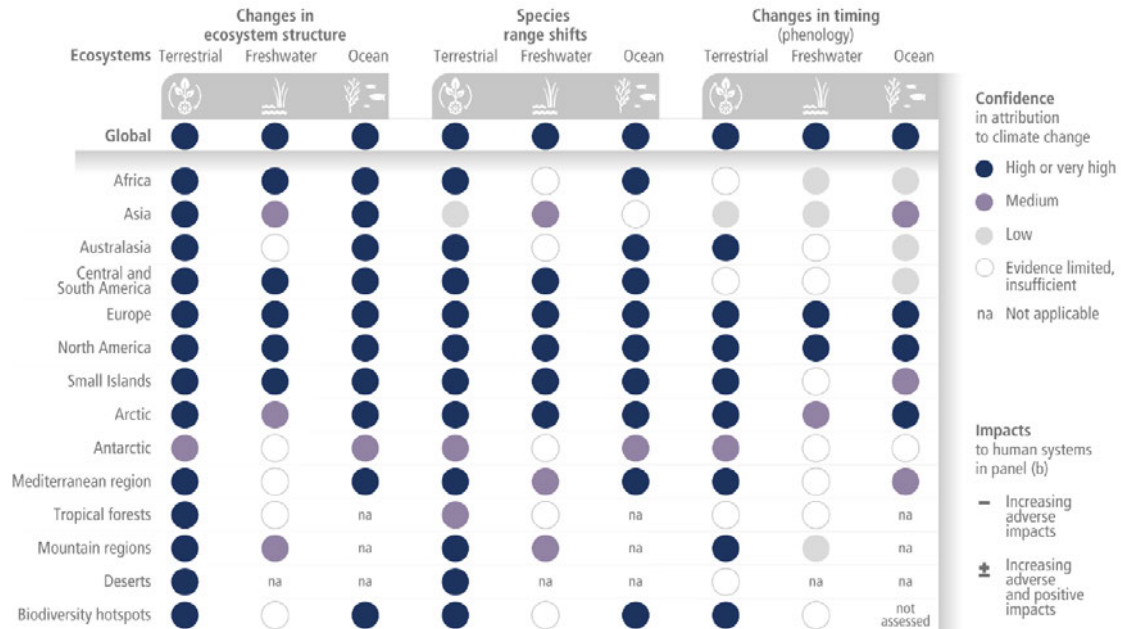
Figure 1 Observed global and regional impacts of climate change on ecosystems [8].

The threat to ecosystems due to climate change involves top-down and bottom-up processes, which are influenced by various factors. These processes do not only influence changes in the behaviour and physiology of consumers, but also the nutrient content of resources. This holistic view of the factors is important in order to be able to assess and classify possible dangers of climate change on ecosystems.

The food resources of animals are dependent on various environmental variables such as temperature, CO_2 content of the environment and the availability of water. These resources in turn influence trophic interactions. Thus, both top-down and bottom-up effects of climate change take place within the food web (Fig.2) [3].

Drought can enhance heat tolerance of photosynthesis, temperature can exacerbate water stress in plants and arthopods

Attack rate
Feeding behavior
Consumption efficiency
Diet preference
Fecundity
Growth/development
Handling time
Metabolism
Phenology
Respiration
Voltinism

Chemical signaling CO_2
Chemical signaling

Predators

Chemical signaling

Feeding behavior
Biomass
Nutrients
H_2O balance

Feeding behavior
Biomass

Feeding behavior
H_2O balance
Metabolism?

Feeding behavior
Consumption efficiency
Consumption rate
Diet preference
Fecundity
Growth/development
Metabolism
Phenology
Respiration
Voltinism

Temperature

Herbivores

Feeding behavior
Consumption rate
Diet preference
H_2O balance
Metabolism

H_2O availability

Feeding behavior
Biomass
Nutrients
H_2O balance

Biomass
Nutrients
Defense

Trophic cascade

Nutrients
Growth
H_2O balance
Photosynthesis
Respiration

Nutrients
Defense
Growth
Phenology
Photosynthesis
Respiration

Plants

CO_2 and temperature can interact to alter effects on plant nutrients

Nutrients
defense
growth

H_2O use efficiency
photosynthesis
respiration

Elevated CO_2 can decrease water stress in plants, drought can limit CO_2 effects on photosynthesis

CO_2

Trends in Ecology & Evolution

Figure 2 Top-down and bottom-up effects of a terrestrial tri-trophic arthrop food web [3]

Consequently, organisms of soil communities are directly affected by environmental conditions (e.g.: temperature, drought) and indirectly by changes regarding food resources. These factors act as stressors on the organisms as individuals and as a community. Many studies investigating interactions within ecosystems provide evidence that climate change affects soil organisms such as collembola. Collembola play an essential role in ecosystems, as they regulate decomposition processes of leaf litter and nutrient cycling [11]. Their impact is particularly important within the biochemical cycles. Collembola are extremely sensitive to environmental conditions like soil temperature. Temperature functions for collembola communities as a demographic parameter and also controls the activity of them. Rising temperatures due to climate change will also have a strong impact on soil organism communities and their response to predation [12]. The biodiversity of these organisms is severely threatened by climate change - and with it their function in ecosystems around the world. The ecologic function of collembola is also based on their high abundance in many different soils. They increase the microbial activity, decomposition and mineralisation. Furthermore, there is a causality

between collembola activity and enhancement of soil fertility [13]. The influence of collembola communities on ecosystems is directly influenced by their feeding on bacteria and fungi. Indirect influence occurs through the comminution of organic material, dissemination of microbial propagules, and the altering of nutrient availability. Among the terrestrial soil fauna collembola is an abundant and ubiquitous microarthropod [14]. The interaction between soil microbes and collembola is important because of their trophic and functional significance within belowground food webs [15]. In these studies, collembola were exposed to the stressor temperature, among other things. Temperature is a determinant of the demography and activity of these arthropods [16]. Thus, increasing temperatures can cause changes between and within species [17]. These changes relate to the competition and feeding behaviour of that soil community. For example, there is not only a reduction in body size to regulate metabolic energy balance, but also altered interactions that occur across trophic levels. Increased external temperature also means that organisms have a faster rate of development. As a result, smaller organisms may have a competitive advantage because they have a low energy expenditure. However, this advantage is also influenced by predation. Similar to prey, the energy demand of predators increases with rising temperature. In the process, action periods shorten and attack rates increase to meet this energy demand. Although prey consumption increases, consumption efficiency decreases and nutrient deficits occur [18]. Thus, studies show that the top-down effect of predators on prey increases with rising temperatures. The predators used (e.g. spiders, centipedes) had a negative effect on the collembola communities [16,19]. However, the predation effect is strongly dependent on habitat size and condition [20]. The majority of studies conducted focus on single stressors, this, however, has its limitations and can be considered unrealistic, due to the stressors occurring in correlation to each other and not separately (shown by Speißer et al. [21]). Thus, it is necessary to consider the effects of multiple, simultaneously-acting stressors, such as climate change and biodiversity loss. The effects of these stressors can act interactively, as for example shown by Santonja et al. [22] and Thakur et al. [17], where predation increases caused by increasing temperature. But they can also be additive, when the effects occur together but there is no effect of one driver on the impact of the other.

To address the knowledge gap of multiple, simultaneously-acting stressors, this thesis will examine the impact of increasing temperature (warming) and predator diversity. The

set-up of the experiment is based on a study by Thakur et al. [17]. In this study, it was investigated how increasing temperatures will influence the predation on and the competition between two Collembola species. It can be expected that increasing temperature, as well as predator diversity, will have an impact on the collembola community. As previous studies showed the increasing of predation with warming but not address the effect of predator diversity. Furthermore, it is likely that these stressors will be mutually dependent. For my thesis I established a microcosm experiment containing collembola as prey and mites and/or chilopods as predators. These microcosms were exposed to a temperature gradient. In addition, the decomposition rate of the collembola was assessed.

2 Aim of the study

The aim of the study was to investigate that increasing temperatures as well as the different predation levels will have an impact on the collembola communities and decomposition rates. Furthermore, it should be researched if these two treatments depend on each other.

3 Materials and Methods

To evaluate the impact of two stressors, temperature, and predation, on collembola communities and decomposition rate, I set up a microcosm experiment with full factorially crossing, which included six climate levels (12°C to 27°C) and four predation levels. This experiment was set-up in reach-in climate cabinets with adjustable light
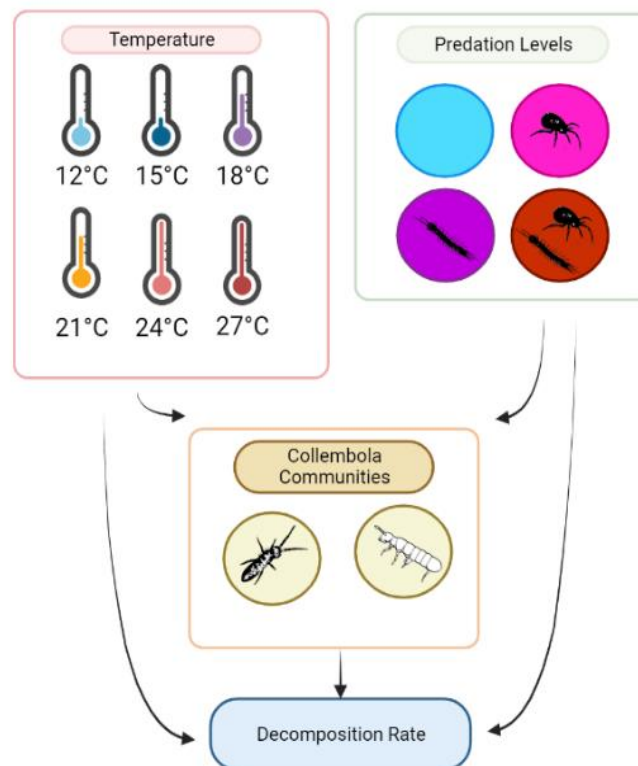
Figure 3 experimental design

3.1 Experimental Set-Up

I used petri-dishes as microcosms with a diameter of 14 cm and a double layer of filter paper. The petri-dishes have small vents (a slightly raised lid) for gas exchange (i.e. to avoid mould in the microcosms). The experiment lasted for 50 days (seven weeks). The following paragraphs are describing the content of the microcosms, which was chosen to create a reasonably realistic environment.

Figure 4 set-up of the microcosm (left), set-up of the bait lamina stripe (right)

XXX day means 8 hours of light, night means 16 hours of darkness

The microcosms were subject to one of two treatments (predation and temperature). Each microcosm contained eight individuals of each species, *H. nitidus* and *F. candida*. Six temperatures were used to span a temperature gradient from 12°C to 27 °C (six climate levels) and represent naturally occurring temperatures for temperate litter communities in summer (Table 1). The light intensity was set by 20% and the humidity by 70% to simulate the natural habitat of a forest ground. Furthermore, there were sixteen hours of light and eight hours of darkness to simulate day and night.

Table 1 temperatures

Temperature Light in °C	Temperature Darkness in °C
12	9
15	12
18	15
21	18
24	21
27	24

The predation treatments had three levels defined by the used predator. Seven replicates of each treatment were provided in order to subsequently determine the impact of the stressors. These treatment levels were full-factorially crossed. The following paragraphs describe the composition of the predation levels:

In **no predator treatment level**, only the two prey species were added to the microcosms. This treatment was used to evaluate the impact of predation on the community. **Mite treatment level** includes eight individuals of each prey species, as well as ten mites, which were functioning as predators. In **Chilopod treatment level**, chilopods were used as predators. One Chilopod was placed in each microcosm. As the chilopods were found to have different body masses, they were categorised by size and the "chilopod" predation replicates of each temperature level received chilopods of body mass spanning a reasonable gradient so that the influence of centipede body mass on the collembola community could later be assessed. **Both predator levels** consisted of using ten mites and one centipede as predator. These treatments were stored at six temperature levels * four predation levels * seven replicates. This resulted in an absolute number of microcosms of 168. Furthermore, **control microcosms** were set up that did not contain any animals, but did include the BLS and the substrate. These microcosms were also stored under the same conditions as the microcosms containing animals. There were four replicates of the controls per temperature, so there were 24 control petri-dishes in total. Consequently, the total number of replicates and controls was 192 microcosms.

To prevent the animals from dying due to desiccation, the microcosms were watered with 1 ml of deionised water every day at the beginning of the experiment and then every third day after one week for seven weeks.

3.2 Organisms

3.2.1 Collembola – *H.nitidus* and *F.candida*

In this experiment two different collembola species were used: *Heteromurus nitidus* and *Folsomia candida*. *F.candida* belongs to the family of Isotomidae and has a length of 1.5 mm to 3 mm at maturity. They are white or faintly yellowish in color and do not bear ocelli. *F. candida* has no visible external eye structure, which is present in *H. nitidus*.

Furthermore, the two species differ in that the posterior three abdominal segments are fused together in *F.candida* and the dorsal part of the first thoracic segment is reduced. *H.nitidus*, on the other hand, has a differently shaped thorax and are easily recognised by their eyes, which consist of a single reddish-brown ocellus on each side of the head. Like other collembola, *F.candida* has a ventral tube (collophore), which is involved in fluid exchange with their environment. In this experiment, *H.nitidus* individuals have longer body length than *F.candida*. In this Experiment, *H.nitidus* has an average body length of 1.9 mm and *F.candida* a length of 0.91 mm. The optimal temperature for *F.candida* is 20°C and for *H.nitidus* 15°C. These species were chosen due to their worldwide occurrence and their ability to function as model organisms [20].

The breeding of both collembola species was carried out in breeding pots filled with a mixture of plaster and activated carbon. Before placing the animals inside, the plaster and activated carbon substrate was moistened. Afterwards, 30 adult individuals were placed in each breeding pot with the help of an exhaustor. The food substrate was dry baker's yeast placed on cellulose. The animals were stored at 12°C for the rearing, as mould had previously formed in the pots at room temperature. The yeast residues were changed regularly every 3 to 4 days and water was added as needed using a pipette. This procedure was carried out for both species. If juvenile individuals were seen, their growth was closely observed and subsequently the adult collembola were transferred to new breeding pots.
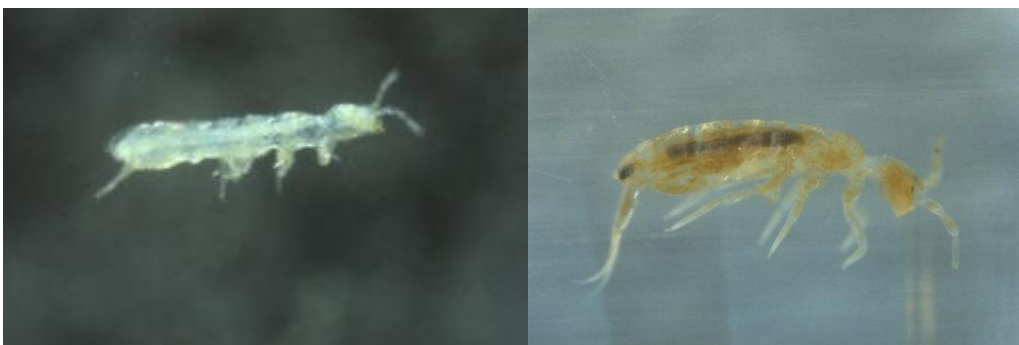
Figure 5 Collembola species – *F.candida* (left), *H.nitidus* (right)

3.2.2 Mites – *Stratiolaelaps scimitus*

The habitat *Stratiolaelaps scimitus* of is located in Europe and North America. The mites have a brownish colouration and adults bear an adult, pointed dorsal shield. The larvae have only 6 legs and are much smaller than the adults. They are living in soils and usually are not found on plants. Their active period is mainly in summer, only females are known

to hibernate. They prefer dark, moist places and are not tolerant to dry conditions. The average body length is 1 mm, body and legs are brown [25]. Their temperature tolerance is between 12°C and 30°C. At a temperature below 10°C, no population growth can be observed. However, growth resumes when the environment warms up slightly. They can survive without food up to four weeks. This species of mites feeds mainly on living insects, such as flies, beetle larvae, nematodes, thrips, springtails and smaller mites [25]. The mites were purchased from the online store www.schneckenprofi.de.
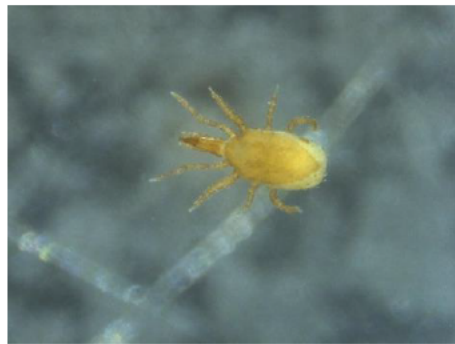
Figure 6 mite - *Stratiolaelaps scimitus*

3.2.3 Chilopoda - *Lithobiidae*

This predator species functions as a predator of Collembola, as chilopods are also living in the upper soil layer [19,26]. They are most reddish brown and the body flattened. The dorsal plates of individual segments are alternately narrow and broad. They have 15 pairs of legs (last two are the longest and the slender antennae are pointed. Subsequent determinations of the chilopods revealed that the majority belonged to the species *Lithobius forficatus*. *Lithobiidae* are known as active predators and are sensitive to desiccation, so that they can be found in dark and moist places [22]. Like collembola they are living in the upper soil layer [19,26]. They were manually collected with tweezers and by sieving litter (Locations: Auwald, Leipzig; Volkspark Kleinzschocher, Leipzig). Most successful was the method to collect them with tweezers under tree bark. In total, I needed

Figure 7 Chilopod – *Lithobiidae*

82 centipedes. However, more were collected, as it was assumed that some would not survive the high temperatures in the climate cabinets for so long. The sizes of the chilopods differed so that it was possible to apply a size gradient. The chilopods were categorized so that there was an even distribution in regard to their size among the treatments. All centipedes were kept separated and fed on collembola.

3.3 Leaf-litter substrate

The leaves of the hornbeam (*Carpinus betulus*) were used as substrate for the microcosms. The hornbeam is a deciduous tree species typically found in Central Europe [24,27].

This litter thus served as a habitat and food resource for the collembola and should form as natural an environment as possible for the animals. The leaves were dried at 80℃ in a drying oven for 48 hours.

3.4 Leaf Discs

To determine the decomposition rate of Collembola, I used leaf discs. For this purpose, circular discs with a diameter of 1.7 cm were punched out of the dried leaves of beech (*Fagus sylvatica*). After drying at 80°C for 48 hours, these were weighed and inserted into the respective microcosms. By weighing them again after the end of the experiment, it should be possible to detect differences in weight, so that the decomposition rate of the Collembola can be concluded based on their feeding on the leaf discs.

3.5 Bait lamina stripes (BLS)

The bait-lamina test was first used and published by Von Törne in 1990 [2]. This test is performed by filling polyvinyl chloride (PVC) strips, which contain 16 small holes, with a suitable bait substance. The activity and density of the soil community are proportional to the eaten material, measured by assessing each of the 16 holes in the stripe [28,29]. For the evaluation, the strips are inserted vertically into the soil, left there for two to three weeks, carefully removed, and then assessed for food marks. For this experiment, it was first tested whether springtails use the BLS as a nutrient source, even though the BLS are not inserted in soil but offered in the microcosms among the leaf litters. This pre-experiment confirmed that BLS could be used for evaluation. The following steps were taken to prepare the BLS:

a mixture of 70 g cellulose, 27 g wheat bran, and 3 g activated carbon was used for the bait substance. For this, the cellulose and wheat bran had to be finely ground and then sieved through a mesh size of 500 µm. The grinding settings for this were:

Cellulose for 10 minutes at f=10/s
Wheat bran for 5 minutes at f=30/s

Then, a small amount was placed in a beaker and distilled water was added until the powder produced a sticky paste. This substrate was filled into the holes using a spatula and excess substrate was removed. The strips were then dried at 40°C for one hour. The mixture contracts as it dries, therefore, both the application of the substrate and the drying process was repeated two to three times depending on the quality of the final product assessed by eye.

The BLSs were prepared with cork pieces (shown in Figure 2) so that the collembola had free access to the bait resource but no ground contact and subsequently evaluated (no food marks = 0; partially eaten holes = 0.5; completely consumed holes = 1)

3.6 Final harvest and heat extraction

Before the contents of the microcosms were transferred to the extraction pots, the leaf discs, BLS, and chilopods were removed.

At the final harvest, after 50 days, I carefully retrieved the chilopods by hand. The assessment of collembola and mite populations was done with the use of heat extraction in a modified Kempson apparatus [30] to carefully and effectively extract all collembola and mites, as well as chilopods having avoided hand-capture. The chilopods were collected so that they could be released back into their natural habitat. They were weighed before release in order to detect weight changes and to calculate the body mass that affected the community during the experiment. Leaf samples were also taken for the subsequent microbial respiration analysis.

The filter paper with the substrate and the animals was then placed upside down in PVC pots. These PVC pots had a height of approx. 4 cm and a diameter of 7 cm and a 2 mm grid at the bottom. The filled pots were placed on top of 250 ml beakers containing 50 ml

of a glycol-water solution (1:1). In addition, a PVC cup was placed over the pots to ensure reliability regarding the purity of the samples and prevent animals from escaping. During heat extraction, the animals with the material in the microcosms are exposed to increasing temperatures. In the Kempson apparatus [30] set-up, heat is emitted from the top while the bottom of the chambers is cooled. The temperature was set to rise from 28°C until it reached 55°C. The heat acts as a stressor for the animals, causing them to crawl down through the substrate to avoid the high temperatures. In doing so, they end up in the glycol-water solution where they are preserved. After six days of heat extraction and reaching 55°C, the animals were transferred from the glycol-water solution to a 70% ethanol solution.

3.7 Microscopy

The animals in the 70% ethanol solution were analysed under a stereomicroscope. The body length of the organisms (without appendages) was determined using an object micrometre (50 mm in 0.1 mm intervals). To determine the abundance of the Collembola the two species were distinguished by their physical traits and their individual number was counted. The body mass was then calculated by a regression of Mercer et al. (2001), based on that the biomass was calculated. Same procedure was performed for the mites. The Chilopods were weight before and after the experiment. They were not heat extracted, except for the case that they were not able to find within the microcosm at the day of the experiment ending.

3.8 Determining respiration activity of soil microbes

To determine the amount of living carbon in the soil, the microbial activity in soil samples can be determined by its oxygen consumption. The modified Scheu apparatus was used for this purpose [31–33]. Its function is based on electrolytic oxygen micro compensation. During the measurement, the pressure difference between a control chamber and the sample chamber is measured with the help of a pressure detector. The sample chamber consists of a glass vessel for the sample and a CO_2 trap, which is connected to the glass vessel by means of a simple joint. The CO_2 trap contains 200 µl of 2 N potassium hydroxide solution. The sample chamber is also connected to a chamber containing a platinum electrode in a saturated copper sulphate solution ($CuSO_4$). The microorganisms consume oxygen during their metabolic processes. The oxygen consumption of the

microorganisms in the sample is compensated by the oxygen production of the electrode. The CO_2 that is excreted during respiration is captured with the help of KOH. So as soon as a lower pressure is measured in the sample chamber, a current pulse of 10 mA (1 s) is applied to the electrode so that the pressure inside this chamber is balanced. In this case, 0.83 µg of oxygen is released from the copper sulphate solution. The amount of oxygen consumed per hour can then be measured by the number of current pulses delivered. To ensure a constant temperature, the vessel units are immersed in a water bath, which has a temperature of 20°C. The oxygen consumption is then measured by the number of current pulses delivered. Therefore, aa dependence on the oxygen consumed and the dry mass of the sample can be detected. The determination of basal respiration is carried out without any addition of substrate, while usually durating 24 hours [31–33]. The measurement of microbial biomass is done by substrate-induced respiration This reaction is induced by glucose in this method. The determination takes 15 hours and is carried out following the measurement of basal respiration [31–33]. Regarding sample preparation, several leaves (2-3 pieces) were taken from the microcosm, cut into pieces, and stored at 20°C. In previous experiments, the volume to be achieved in the methodology was determined and the corresponding mass was noted by me. The total mass of the leaves taken from the microcosms was approx. 200 mg.

3.9 Statistical analysis

The aim of the statistical analysis was to identify if temperature and predation have an effect on the Collembola community and decomposition rate. These predictors were tested on their own but also in their interaction to assess if the effects were interactive or additive. The predictors were always first tested in the models with an interaction, if the interaction showed no significance, an additive model was used. Further simplifications of the models were made if no significant influence of the predictors was shown. The following table provides an overview of the response variables and predictors.

Table 2 tested predictors and response variables

Predictors	Temperature Predation Chilopoda Body Mass Mite Abundance Absence/Existence of any Predator	
		Absence/Existence of Chilopoda Absence/Existence of Mite

Response variables	Collembola	
		Abundance Biomass Body mass Survival
	Basal respiration Microbial biomass carbon	

R version 4.1.3 (R Development Core Team, 2022) has been used for the evaluation of the results with the carData-package (version: 3.0-5), MASS (Version: 7.3-58.3), lmtest (Version: 0.9-40), ggplot2 (version 3.3.6) and the performance package (Version: 0.10.2). These packages were used to check the models and their fitting and to generate graphs. Zero values of collembola abundance were not removed from the obtained heat extraction data as they were recognized as extinction events and were thus retained in the analysis. The used models differed slightly depending on the data type of the respective response variable. These response variables included the heat extraction data of each collembola species, *F.candida* and *H.nitidus*, as well as the overall collembola community. Excluded from the heat extraction data were the measurements of the 18°C regime, which showed no living animals (neither prey nor predators). The response variables were tested against temperature and predation and the interaction of both drivers. To specify the predation effect, several more specific predictors of it were examined in more detail. These predictors included mite abundance, chilopod body mass, as well as the effect of the absence or presence of any predator. The factor of predator occurrence was further specified regarding the two predator species so that mite and Chilopod existence were also predictors. If any predator, either mite or Chilopod, was present in the microcosm it was coded as 1 in the data, other way the predictor was coded as 0. The predictors were equally tested for their effect on biomass, body mass, basal respiration and microbial

biomass carbon. All these response variables were tested against the predictors in different models.

To analyze the abundance of collembola and test the hypotheses, generalized linear models (GLMs) with a Poisson distribution error were run. These models were chosen to explain variation in animal population by temperature and predation levels. They led to an over-dispersion (residual deviance $>>$ degrees of freedom) and zero inflation caused by many zeros in the abundance data. To overcome this problem, zero inflated models (ZIMs) with a Poisson distribution error were used. The ZIMs proved to be a better model fit to the data and also no overdispersion. These models are handling zeros and positive integers separately [34]. To analyse the ZIMs, the R packages pscl (version 1.5.5) and lmtest (version 0.9.40) were used.

The effects of temperature and predation levels on biomass of the collembola was calculated based on the body mass (covered with body length-mass regression by Mercer et al. [35]) of Collembola and examined with GLMs. This model showed the best fitting according to the data. The same model was chosen in regard to the body mass of Collembola. The model fit was checked by using anova to compare the interactive and additive models, this goes for all GLMs.

For the analysis of the Collembola survival, a GLM was used. This model checked the effect of predictors on the coexistence and survival of the Collembola species. To process this, the presence of Collembola was coded as 0 (no Collembola) or 1 (found Collembola in microcosm). Hence, a GLM with binomial distribution error was used.

For the basal respiration and microbial biomass carbon, GLMs with gaussian distribution were chosen.

4 Results

The following sections describe the results of the statistical analysis. I tested the effect of temperature and predation on collembola communities and decomposition using GLMs and ZIMs as mentioned in the methods section. The predictors were always first tested in the models with an interaction, if the interaction showed no significance, an additive model was used. Further simplifications of the models were made if no significant influence of the predictors was shown. If the additive model shows no significance the predictors were tested on their own without an interactive or additive system. All lines in the tables are associated with one tested model.

The abundance of the springtails was checked with ZIM against the interaction of temperature and predation. This model showed no significance. After a simplification of the model by removing the predictor of predation, temperature showed a high significance as a predictor and had a high impact on the whole collembola community and on each collembola species. Furthermore, *F.candida* showed significance in an additive model structure with predictors temperature and mite abundance. This can also be observed for the total collembola abundance. Only *H.nitidus* showed significance in the interaction of temperature and mite abundance (Table 3).

Table 3 tested models of the Collembola abundance with z-value, p-value and significance

Total collembola abundance			
Predictors	z-value	p-value	Significance
Temperature (T)	4.339	1.43e-05	***
Temperature + Mite Abundance	0.3554	0.000144	***
	-1.974	0.048409	*
Heteromurus nitidus abundance			
Predictors	z-value	p-value	Significance
Temperature (T)	5.760	8.43e-09	***
Temperature x Mite Abundance	-2.171	0.0299	*
Folsomia candida abundance			
Predictors	z-value	p-value	Significance
Temperature (T)	5.760	8.43e-09	***
Temperature +	3.524	0.000426	***

Mite Abundance	-1.716	0.086239	.

Temperature showed the highest significance regarding the abundances of the Collembola. Increasing temperature showed a positive effect on the *F.candida* population, which peaked at 21°C. At the two highest temperature levels, an extinction of both species was observed. The abundance of *H.nitidus* populations was interactive affected by temperature and mite abundance and showed only a slight increase at 21℃. A strong peak of *H.nitidus* abundance can not be observed. This springtail species also went extinct at the highest temperatures (24°C and 27°C). Despite different combinations being tested in the models, the occurrence as well as the body mass of centipedes had no significant effect on either of the species. To summerize this collembola abundance was driven by temperature across species and additionally influenced by mite abundance, in the case of *H.nitidus* even with a significant interaction of mite abundance and temperature (Fig.8). The juvenile and adult individuals of the Collembola species were determined by their body length, individuals with a body length longer than 1.5 mm was noticed as adults and smaller than this they were counted as juveniles (Fig.9).
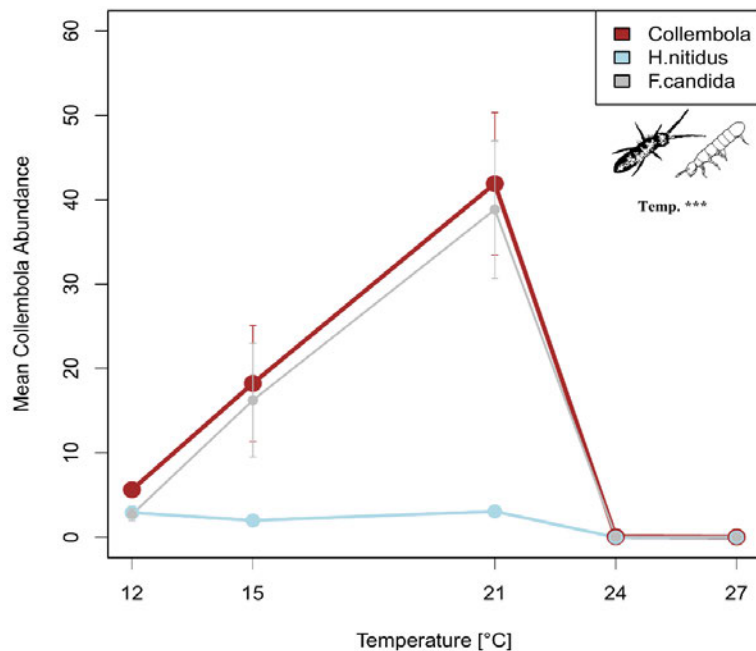

Figure 8 mean Collembola abundance with standard error and temperature (interaction significance with mite abundance *)
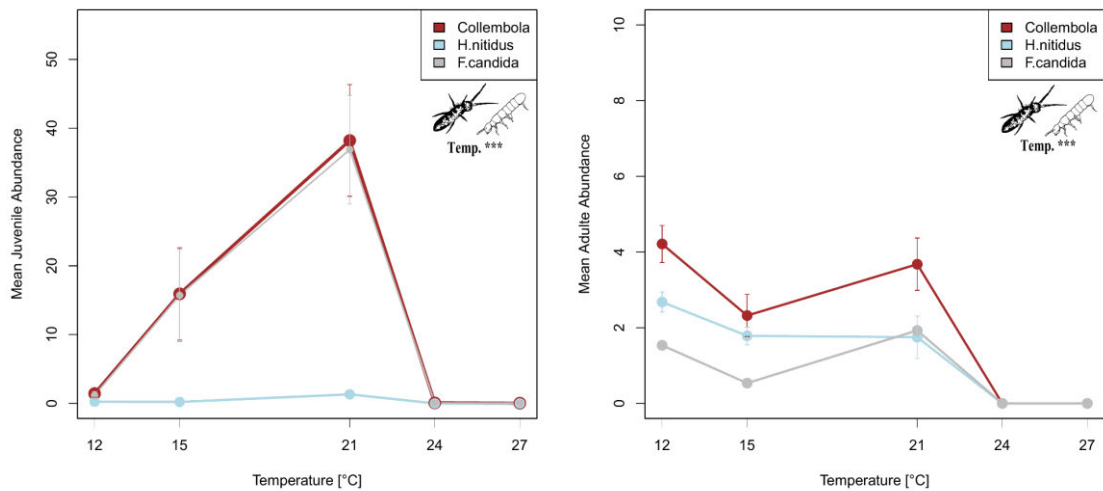
Figure 9 Mean juvenile abundance of Collembola with standard error (left), mean adult abundance of Collembola with standard error (right)

First, the biomass of the whole collembola community was tested and after that each of the species, separately. The biomass was tested with a GLM, because this model showed the best coverage of the data. It showed an interactive effect of temperature and mite abundance on the whole collembola community. There was a significant effect of mite abundance.

Table 4 tested models of the Collembola biomass with z-value, p-value and significance

Total collembola			
Predictors	z-value	p-value	Significance
T* Mite Abundance	2.306	0.0226	*
Mite Abundance	3.652	0.000369	***
Heteromurus nitidus			
Predictors	z-value	p-value	Significance
Temperature (T)	-3.860	0.000173	***
Predator Absence/Presence	-1.952	0.0529	.
Predation	-1.849	0.0667	.
Folsomia candida			
Predictors	z-value	p-value	Significance
T*Chilopoda Body Mass	-2.002	0.04533	*
T*Mite Abundance	3.849	0.000119	***
T * Mite Absence/Presence	-3.862	0.000112	***

On the biomass of *H.nitidus,* the temperature showed a highly significant effect. The species was also affected by the existence of any predator (either mite or Chilopod) in the microcosm. The biomass of *F.candida* depicted an interactive effect by temperature and mite abundance/occurrence. The Chilopod body mass showed some significance in the GLM. There was a a steady increase in biomass of *F.candida* with warming temperatures and a peak at 21°C (Fig. 10). At higher temperatures (24°C and 27°C), the species went extinct like *H.nitidus*, which showed also a low biomass at colder temperatures.
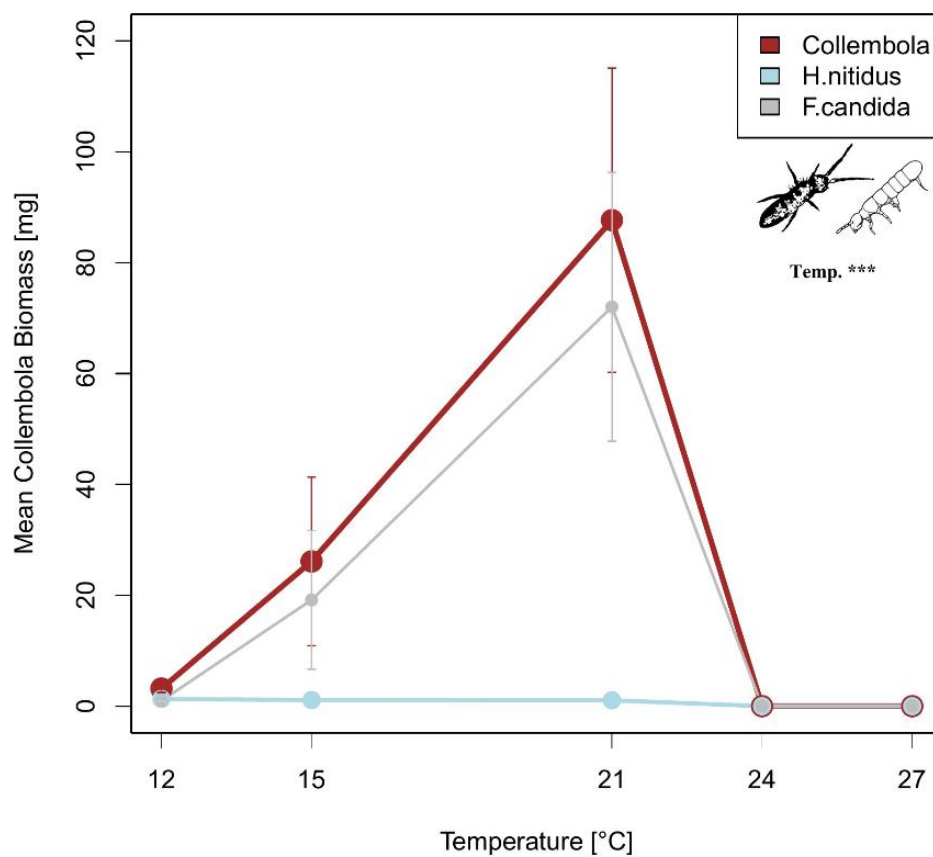

Figure 10 mean Collembola biomass with standard error and temperature (interaction significance with mite abundance *)

The body masses were calculated to assess the impact of the predictors on the life cycles of the prey species, because of the lighter weight of juvenile collembola. In the tested GLM (Table 5), temperature and mite abundance showed an interactive effect (Table 5, Figure 11). Furthermore, the body mass of both species was significantly affected by the temperature itself. Body mass of *F.candida* is stronger impacted by the temperature than *H.nitidus* (Fig 11) The body mass of *F.candida* and the whole collembola community was affected by an interaction of temperature and mite abundance.

Table 5 tested models of the Collembola body mass with z-value, p-value and significance

Total collembola			
Predictors	z-value	p-value	Significance
Temperature (T)	-2.551	0.0107	*
T * Mite Abundance	2.278	0.02275	*
Heteromurus nitidus			
Predictors	z-value	p-value	Significance
Temperature (T)	-2.965	0.00302	**
Folsomia candida			
Predictors	z-value	p-value	Significance
T * Mite Abundance	2.124	0.0337	*

At a temperature of 12°C, Fig. 11 showed a higher mass of *H.nitidus* than *F.candida*. At 15°C the biomass of the two species was very similar. *F.candida* body mass peaked at the temperature of 18°C and the population went nearly extinct at the two highest temperatures. The biomass of *H.nitidus* decreases with the increasing temperature and the population went extinct at the highest temperatures. The increasing temperature between 15°C and 21°C has no significant negative effect on the body masses of the springtails. It can also be seen that the body mass of the collembola was almost zero at 24°C and eventually went zero at 27°C.
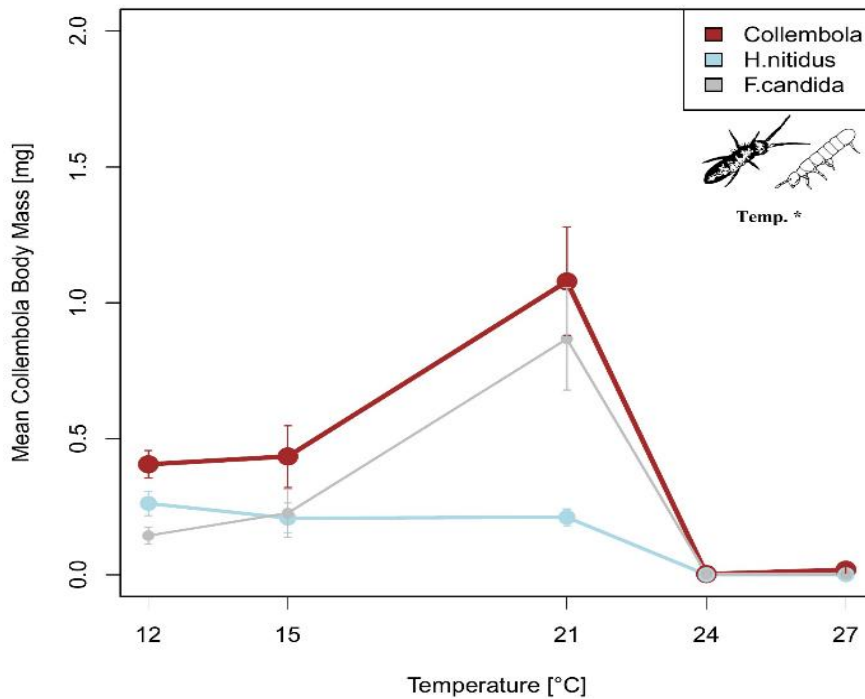
Figure 11 mean Collembola body mass with standard error and temperature (interaction significance with mite abundance *)

The survival rate was examined to assess the survival of each Collembola species. On predation level it shows in the tested models, that only mite abundance and temperature showed a significant interactive effect on the prey species (Table 6, Figure 12). But also temperature itself had a significant effect on *F.candida* and *H.nitidus*. So not only does it show a high significance for the collembola community, but also for each species, separately. Furthermore, the interaction of mite abundance and temperature showed the highest significance regarding the whole community. The interactive effect on *H.nitidus* was not as significant as on *F.candida*. Temperature was a determining factor in the survival of springtails. The survival of *H.nitidus* is verifiable at temperature below 18℃. With increasing temperature, the number of *H.nitidus* decreases and so also the coexistence of the species. *F.candida* survives above 18°C.

Table 6 tested models of the Collembola survival with z-value, p-value and significance

Total collembola			
Predictors	z-value	p-value	Significance
Temperature	-5.609	5.35e-07	***
T *	3.082	0.00206	**

Mite Abundance			
Heteromurus nitidus			
Predictors	z-value	p-value	Significance
Temperature	-6.221	4.94e-10	***
T * Mite Abundance	2.383	0.0172	*
Folsomia candida			
Predictors	z-value	p-value	Significance
Temperature	-5.886	3.96e-09	***
T * Mite Abundance	2.952	0.00316	**
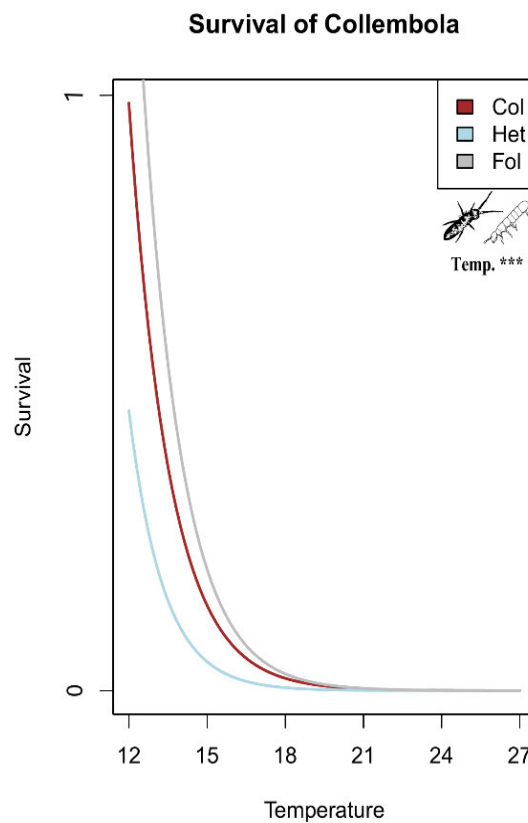
Figure 12 Collembola survival depending on temperature (interaction significance with mite abundance:*)

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Basal respiration was measured to assess the microbial activity within the microcosms. The increasing temperature had a high significance on the microbial activity (Table 7, Fig. 13). Figure 13 shows the basal respiration depending on the temperature. It can be seen that the basal respiration decreases with increasing temperature. Furthermore, it is

detectable that microcosms with Chilopods as predators have a higher basal respiration. This suggests that these microcosms also have a higher microbial activity.

Table 7 final model of basal respiration with z-value, p-value and significance

Basal Respiration			
Predictors	z-value	p-value	Significance
Temperature	-5.134	9.84e-07	***
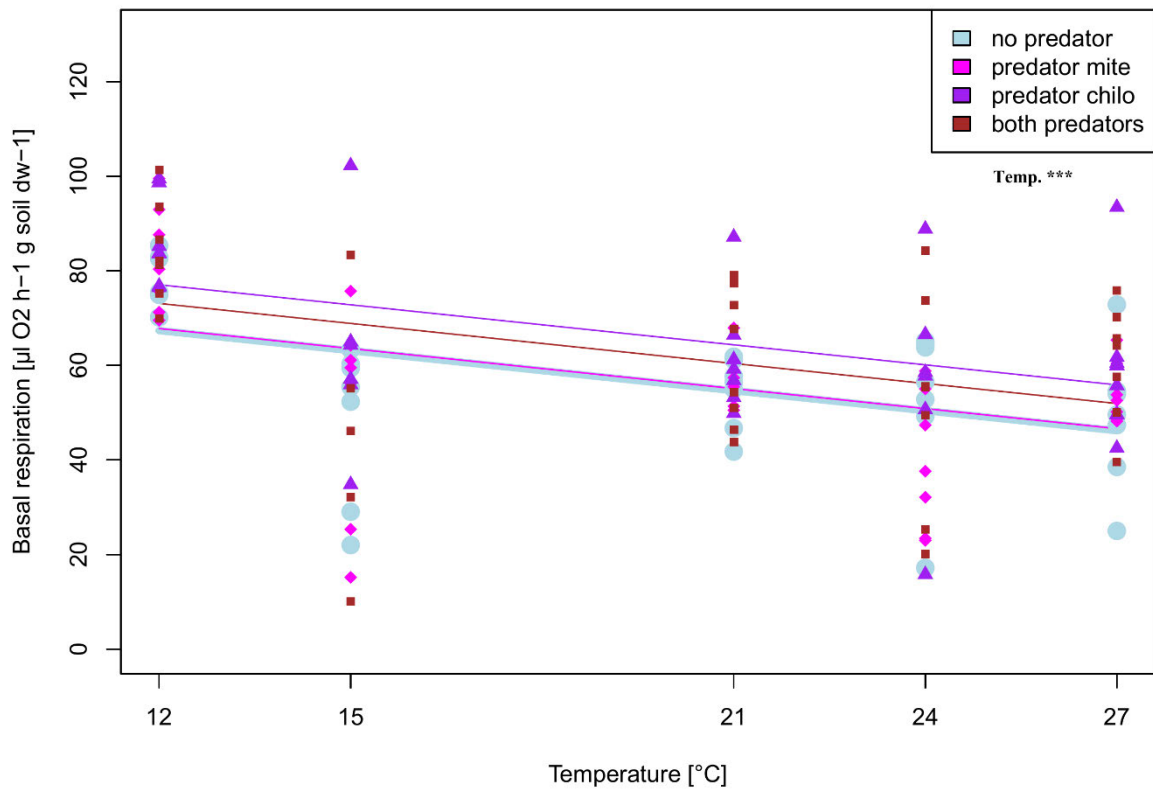
Figure 13 Basal respiration with prediction of the predator levels depending on temperature

Microbial biomass carbon is the carbon contained in the living components of soil organic matter. This was measured together with basal respiration to obtain an indication regarding the influence of the predictors on biological activity. Microbial biomass carbon was tested with the same model as basal respiration. The impact of temperature has the highest significance. The predation predictors showed only an additive effect with temperature on the microbial biomass carbon. These predation predictors included the occurrence of a centipede and the Chilopod body mass.

Figure XXX (pred sig) shows the microbial biomass carbon depending on the temperature and the impact of the different treatments as well as their prediction based on the tested model. With increasing temperature, the carbon microbial biomass carbon decreases. It can also be seen that the microcosms with the predation level mite have the lowest carbon. The highest microbial biomass carbon can be detected in the microcosms with centipedes as predators and at the coolest temperature.

Table 8 tested models of microbial biomass carbon with z-value, p-value and significance

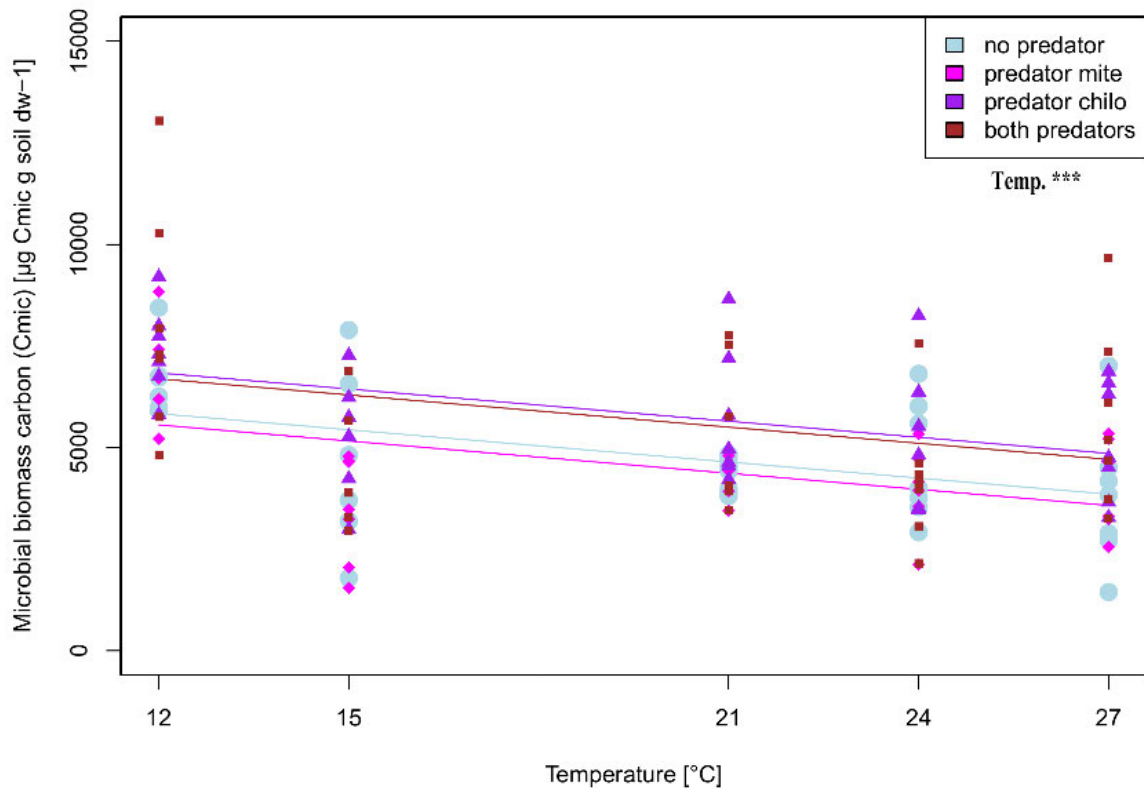| Cmic			
Predictors	z-value	p-value	Significance
Temperature	-4.769	4.79e-06	***
T+		6.261e-07	***
Predation		0.003427	**
T+		5.521e-07	***
Chilopoda Absence/Presence		0.0002764	***

Figure 14 Microbial biomass carbon with prediction of predation levels (additive significance with Chilopod Absence/Presence: ***)

5 Discussion

The aim of the study was to investigate the experimental impact of temperature and predator diversity on Collembola communities and to examine the decomposition rate. At the beginning of the experiment, it was hypothesized that the temperature as well as the predation levels will have an effect on the prey species. In addition, it was suggested that the impact of the two treatments will depend on each other.

The results on this research question can be summarized by two key points. First, the temperature had a major effect on all the investigated response variables, which are including the Collembola abundance, biomass, body mass and basal respiration as well as microbial biomass carbon. Second, it was found evidence of an interactive effect of temperature and mite abundance on the Collembola community. The observed temperature effect can be confirmed by many studies before. So was shown in the experiment, that the Collembola are sensitive to environmental conditions like temperature [19,20] which also explains that both species almost went extinct at the highest tested temperatures. This sensitivity was shown clearly by their abundance decrease at the highest tested temperatures and was observed in many studies before [17,22]. Both Collembola species showed an increasing of abundance, biomass and body mass within the temperature range of 15°C to 21°C, which also confirmed the optimal temperatures for reproduction [20,36]. Especially *F.candida* shows a peak at 21°C of juveniles. Contrary to studies like Xu et al. (2012) [37] and Kardol et al. (2011) [38], which showed that temperature only had little effect on Collembola, the temperature was a determining factor for Collembola abundance, biomass and body mass of *H.nitidus* and *F.candida* in this experiment. Overall, temperature had a major impact on the tested response variables and showed almost in every tested model the highest significance.

The temperature showed also an interactive effect with the predictor of mite abundance. This interaction was also observed by Thakur et al. (2017) [17]. Despite the fact that the present performed experiment cannot confirm, that the predation effect on the smaller Collembola species (here *F.candida*) has increased with warming temperatures. In regard to the predation effect only mites were detected to have a significant interaction whereas the Chilopods did not exert any interactive effect with temperature. Hence, no statement

can be made about the impact of predator diversity in interaction with temperature on the Collembola community. The different impacts of smaller and larger predators on Collembola were also observed by Schneider et al. (2012) [39]. In this study, Schneider et al. showed that the prey species suffers from smaller predators like mites and benefits from larger predators. This is caused by trophic cascade in which the larger predator feeds within the predator guild while the smaller predator feeds directly on the prey [39]. The possibility of a trophic cascade also exists for the results obtained in particular with regard to basal respiration and microbial biomass carbon. In comparison within the four predation levels are differences regarding these measurements recognizable. The differences within the basal respiration and the microbial biomass carbon may be related to the feeding of the Collembola on bacteria and fungi [40]. The basal respiration decreases when the Collembola feed on the bacteria as well as on fungi and it increases when the feeding behaviour of the Collembola is influenced by predation. Thus, it can be observed that the predation level of both predators has the second highest basal respirations, which leads to the suggestion that the chilopods fed within the predator guild and therefore the Collembola fed on the bacteria and fungi (Fig. 13).

According to the results of the microbial biomass carbon it seems similar, except that the mites have a bigger impact on the Collembola, hence, the microbial biomass carbon of microcosms with mites is the lowest among the predation levels. Temperature showed a significant influence as well as its interaction with mite abundance. However, the influence of predator diversity could not be proven, as it did not show significance, which contrasts with the statement of Schneider et al. (2012). The reason for the significance difference between the temperature effect and the predation effect of Chilopods could be due to the fact that the Chilopods were added one week after the microcosms with the Collembola had been established. The reason for this delay was to allow the Collembola to get used to the environmental conditions and the assumption that Chilopods with high body mass will have an increased metabolic demand with warming temperatures [12]. This would have led to the extinction of Collembola within the microcosms before any effect will be visible. Due to this delayed onset, the temperature may have already had such a great influence on the community that only an effect of Chilopod body mass on *F.candida* was detectable. Nevertheless, a further predation effect by the mites could be detected. The reason for this could be that animals with a smaller body mass have a greater

increase in metabolic demand and are therefore significantly more active than large predators [41]. Another reason for the higher temperature significance can be, that the individual number of the prey species was too low. Different from Thakur et al. (2017) [17] only eight individuals of each species were used. Caused by moulding in the breeding pots the rearing in regard to the *H.nitidus* species was very difficult and took longer time than expected. This could also have had an influence on the reproduction of this species. The consequences of this are resulting in much lower abundances than shown in Thakur et al. (2017) and Santonja et al. (2018) [22]. Furthermore, the survival of *H.nitidus* within the microcosms was examined and showed that *H.nitidus* has not the necessary capacity to adapt on the warming - at least not at the scale tested here.

According to the six tested temperatures, the cabinet which was pre-set at a temperature of 18°C showed no survival of Collembola, which was noticed during the microscopy. This contradict the findings of many studies [19,20]. Based on the results, which are showing that individuals survive below and above 18°C and the fact that the installed temperature loggers showed no difference to the pre-set temperature, it was decided to not consider this effect. So, the data of the 18°C climate cabinet was excluded from the analysis.

As mentioned in the method chapter, BLS and leaf discs were used to determine the decomposition rate of the Collembola. After the experiment it was observed that no feeding of Collembola was shown neither on the BLS nor on the leaf discs. BLS are a typical measurement to assess the activity of soil fauna [3,28,29] and showed that the Collembola will also fed on them in a different environment (showed by pre-experiments). Despite this fact of missing feeding marks on the BLS can be caused by the preference of food choice of the Collembola species. The leaf discs' weight indifference could be attributed to this as well.

6 Summary

In order to assess the impact of climate change on ecosystems, the interactions of organisms within these ecosystems must be understood. This has been done in various studies, including Thakur et al. (2017), but the multifactorial reference was not included, and the aim of this thesis was to fill this knowledge gap. In particular, the temperature effect as well as the effect of predator diversity were considered and how their interaction affects Collembola communities and their decomposition rate. The experimental impact was investigated with microcosms, which were stored by six different temperatures (12°C,15°C,18°C,21°C,24°C,27°C) and populated with Collembola (*H.nitidus* and *F.candida*) and predator species (mites and Chilopods). After the experiment the animals were extracted by a modified Kempson apparatus (Kempson et al. 1963) and the species abundance was determined. The set-up of the microcosms was similar to the microcosms, which were used in the experiment of Thakur et al. (2017). During the microscopy, the body length was measured followed by the calculation of biomass and body mass. In the following analysis the response variables of Collembola abundance, biomass and body mass as well as basal respiration and microbial biomass carbon were examined. The analysis was performed with ZIMs (abundance) and GLMs (biomass, body mass, basal respiration and microbial biomass carbon). To assess the predation effect, the predation was investigated by detail. The predation predictors included the occurrence of a predator (mite or Chilopod), the mite abundance and the body mass of Chilopods. Based on the results the hypothesis of the temperature and predation levels effect can be confirmed in regard to the temperature effect and an interactive effect of temperature and mite abundance. Thus, the second hypothesis of the dependence of the two treatments can also be confirmed. It could be proven, that the body mass of Chilopods has an impact on Collembola and that their presence shows significance in an additive system with temperature. It is possible to interpret the results of basal respiration and microbial biomass carbon in that way, that there might be a trophic cascade. But the temperature showed in all models the highest significance. This means that the soil fauna is much more impacted by the temperature, which will increased caused by climate change, than by the predation. Also, there was no evidence found, that especially predator diversity has impact on prey species. It was shown, that the temperature above 24°C has a supressing effect on Collembola abundance, biomass and body mass. If this effect is

considered on a large scale, very high temperatures in summer would affect soil organisms in such a way that this could have an impact on the decomposition of organic material and consequently on the entire ecosystem.

A repetition of the experiment would be fruitful if the Collembola were used with a higher number of individuals and the temperature range would be chosen to be smaller so that the temperature effect could not mask the predation effect. Furthermore, with the help of regressions from the existing data of basal respiration and microbial biomass carbon, the decomposition rate of Collembola could be concluded. Further research is encouraged, specifically on multifactorial cross-over experiments investigating predictor diversity and its influence on the ecosystem, because the impacts of the climate change are not limited to one factor and the especially soil organisms are important regulators within ecosystems. Only with experiments which are including various factors a realistic assessment of the risks of climate change can be made.

8 Zusammenfassung

Um die Auswirkungen des Klimawandels auf Ökosysteme beurteilen zu können, müssen die Interaktionen von Organismen innerhalb dieser Ökosysteme verstanden werden. Dies wurde in verschiedenen Studien getan, darunter Thakur et al. (2017), aber der multifaktorielle Bezug wurde nicht einbezogen, und das Ziel dieser Arbeit war es, diese Wissenslücke zu schließen. Insbesondere wurden der Temperatureffekt sowie der Effekt der Räuberdiversität betrachtet und wie sich deren Interaktion auf Collembola-Gemeinschaften und deren Zersetzungsrate auswirkt. Die experimentellen Auswirkungen wurden mit Mikrokosmen untersucht, die bei sechs verschiedenen Temperaturen (12℃, 15°C, 18°C, 21°C, 24°C, 27°C) gelagert und mit Collembola (H. nitidus und F. candida) und Räuberarten (Milben und Chilopoden) besiedelt wurden. Nach dem Versuch wurden die Tiere mit einer modifizierten Kempson-Apparatur (Kempson et al. 1963) extrahiert und der Artenreichtum bestimmt. Der Aufbau der Mikrokosmen war ähnlich wie bei den Mikrokosmen, die im Experiment von Thakur et al. (2017) verwendet wurden. Während der Mikroskopie wurde die Körperlänge gemessen, gefolgt von der Berechnung der Biomasse und der Körpermasse. In der folgenden Analyse wurden die Reaktionsvariablen Collembolenhäufigkeit, Biomasse und Körpermasse sowie die Basalatmung und die mikrobielle Biomasse Kohlenstoff untersucht. Die Analyse wurde mit ZIMs (Abundanz) und GLMs (Biomasse, Körpermasse, Basalatmung und mikrobieller Biomassekohlenstoff) durchgeführt. Zur Bewertung des Prädationseffekts wurde die Prädation im Detail untersucht. Zu den Prädiktoren für die Prädation gehörten das Vorkommen eines Räubers (Milbe oder Chilopode), die Milbenhäufigkeit und die Körpermasse der Chilopoden. Anhand der Ergebnisse kann die Hypothese des Effekts von Temperatur und Prädationsebenen in Bezug auf den Temperatureffekt und einen interaktiven Effekt von Temperatur und Milbenhäufigkeit bestätigt werden. Somit kann auch die zweite Hypothese der Abhängigkeit der beiden Behandlungen bestätigt werden. Es konnte nachgewiesen werden, dass die Körpermasse der Chilopoden einen Einfluss auf die Collembola hat und dass ihr Vorhandensein in einem additiven System mit der Temperatur von Bedeutung ist. Die Ergebnisse der Basalatmung und des mikrobiellen Biomasse-Kohlenstoffs können dahingehend interpretiert werden, dass es eine trophische Kaskade geben könnte. Aber die Temperatur zeigte in allen Modellen die höchste Signifikanz. Das bedeutet, dass die Bodenfauna viel stärker von der Temperatur

beeinflusst wird, die durch den Klimawandel steigen wird, als von der Prädation. Es wurde auch kein Hinweis darauf gefunden, dass insbesondere die Vielfalt der Räuber einen Einfluss auf die Beutetierarten hat. Es wurde gezeigt, dass die Temperatur über 24°C eine unterdrückende Wirkung auf die Abundanz, Biomasse und Körpermasse von Collembola hat. Betrachtet man diesen Effekt in großem Maßstab, so würden sehr hohe Temperaturen im Sommer die Bodenorganismen so beeinflussen, dass dies Auswirkungen auf die Zersetzung von organischem Material und damit auf das gesamte Ökosystem haben könnte.

Eine Wiederholung des Versuchs wäre fruchtbar, wenn die Collembola mit einer höheren Individuenzahl eingesetzt und der Temperaturbereich kleiner gewählt würde, damit der Temperatureffekt den Prädationseffekt nicht überdeckt. Außerdem könnte mit Hilfe von Regressionen aus den vorhandenen Daten zur Grundatmung und zur mikrobiellen Biomasse Kohlenstoff auf die Zersetzungsrate der Collembola geschlossen werden. Da die Auswirkungen des Klimawandels nicht auf einen Faktor beschränkt sind und insbesondere die Bodenorganismen wichtige Regulatoren innerhalb von Ökosystemen sind, werden weitere Forschungen angeregt, insbesondere zu multifaktoriellen Cross-Over-Experimenten, die die Vielfalt der Prädiktoren und deren Einfluss auf das Ökosystem untersuchen. Nur mit Experimenten, die verschiedene Faktoren einbeziehen, kann eine realistische Einschätzung der Risiken des Klimawandels vorgenommen werden.

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig und nur unter Verwendung der angegebenen Literatur und Hilfsmittel angefertigt habe.

Stellen, die wörtlich oder sinngemäß aus Quellen entnommen wurden, sind als solche kenntlich gemacht.

Diese Arbeit wurde in gleicher oder ähnlicher Form noch keiner anderen Prüfungsbehörde vorgelegt.

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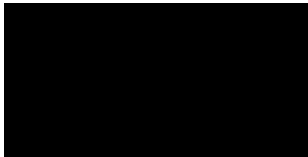
Susanne Jahn

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