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Jonathan Bonfanti, Mickael Hedde, Jérôme Cortet, Paul Henning Krogh, Klaus Larsen, Martin Holmstrup

Version of Record: https://www.sciencedirect.com/science/article/pii/S0031405622000014
Manuscript_2baf2da5438f461b11fa2a494ad6720e

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Journal: Pedobiologia

Authors & affiliations:

Jonathan Bonfanti [a], Mickaël Hedde [b], Jérôme Cortet [a], Paul Henning Krogh [c], Klaus S. Larsen [d], Martin Holmstrup [c]

[a] CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3, Montpellier, France

[b] Eco&Sols, INRAE, Université Montpellier, CIRAD, IRD, Montpellier SupAgro, Montpellier, France

[c] Department of Bioscience, Aarhus University, Vejlsøvej 25, DK-8600 Silkeborg, Denmark

[d] Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg, Denmark

Corresponding author:

Jonathan Bonfanti

E-mail: jonathan.bonfanti@gmail.com (permanent) / jonathan.bonfanti@cirad.fr (current)

Postal address: CEFE, Bâtiment J, Université Paul-Valéry Montpellier 3, Route de Mende, 34199 Montpellier (France)

Abstract

Soil ecosystems, and the fauna they host, are known to provide many services and communities of Collembola can be used as bioindicators of soil functionality. Climate change is often expected to threaten Collembola, however, it is possible that it could also favour them. Previous studies have shown that the structure of collembolan communities can be shaped by long-term adaptation to climate, and that temperature plays a major role in the variation of species traits. In this study, we evaluated how the functional composition and structure of collembolan communities are impacted by climate change using an experimental climate manipulation design. The study used data from the CLIMAITE experiment, which was carried out in Denmark in an unmanaged heath/grassland ecosystem that was subjected to the simulated predicted climate for the year 2075. The climate manipulation experiment parameters included elevated temperature, elevated concentration of atmospheric CO_2 and extended drought, which were tested alone and in combination on a total of 48 plots, including controls. Collembola were sampled using 10-cm-depth soil cores after 1, 2 and 8 years of climate manipulation. We posited (i) that a stimulating factor (elevated CO_2) would increase mean body length, and (ii) that an inhibiting factor (drought) would favour traits indicating a euedaphic life or an ability to present resistance mechanisms (scales, ecomorphosis) and would reduce functional structure indices through environmental filtering. The results did not support these hypotheses. While the findings showed sporadic effects of the climatic treatments on the functional composition and structure, they did not demonstrate any general community response pattern. This may be due to limitations of the study in terms of climatic intensity or community assembly, opening perspectives for future experiments in terms of the choice of traits and measurements.

Keywords: trait, climate change, Collembola, community-weighted mean, resilience, soil fauna

Highlights

1. In an 8-year field experiment we increased temperature, atmospheric CO_2 and drought duration

2. Collembolan communities were sampled under different climatic treatments and controls

3. Their short-term, mid-term and long-term functional responses were scrutinised

4. Only minor effects of climate change on collembolan traits were observed

5. Collembola appear functionally resilient to climate change of moderate intensity

1. Introduction

The world is currently experiencing a series of global changes due to human activities. One of these is climate change, which is expected to occur at a rapid rate over the 21st century. The increasing concentration of CO_2 in the atmosphere is causing rising temperatures and increased variation in precipitation patterns, including extended periods of summer drought (IPCC, 2018). These environmental factors – and their interactions (Rillig et al., 2019) – are expected to have an impact both on soil organisms and the physico-chemical properties of soil, potentially threatening soil ecosystem functioning. As soil ecosystems provide numerous ecosystem services, in the context of climate change, research into these systems is urgent (Wall & Six, 2015).

Soil invertebrates and Collembola in particular contribute to several ecological functions in soil, such as organic matter decomposition, microbial activity regulation, soil structure, etc. (Hopkin, 1997; Lavelle et al., 2006) and this contribution is climate dependent (Wall et al., 2008). Yet the impacts of commonly projected climatic scenarios based on temperature, drought or CO_2 on soil biota in general may differ (Blankinship et al., 2011; Meehan et al., 2020). The links between organisms and ecosystem functioning are increasingly explored by studying functional traits (Violle et al., 2007). Such trait-based studies have been widely used in plant ecology, notably to explore trait–climate relationships in a changing world (Wieczynski et al., 2019). A growing body of evidence shows that functional diversity helps to understand how terrestrial ecosystems – including soil fauna – respond to climate change at a community level (Bardgett & van der Putten, 2014). To date, the complexity of the links between soil fauna and soil ecosystem functioning has been little studied in a climate change context (Wolters et al., 2000). However, trait-based approaches are becoming more common in soil fauna studies (Pey et al., 2014) given the current need for relevant descriptive data concerning soil invertebrates (Phillips et al., 2017) and the ability of species traits to explain soil functioning in complement to taxonomic indicators (Heemsbergen, 2004). In the present study, we aim to investigate the links between collembolan communities – bioindicators within soil fauna – and climate change using a trait-based approach.

Elevated temperature may have (i) direct positive effects on soil fauna, by bringing species closer to their performance optimum, especially at high latitudes (Deutsch et al., 2008), as well as (ii) indirect positive effects, notably on food supply: for decomposers through increased plant growth (Dietzen et al., 2019; Rustad et al., 2001) and for grazers through changes in the fungi:bacteria ratio (Haugwitz et al., 2014). Elevated atmospheric CO_2 may also have indirect positive effects, by contributing to an increase in plant litter C:N ratios, net primary production (Pendall et al., 2004) and plant biomass (Wang et al., 2012), and thus of food supply available for decomposers. C:N ratio was thus positively affecting collembolan communities' diversity in heathland after 2 years of elevated CO_2 condition (Holmstrup et al., 2017). Moreover, an increase in both temperature and CO_2 might potentially reinforce one another (Bradford et al., 2016). In contrast, extended summer droughts are expected to have negative effects on soil fauna, as the precipitation regime is considered to have a greater general impact on soil biota than temperature and CO_2 (Blankinship et al., 2011). Drought is also expected to impact community assembly processes in Collembola since these animals express a moisture preference gradient at a species level from drought tolerant to drought sensitive species. The species' abundances are thus expected to vary with soil moisture when facing a drought event e.g. during the summer season (Verhoef & Selm, 1983). These effects might be lethal, or they may lead to non-lethal adaptations, such as triggering resistance mechanisms in these organisms (Holmstrup & Bayley, 2013) or behavioural avoidance responses (Tsiafouli et al., 2005).

Communities of Collembola are known to respond along several gradients, such as land use (Joimel et al., 2017) or their vertical position in the soil profile (Cortet & Poinsot-Balaguer, 1998). Furthermore, in the face of temperature and/or moisture stress, some collembolans are able to form climate-specific resistance stages through so-called ecomorphosis (Cassagnau, 1974). Trait–environment relationships have been studied in Collembola on a range of scales, from local (Santorufo et al., 2015) to large areas (Salmon et al., 2014). These relationships can be explored through single-trait (Garnier et al., 2004) and multi-traits (Mouillot et al., 2013) metrics. In a context of climate change, it is thus relevant to explore the impacts of increasing temperatures, CO_2 and drought on Collembola traits in soils.

To test for the effects of different climatic parameters on the functional composition and structure of collembolan communities, we used data from the CLIMAITE experiment in Denmark, which has been simulating realistic climate change modifications in a semi-natural ecosystem (Mikkelsen et al., 2008). In this experiment, all combinations of three climatic parameters – elevated temperature, elevated atmospheric CO_2 and extended summer drought – were tested. Their consequences on soil biodiversity were measured over a period of eight years, in order to track the temporal dynamics of soil biodiversity responses. However, hypothesizing the trait–environment relationships in such a dynamic and complex system can be a challenge since multiple possible effects and interactions between such effects are to be expected in a full-factorial experiment. For simplicity, we therefore stated the following hypotheses on the relationships between traits and environment:

(1) We expected elevated CO_2 to enhance the availability of organic matter in soils leading to larger collembolan body size.

(2) As drought exposure is most pronounced at the soil surface, we expected extended drought to threaten species living there (i.e. epiedaphic) and to favour soil-inhabiting species (euedaphic) and/or species with resistance abilities, e.g. via ecomorphosis (Cassagnau, 1974) or scales (Cortet & Poinsot-Balaguer, 1998). In addition, we expected this stressful environmental factor to reduce functional diversity through environmental filtering processes (Cornwell et al., 2006) through which the environment constraint trait values to narrower ranges thus filtering individuals and species in realized communities.

2. Materials & methods

2.1 Experimental site and climatic treatments

The CLIMAITE experiment is extensively described by Mikkelsen et al. (2008). The experimental site is located in Brandbjerg, Denmark (55°53′ N, 11°58′ E) on a hilly, nutrient-poor sandy substrate. It consists of heathland and grassland dominated by the grass *Deschampsia flexuosa* L. and the dwarf shrub *Calluna vulgaris* Hull, 1808. Long-term annual mean precipitation and air temperature (1961–90) for the area was 613 mm and 8.0°C, respectively (www.dmi.dk in Mikkelsen et al., 2008), while the mean data from the site's meteorological station during the study period (2006–13) showed mean annual precipitation and air temperature of 648 mm and 9.7°C (Larsen et al., 2019). An experimental design using automated curtains allowed the control of three climatic parameters: elevated temperature (aiming for +2°C), elevated atmospheric concentration of CO_2 (aiming for 510 ppm) and reduced soil moisture (aiming to simulate a more intense summer drought). The effect of the temperature and drought conditions are presented in Annex 1. These climatic modifications were consistent with the expected climate in 2075 in Denmark at the time the experiment was designed (IPCC, 2001). The experiment started in October 2005. A full-factorial design was used, allowing each parameter to be tested alone (T: elevated temperature, D: extended drought period, CO_2: elevated CO_2) and in each combination (TD for 'Temperature x Drought', and the following DCO_2, TCO_2, $TDCO_2$), resulting in 7 climatic treatments in addition to control plots (A: ambient controls). Each of these climatic treatments and the controls were replicated 6 times on a total of 48 plots. The efficacy of treatments have been documented in several studies (Holmstrup et al., 2015; Vestergård et al., 2015): the actual increased air concentration of CO_2 was very close to the target of 510 ppm, and the extended drought (3–4 weeks) resulted in a water content of 4–5 vol%. However, the average soil temperature in warmed plots was not more than 0.5–1°C.

2.2 Collembola abundance data

Collembola were sampled at different phases of the experiment: after **short-term** exposure (October 2006), after **medium-term** exposure (October 2007), and after **long-term** exposure (2012–13). For the latter, there were three sampling dates: August 2012 (summer, after the 'Drought' treatment); April 2013 (mid-spring, before the 'Drought'); June 2013 (early summer, just at the end of the 'Drought'), resulting in a total of five sampled temporal phases. In total, our data gathers 240 communities (5 temporal phases * [7 treatments + 1 control] * 6 replicates).

Soil mesofauna was sampled using one cylindrical soil core (diameter 5.5 cm; depth 10 cm, except for June 2013 when the soil core depth was 5 cm) per plot, and was extracted with a Macfadyen-type high thermal gradient device (Macfadyen, 1961). Collembola were then isolated and identified to species level (Fjellberg, 1998, 2007; Zimdars, 1994 and 'Synopses'). For our study, individuals that could be identified only to genus level were counted as their morphologically closest local species as a proxy; these attribution choices are detailed in our Raw data files. Individuals that could not be identified at least to genus level were removed from our analysis; this represented a low proportion of the total individuals (and all belonged to the *Symphypleona* order): 0% of individuals were removed in 2006, 4.3% in 2007, 3% in 2012, 6.3% in April 2013 and 8.4% in June 2013. These proportions are much lower than those of the dominant species of Collembola in CLIMAITE communities and are thus unlikely to impact conclusions based on community-weighted metrics.

2.3 Collembola trait data

Trait data was extracted at species level from the open-access BETSI database (https://portail.betsi.cnrs.fr). We first selected trait values from Scandinavian sources, then completed the dataset with Gisin (1960) and Zimdars (1994 and 'Synopses') values, as recommended by Bonfanti et al. (2018). Computation of several literature sources – thus trait values – per trait per species, were made possible by using a fuzzy coding procedure: splitting traits into binary attributes coded in percentage (except for body length, continuous value in mm) as described in Hedde et al. (2012). Five morphological traits were used from this dataset (pigmentation, furca, body shape, scales, body size). **Absence of pigmentation** and **absence of a furca** are both sensitive traits that reveal a species' preference for the vertical position in the soil habitat: pigmentation, when present, is a protection against sunlight and indicative of a hemiedaphic or epiedaphic life form. A furca, when present and developed, confers high immediate motility through springing (e.g. to avoid danger). **Body shape** might be partly linked to the species' vertical position in the soil, so we also considered that it reflects the sensitivity of a species to desiccation. Cylindrical body shapes have a higher surface-to-volume ratio than spherical body shapes, relatively increasing their risk of desiccation (Kaersgaard et al., 2004). The **presence of scales** is expected to strengthen the cuticular impermeability of a species and can generally be considered to protect against evaporative water loss. We selected **body size** as a general performance trait. We considered that body size is notably linked to energy transfers in soil ecosystems – Collembola being both a very abundant group of microbial feeders and a very abundant pool of prey for taxa of higher trophic levels. Additionally, we also considered the ability of a species to display **ecomorphosis** as a feature of interest, here used as a trait in further analysis. This strategy allows an individual to switch into specific resistance stages triggered by stressful environmental conditions, notably temperature increase and drought during the summer season. The data on ecomorphosis ability was obtained from Bonfanti (2021). A summary of these traits and their links to our hypotheses is given in Table 1. Species trait values used in the analysis are listed in raw data files.

2.4 Statistical analysis

2.4.1 Communities' functional composition and structure

Based on these six traits, we investigated: (i) the functional composition of a community and (ii) its functional structure. To do this, we calculated the community-weighted mean (CWM) metric (Garnier et al., 2004) as follows: $CWM_{j,y} = \sum_{k=1}^{n_j} A_{k,j} \cdot z_k$, where n_j is the number of species sampled in plot j, $A_{k,j}$ is the relative abundance of species k in plot j, and z_k is the mean value of species k. To visualize the multidimensional response of communities' functional composition to time and climatic treatments factors, we built a functional space using a Principal Component Analysis (PCA) ran on the 240 communities (lines), described by their six CWM trait values as quantitative variables (columns), from which we display the two first axes. Additionally, to visualize how n species (e.g., the experimental site species pool from one temporal phase) are located within the same trait space, we ran a PCA on these n species (lines), described by their six trait values as quantitative variables (columns), from which we display the two first axes.

We then calculated three complementary distance-based functional diversity indices revealing different facets of a community's functional structure: functional richness (FRic) that represents the volume of the functional space occupied by the community, functional evenness (FEve) that expresses the regularity of the distribution of species abundance in this volume, and functional divergence that represents the divergence in the distribution of abundance in this volume (FDiv) (Villéger et al., 2008).

2.4.2 Effects of climatic parameters on community metrics

To test the effect of each climatic treatment on CWM trait values and on functional diversity indices in each community, we used linear mixed-effects models, with the position of each plot in Blocks then in Octagons as random variables, as in Vestergård et al. (2015). For CWM trait values expressed in percentages, a logit transformation was applied beforehand as suggested by Warton & Hui (2011). The statistical significance of models was tested with type-II Anova. We then investigated the significance of post-hoc pairwise comparisons between the seven climatic treatments and the controls with multiple comparisons of means by Tukey contrasts.

Then the main effects of the three modified climatic parameters ('Temperature', 'Drought' or 'CO_2') were characterized with a standardized effect size mean difference: $\theta = \frac{\mu_1 - \mu_0}{\sigma}$, where μ_1 is the mean CWM value in plots containing a modified climatic parameter, and μ_0 the mean CWM value in plots used as controls (i.e. not subject to this modified climatic parameter), and σ is the standard deviation of the whole CWM value series for each climatic parameter.

The analyses were performed in R software, version 3.4.0 (R Core Team, 2017), using the following R packages: “FD” (Laliberté & Legendre, 2010), “lme4” (Bates et al., 2015), “car” (Fox & Weisberg, 2011), “multcomp” (Hothorn et al., 2008), “ggplot2” (Wickham, 2016), “ggalt” (Rudis et al., 2017), “FactoMineR” (Lê et al., 2008), “factoextra” (Mundt & Kassambara, 2020).

3. Results

3.1 Effects on community functional composition

3.1.2 Pairwise comparisons of climatic treatments

The mean CWM trait values per climatic treatment for every temporal phase are presented in Table 2, and the detailed CWM trait values in Annex 2. All the statistical tests outputs used to conclude on the effects of climatic treatments on CWM values are detailed in Annex 3. After **short-term** exposure, we generally observed no effect of treatments on mean trait values (Figure 1). In this temporal phase, on average, the absence of pigmentation varied from 30–55%, cylindrical body shape from 54–72%, the presence of ecomorphosis from 1–7%, the presence of scales from 13–20%, the absence of furca from 33–47%, and body length from 0.83–0.99 mm. We noted a significant difference in the presence of ecomorphosis, with 'Temperature' treatment exhibiting higher values than 'Temperature x Drought' treatment (Anova χ^2=21.6; df=8; p<0.01).

After **medium-term** exposure, we observed no effect of treatments on trait values. In this temporal phase, on average, the absence of pigmentation varied from 40–62%, cylindrical body shape from 72–91%, the presence of ecomorphosis from 4–18%, the presence of scales from 0–7%, the absence of furca from 32–55%, and body length from 0.96–1.39 mm.

After **long-term** exposure, we generally observed no effect of treatments on trait values. In this period, in which samples were taken at three temporal phases, on average, the absence of pigmentation varied from 38–79%, cylindrical body shape from 63–94%, the presence of ecomorphosis from 0–6%, the presence of scales from 0–10%, the absence of furca from 13–55% and body length from 0.85–1.50 mm. We noted a significant difference in the absence of furca in spring 2013, with 'Drought' treatment exhibiting higher values than 'Temperature x CO_2' treatment (Anova χ^2=85.9; df=8; p<0.001).

Finally, after long-term exposure, the multidimensional response of the communities' functional composition to climatic treatments shows no clear pattern and especially no difference between the Controls (A) and the full factorial climatic simulation treatment ('Temperature x Drought x CO_2', $TDCO_2$) as shown by the large overlap of the ellipses on PCA in Figure 2. This absence of response pattern can also be observed at all the other temporal phases (Annex 4).

3.1.1 Main effects of climatic parameters

The main effects of each climatic parameter on CWM trait values and for each temporal phase are presented in Annex 5. We show only the cases for which a significant effect ($p<0.05$) was found and for which no interaction effect was found. Of the 90 main effects tested (3 parameters * 6 traits * 5 temporal phases), seven were significant. After medium-term exposure, elevated CO_2 led to a higher presence of cylindrical body shape. After long-term exposure, each modified climatic parameter led to a higher presence of cylindrical body shape, while extended drought led to a higher absence of pigmentation, and elevated CO_2 led to a higher presence of ecomorphosis and of scales.

3.2 Effects on community functional structure

We generally observed no effect of the climatic treatments on functional diversity indices, either after short-term, medium-term or long-term exposure (Table 2). After short-term exposure and for all treatments, functional richness varied from 0.06 to 0.83, functional evenness from 0.15 to 0.85 and functional divergence from 0.52 to 0.99. After medium-term exposure and for all treatments, functional richness varied from 0.02 to 0.95, functional evenness from 0.08 to 0.97 and functional divergence from 0.34 to 0.96. After long-term exposure and for all treatments, functional richness varied from 0.00 to 0.85, functional evenness from 0.10 to 0.97 and functional divergence from 0.42 to 0.99. We did note a significant difference in functional divergence in spring 2013, with 'Drought' treatment exhibiting higher values than 'Temperature x CO_2' treatment (Anova χ^2=1148.6; df=8; $p<0.001$). A high intra-treatments variability of scores is observed.

4. Discussion

Generally, the results did not indicate any marked effect of the climatic treatments on the chosen community metrics, in contrast to what we had expected. While our hypotheses were based on independent climatic parameters, climatic treatments resulting from combinations of factors were more complex to postulate. Nonetheless, we expected an elevated temperature combined with an extended drought to be even more stressful, as elevated temperatures increase evaporation and thus reduce moisture in soils. However, such an additive effect was not observed. The full factorial climatic simulation treatment ('Temperature x Drought x CO_2') allowed us to explore to what extent a combination of both stressful and stimulating factors would result in a balanced situation. This simulation of a future climate scenario showed no effect on community functional structure or composition – whether this is due to balance is hard to determine.

4.1 Almost no effect on functional structure and composition

According to our first hypothesis, we expected higher body size values resulting from CO_2 elevation. Conversely, our second hypothesis expected lower functional diversity values resulting from physiological constraints caused by drought.

In fact, few significant main effects of climatic parameters were observed and, of these, all were positive, meaning that they led to higher CWM values for every concerned trait. These significant effects were found only in three temporal phases and for four traits. Cylindrical body shape was slightly favoured by each of the climatic parameters and thus cannot be interpreted according to our hypotheses. Absence of pigmentation was slightly favoured by extended drought, which may indicate that euedaphic species might be more tolerant to this stress in the observed conditions, or that species confined to deeper soil layers are less exposed to drought, which may support our second hypothesis. But resistance traits such as the presence of ecomorphosis and the presence of scales were favoured by elevated CO_2, which goes against our first hypothesis, which expected this to be more a stimulating than a stressful factor. The two traits (presence of scales and ecomorphosis) that exhibited moderate effect sizes from climatic parameters (0.5–1 sd) also had very low CWM values (0–5%); in all other cases, the effect sizes were low. In general, the main effects were marginal considering the number of tests, and no clear pattern could be seen.

The multidimensional response of communities' functional composition showed a slight site-level temporal trajectory over the years, 2006 ellipse being relatively located apart from the others (Annex 4). This could be explained by a recovering process from the initial experimental set up considered as a perturbation, or by long-term dynamics of the communities responding to environmental factors (Jucevica & Melecis, 2006). We notice that these temporal dynamics seem to be expressed on the axis-1 related to traits indicating the affinity to euedaphic life habits, 2006 communities showing relatively more epiedaphic communities on average. Moreover, within the long-term phase, since the three ellipses seem also differentiated, we might observe a seasonal variability between samples. These three drivers – initial perturbation, annual and seasonal dynamics – may not be mutually exclusive and can bring variability to the communities' responses to the experimentally modified climatic parameters that we study.

Any significant differences that did exist between the effect of climatic treatments in CWM trait values went against our hypotheses, especially the second hypothesis. For example, we observed that the presence of ecomorphosis was highest in 'Temperature' (T) plots and lowest in 'Temperature x Drought' (TD) plots, in autumn 2006. At this period, two species were able to display ecomorphosis: *Folsomia quadrioculata* (Tullberg, 1871) and *Isotomurus palustris* (Müller, 1776) (raw data). Looking at the relative abundance of these species (raw data), the latter was only present in control plots (moreover, at a very low density), while *F. quadrioculata* was present in all treatments. Thus, the ecomorphosis was mainly explained by fluctuations in *F. quadrioculata* density, which was highest in T plots – ca. 7% – while it was only 0.7% in TD plots. We should note that we have a slight doubt concerning the proportion of ecomorphosis due to *I. palustris* abundance: in the dataset, we inferred this species as a proxy for collected *Isotomurus* individuals (raw data), but the literature mentions a *palustris*-complex (Potapov, 2001), and the status of different forms remains unclear. However, the neotype was described from individuals collected in Denmark, which reduces the misidentification risk about this Holarctic species in our study (Carapelli et al., 2001).

We also observed, in spring 2013, that the absence of furca was highest in 'Drought' (D) plots and lowest in 'Temperature x CO_2' (TCO_2) plots. Looking at species relative abundance (raw data), *Isotomiella minor* Schäffer, 1896 was particularly abundant in TCO_2 plots, and this species has a furca. At this period, its relative abundance reached an average of ca. 70% in TCO_2 plots. Conversely, its relative abundance was lower in D plots, where the communities were dominated mainly by *Mesaphorura macrochaeta* Rusek, 1976; this species does not have a furca and reached an average ca. 51% of relative abundance in these plots.

In both of these examples, the marginal effects of climatic treatments on ecomorphosis and on the absence of furca may be attributable to variation in a single species' relative abundance – *F. quadrioculata*, *I. minor* or *M. macrochaeta* – thus strongly driving the CWM values in the concerned communities. Since the presence of *I. minor* and, to a lesser extent, *M. macrochaeta* in such high abundance has been observed in the same plots over the years, we may suspect a 'foundation effect' (Schöb et al., 2012), i.e. a dependency on the high abundance of a species locally present at the setup of the experiment, more than a true climatic effect.

Following the same trend, community functional structure, through functional diversity indices calculations, mostly did not allow us to detect any effect of climatic treatments in this study. The effect found on functional divergence (FDiv) in spring 2013 followed the previously described pattern ('Drought' vs 'Temperature x CO_2' plots). This can again be explained by looking at species dominance, FDiv being sensitive to relative abundance. In the spring 2013 trait space (Annex 6) based on our six traits, we can see that *I. minor*, dominating in TCO_2 plots with a low FDiv value, is located in the centre. Thus, switching community dominance to *M. macrochaeta* (in D plots) results in a wider FDiv volume since the latter species is located more externally in the trait space (see e.g. Mouillot et al., 2013). Furthermore, in CLIMAITE communities at any sampling date, the most abundant species were in most cases either *I. minor*, *M. macrochaeta* or *Parisotoma notabilis*

(Schäffer, 1896). They may represent a slight gradient of euedaphic life habits, observed on axis-1 in Annex 6, as they differ in terms of pigmentation, furca and body length (raw data).

In addition to these slight discrepancies in the traits of dominant species, considering the relatively low number of species present in plots and the species richness ranges present within treatments, it can be mathematically expected to observe a wide range of functional richness values, which are directly linked to species richness. Likewise, a wide range could be expected in functional evenness and functional divergence values, which exhibit high variability when there are a low number of species in a community (Schleuter et al., 2010). These amplitudes of functional diversity indices responses may actually blur discrepancies that could be caused by any climatic effect in the experiment, and we may speculate to what extent the community assembly occurred under neutral processes, rather than under environmental (climatic) filtering processes, which remains to be tested (Mouchet et al., 2010).

4.2 Comparison with similar studies

In another field experiment with a similar design conducted on an old-field grassland, the effects of climatic parameters on Collembola after long-term exposure were contrasted (Kardol et al., 2011). While functional traits were not studied, taxonomic responses revealed low impacts of climatic treatments even at a higher magnitude (e.g. warming of ca. +3°C) than in the CLIMAITE experiment. Collembola abundance tended to decrease with a reduction in precipitation, while the low effects of elevated temperature and CO_2 were probably indirect, i.e. mediated through availability of water in the soil. However, the authors mention shifts in community composition, which we did not observe in our experiment, and that might have driven changes in CWM trait values, which remains to be tested. Kardol et al. (2011) also mentioned high within-treatments variation in microarthropods responses, possibly blurring discrepancies in communities' responses across different treatments.

A more recent field experiment showed that collembolan community functional diversity is sensitive to elevated temperature (Holmstrup et al., 2018). However, the magnitude of the maximum temperature increase was much larger (up to +10°C) than in our study and was due to geothermal activity. Moreover, this effect was observed after 6 years but was not detected after 50 years, suggesting the high functional resilience of Collembola in a long-time horizon. Finally, the authors mention a negative correlation between temperature and CWM body size, thus illustrating metabolic scaling rules that result in smaller species being favoured at higher temperatures due to higher individual and population growth rates (Brown et al., 2004).

In a plant–soil mesocosm experiment, soil fauna was impacted by +3.5°C warming after medium-term exposure (2 years), resulting in a decrease of epigeic soil fauna and increased diversity in fungivore species (Briones et al., 2009). Again, we did not observe such changes in our study, likely due to the modest warming of 0.5–1°C. Traits that might reveal facets of a euedaphic life forms, such as small body size, absence of pigmentation or absence of scales, were not sensitive to warming in this range of temperature increase.

Lastly, we note that CLIMAITE community abundance was consistent with that found in the literature. Collembola mean density per plot ranged mostly from 2.10^3 to 9.10^3 ind./m^2 (raw data), which is slightly lower than the mean 10 to 12.10^3 ind./m^2 found in French grasslands (Joimel et al., 2017), while maximum density values were the same (ca. 40.10^3 ind./m^2 in both cases).

4.3 Why were so few effects observed in our study?

A comparison with related literature allowed us to identify two notable causes for the lack of effects of climate modifications found in our study: high stochasticity in community composition and climatic intensity modifications that were possibly too low regarding the tolerance limits of the studied species.

4.3.1 High community stochasticity

Our results showed high amplitude in functional diversity indices values, which may be due to high variability in community structure and composition within the climatic treatments and may explain the lack of difference in comparisons between the different treatments. The local stochasticity in community composition mentioned by Kardol et al. (2011) should be considered regarding the relative body size of our biological model compared to the scale of the experimental design. Theory has predicted how sampling scale can influence the relative importance of environmental factors (such as those in our hypotheses) versus neutral factors (Chase, 2014). We based our hypotheses on the effect of environmental (i.e. niche) factors while, in fact, collembolan communities may be assembled under mainly neutral (i.e. stochastic) factors, thus hindering responses between different conditions. This assumption of high stochasticity has been observed for collembolan species at a small scale (Van Der Wurff et al., 2003), and more generally for mesofauna species in soils on a 12-ha experimental site (Zinger et al., 2018), and is also consistent with the fine-scale and meso-scale horizontal distribution of soil mesofauna described by Berg (2012). In other words, while our experiment tried to intentionally shift the macro-scale ecological preferences of species by modifying the ambient climatic conditions, we observed them at an experimental scale in which communities are too stochastically assembled to detect significant discrepancies.

4.3.2 Climatic intensity modifications that were too low given the organisms' thermal tolerance

Another possible explanation for our results could be the moderate intensity (although consistent with e.g. Barreto et al., 2021) of climatic changes applied in the experiment (Blankinship et al., 2011), with the consequence that the individuals were not stressed to any significant degree, and the ecological preferences of species were not threatened. A similar subtlety in the effects of temperature elevation on collembolan traits was observed even following an 'extreme' event of +4°C during 17 days (Krab et al., 2013).

If we look at the thermal tolerance of soil animals, it has been observed that terrestrial ectotherms' warmer distribution range boundaries do not indicate their maximum heat tolerance (Sunday et al., 2012), and that soil ectotherms in northern European latitudes (CLIMAITE site: ca. 55°N) exhibit the broadest thermal tolerance (Deutsch et al., 2008). These species are thus currently living in climates that are cooler than their optimum and are consequently not threatened by moderate warming; in fact, this probably has a stimulating effect. The same assumption may apply to other climatic parameters as well, if the relative changes are too small to trigger a threat to local species and/or populations. Indeed, the three species dominating CLIMAITE communities (*I. minor*, *M. macrochaeta* and *P. notabilis*) are known to be eurytopic, meaning they are commonly found across several European regions, and especially in northern Europe (Dunger & Schlitt, 2011; Potapov, 2001), in different biomes and climates. They are thus likely to have a wide climatic tolerance range and to exhibit wide phenotypic plasticity.

The magnitude of plasticity per se may yet depend on the environment (Liefting & Ellers, 2008). These authors mentioned that elevated temperature positively increased the growth rate of animals generally, which is consistent with the theory of performance–temperature relationships. Both are expected to be positively correlated, not necessarily in terms of maximum attainable adult body length (which is species-specific and determined by the species' plasticity), but also in terms of growth rate (Angilletta, 2009). However, this effect was higher in forest populations than in heathland populations of *Orchesella cincta* (Linnaeus, 1758), a broadly distributed epiedaphic Collembola species. This discrepancy was unexpected, heathlands being more climatically variable than forests, thus susceptible to select for populations with higher plasticity. Liefting & Ellers (2008) concluded that fitness traits (i.e. functional traits *stricto sensu*) and morphological traits can follow opposite directions in this case, illustrating a trade-off between the energy involved in strategies 'to remain plastic' versus strategies 'to remain performant'. Habitat-specific relationships were shown, but the general costs of thermal plasticity were considered to be still poorly understood in these animals.

4.4 Perspectives: how to track changes in soil biodiversity?

4.4.1 On the difficulty to build proper hypotheses

The links between climatic parameters and collembolan traits at the community level and on a field study were difficult to hypothesize on. Notably, the links between body size and temperature are complex. Assuming a correlation between temperature and latitude, Bonfanti et al. (2018) showed that mean body size between several collembolan populations (intraspecific trait variability) peaked in northern Europe, but the observed geographical gradient was limited to 55–60°N. In contrast, Ulrich & Fiera (2010) showed that species body size (interspecific trait variability) peaked around 45°N, with an observed gradient going up to 80°N. Moreover the duration of exposure to elevated temperatures may also play a role in community assembly processes (Rezende et al., 2014). Thus, interpreting a temperature elevation as a "moving south" gradient for local Danish species initially around 55° N we can imagine that: (i) after short exposures, intraspecific trait variability would play a greater role – the community dealing with species already present at the experimental start – resulting in a reduced body size and thus following 'downsizing' hypotheses (Lindo, 2015); whereas (ii) after long exposures, species out of their thermal niche could be replaced, making interspecific trait variability play a greater role, which would result in an elevated body size. It is also possible to consider a direct physiological effect of temperature on the development of individuals. In cold environment, although they are adapted, individuals' development may be still limited by low temperatures, a temperature elevation resulting in a faster growth (Birkemoe & Leinaas, 2000). We thus question the opportunity to involve in our analysis more traits – e.g., linked to physiology – and/or individual measurements of trait values.

4.4.2 Searching for sensitive and functionally important traits

As mentioned, the climate modifications in our study may not have been sufficient to move species out of their tolerance range, and probably moved them closer to their performance optimum. Nor did we observe negative effects from the 'Drought' treatment, although this factor was expected to induce physiological constraints on the organisms. Even in stressful temperature conditions, desiccation has been shown to be even more threatening, such as in termites and other soil ectotherms (Woon et al., 2019). The ecomorphosis trait did not reveal any response to drought (except for those we inferred to a 'foundation effect'). So which traits would be good indicators of effects related to climate change? Bahrndorff et al. (2006) showed that in a eurytopic species (*O. cincta*) intraspecific trait variability is observable in climatic stress-related traits, and mentioned the genetic adaptation of populations. Over an approximately 2000-km north-to-south European gradient, latitudinal clines were shown in traits related to resistance to high and low temperatures, desiccation, water loss rate, water pool and body size between populations. Individuals from the most northern and southern populations had the highest desiccation resistance. This pattern had been previously observed (Poinsot-Balaguer, 1990), suggesting that hydric stress, occurring in low or high temperature climates, induces convergent long-term physiological adaptations. It also suggests that northern European populations, such as the ones in CLIMAITE, may be adapted to cold conditions and thus have a high drought tolerance (Block, 1996; Holmstrup, 2014). This argument adds support to our explanation that the climatic modification in our study was too moderate to induce stress on the animals, which remained in the core of their climatic tolerance range and/or ecological preference. However, moderate changes in temperature may lead to other examples of sublethal reactions in collembolan individuals, such as body and membrane fatty acid composition (van Dooremalen & Ellers, 2010). In that study, storage lipids became more saturated over time during warm acclimation, while they became more unsaturated during cold acclimation. These reactions to cold were also in line with reactions to drought acclimation (Holmstrup et al., 2002). Other studies have found that Collembola can significantly acclimate to moderate drought stress and thus consistently elevate their survival rate when subject to acute drought stress (Sjursen et al., 2001). Hence, acclimation can improve the climatic stress tolerance of populations, and thus the resilience of communities, in a climate change context in which periods of drought are expected to increase in length and intensity.

4.4.3 Enhancing precision through measuring intraspecific trait variation

While we used trait values collected from the literature to make comparisons within our data, measurements of trait responses in the context of sub-lethal reactions led us to consider local intraspecific trait variability (ITV). Other evidence has shown that ITV may alter our perception of climate impacts on thermal tolerance in ectotherms (Herrando-Pérez et al., 2019). More generally, ITV has recently been observed in Collembola at biogeographical scales (Bonfanti et al., 2018) in a performance trait, namely body size. In other organisms, it has also been observed at regional or local scales, and it can account for a non-negligible part of the total trait variation in communities along ecological gradients (Siefert et al., 2015). We speculate as to what extent ITV may have helped in our CLIMAITE experiment to detect fine-scale changes in Collembola morphology, physiology and performance, as a growing body of research considers ITV an important facet to be taken into account in community ecological dynamics (Raffard et al., 2019). This opens up a potential interest in measuring individual traits – within the local population – in these communities, as it has recently been standardized in soils by Moretti et al. (2016), although the degree of precision is under discussion (Griffiths et al., 2016). For such abundant animals as Collembola, acquiring individual (and thus ITV) data would represent an extensive effort in such a large sampling experiment as CLIMAITE; the feasibility of these practices is currently being evaluated for several morphological traits (Raymond-Léonard et al., 2019).

Acknowledgements

JB received a PhD grant from Université Paul-Valéry Montpellier 3. The CLIMAITE experiment was supported by the Villum Foundation, Air Liquide Denmark A/S, DONG Energy and the INCREASE project ('Integrated Network on Climate-change Research Activities on Shrubland Ecosystems') (EC FP7-Infrastructure-2008-1 Grant Agreement 227628). The authors would like to thank all the BETSI database project managers and contributors. JB is grateful for the constructive remarks on the preliminary results from his colleagues during the TEBIS network annual meeting and the SFE^2 2018 International Conference on Ecological Sciences. The authors would also like to thank Zdenek Gavor for his helpful expertise on Collembola identification. We are thankful to C. Barreto and Z. Lindo for leading this special issue and to the reviewers who helped us improving our manuscript.

Data accessibility

Raw data (species identification and proxies' choices, species present in CLIMAITE and their trait values, communities' taxonomic composition for each temporal phase) are freely accessible online (https://doi.org/10.5281/zenodo.5795710). Trait data were obtained from the open-access BETSI database (https://portail.betsi.cnrs.fr). Collembola ecomorphosis data came from the literature analysis described in JB's PhD thesis (Bonfanti, 2021).

Supplementary materials

Annex 1 presents the mean soil temperature and soil water content values for the five temporal phases.

Annex 2 presents the detailed CWM trait values per plot for the five temporal phases.

Annex 3 presents the results and outputs of Anova tests and post-hoc pairwise comparisons on the effects of climatic treatments on CWM trait values and on FD indices.

Annex 4 presents the PCA displaying the functional space gathering the 240 communities responding to time and to climatic treatments.

Annex 5 presents the main effect of 'Temperature', 'Drought' and 'CO_2' modified parameters on CWM trait values in the communities.

Annex 6 presents the trait space filled by all species present in the spring 2013 temporal phase.

Tables

Table 1 – Summary of the 6 species features used in the analysis with their trait-related status according to the literature and the link to the tested hypothesis regarding the influence of elevated temperature, elevated CO_2 and extended drought on Collembola at a community level.

Species features	Status	Links to the hypotheses	Abbreviations used
Body shape	MPPB traits (Pey et al., 2014); Euedaphic life habit indicators (Martins da Silva et al., 2016)	"Cylindrical" confers susceptibility to Drought	BS_cyl
Furca		"Absence" favoured by Drought	Furca_0
Pigmentation		"Absence" favoured by Drought	Pig_0
Scales		"Presence" favoured by Drought	Scales_1
Body size	Performance trait (Pey et al., 2014)	Promoted by elevated temperature & CO_2	Body length
Ecomorphosis	Resistance strategy (Bonfanti, 2021; Cassagnau, 1974)	"Presence" confers resistance to Temperature and Drought	Ecom_1

Table 2 - Effects of climatic treatments on collembolan communities functional composition and functional structure after short-term, medium-term and long-term exposure. Mean and standard deviation values were estimated from raw indices values. Effects of climatic treatments were tested with type-II Anova on linear mixed-effects models, and post-hoc pairwise comparisons with multiple comparisons of means by Tukey contrasts. Bold values indicate that Anova and pairwise comparisons between treatments were significant (with a threshold of p<0.05). Treatments: A = control plots, T = elevated temperature, D = extended summer drought, CO_2 = elevated CO_2, and combined letters for the combinations of factors. Functional composition presents the average ± sd community-weighted mean trait values across all treatments. Traits/characteristics: Pig_0 = absence of pigmentation, BS_cyl = cylindrical body shape, Ecom_1 = presence of ecomorphosis, Scales_1 = presence of scales, Furca_0 = absence of furca (all these attributes are in %), Body length = body length (in mm). Functional structure presents mean functional diversity indices values across all treatments. Functional diversity indices: FRic = functional richness, FEve = functional evenness, FDiv = functional divergence.

	Short-term	**Medium-term**	**Long-term**		
	Autumn 2006	Autumn 2007	Summer 2012	Spring 2013	Early summer 2013
			Functional composition (mean ± sd)		
Pig_0	41 ± 19	50 ± 25	53 ± 21	68 ± 19	46 ± 21
BS_cyl	63 ± 17	81 ± 20	87 ± 10	89 ± 10	77 ± 17
Ecom_1	**2 ± 4** **T (a), TD (b), all other (ab)**	8 ± 11	0 ± 1	0 ± 1	1 ± 5
Scales_1	17 ± 12	3 ± 6	5 ± 9	1 ± 2	5 ± 7
Furca_0	39 ± 20	46 ± 23	23 ± 16	**35 ± 24** **D (a), TCO_2 (b), all other (ab)**	39 ± 23
Body length	0.90 ± 0.16	1.08 ± 0.31	1.21 ± 0.36	0.99 ± 0.16	0.98 ± 0.25
			Functional structure (mean ± sd)		
FRic	0.42 ± 0.19	0.53 ± 0.24	0.21 ± 0.12	0.13 ± 0.11	0.31 ± 0.14
FEve	0.49 ± 0.16	0.59 ± 0.16	0.61 ± 0.11	0.49 ± 0.13	0.64 ± 0.15
FDiv	0.80 ± 0.12	0.76 ± 0.14	0.80 ± 0.12	**0.74 ± 0.12** **D (a), TCO_2 (b), all other (ab)**	0.75 ± 0.11

Figures

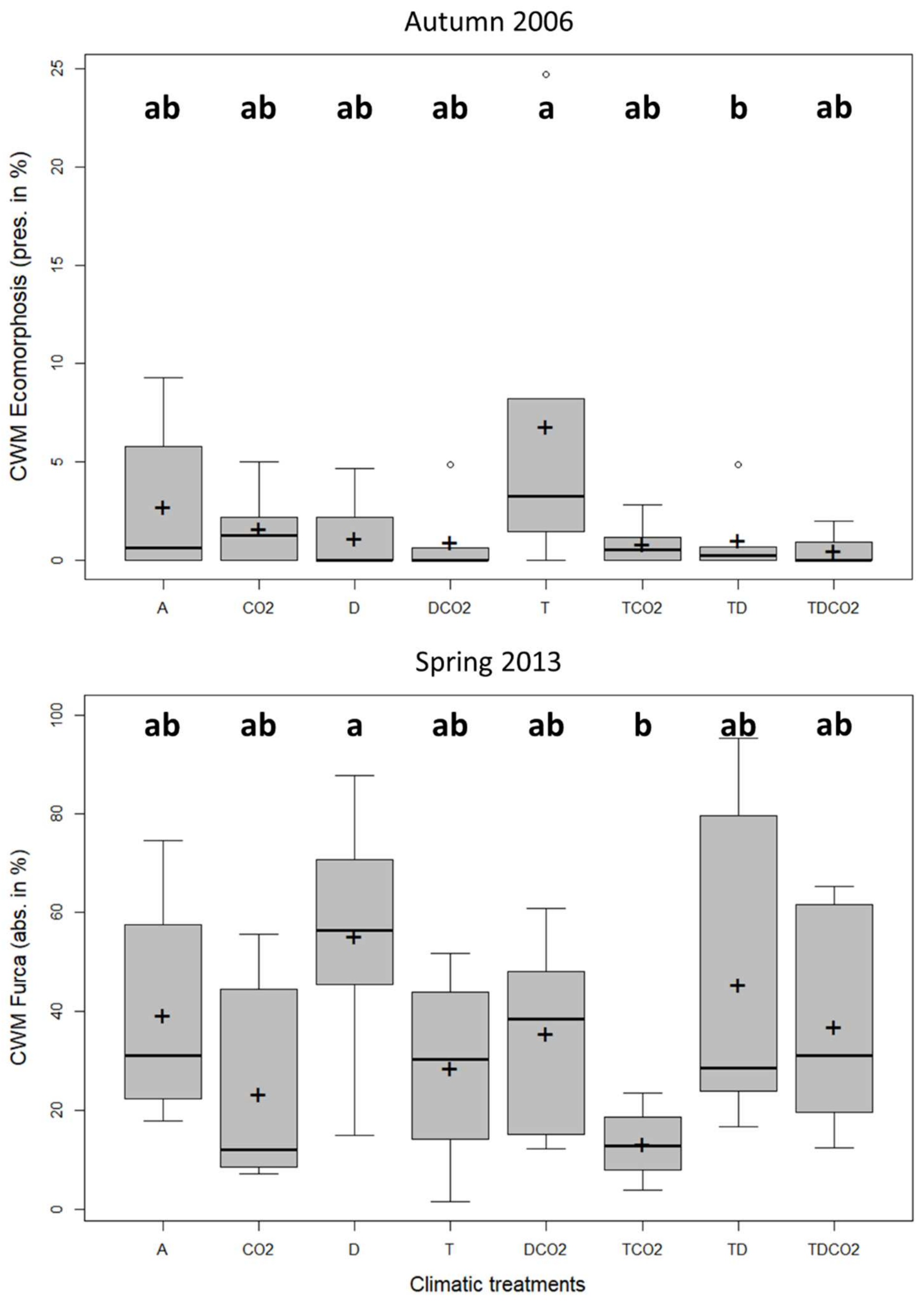

Figure 1 – Effect of climatic treatments on CWM trait values: (top) presence of ecomorphosis (Autumn 2006) and (bottom) absence of furca (Spring 2013) in collembolan communities. CWM trait values are presented in boxplots, with the bold line indicating the median and the plus sign the mean. Lowercase letters indicate significant differences between treatments, with a threshold of $p<0.05$. Effects of treatments were tested with type-II Anova on linear mixed-effect models, and post-hoc pairwise comparisons with multiple comparisons of means by Tukey contrasts. Treatments: A = control plots, CO2 = elevated CO_2, D = extended summer drought, T = elevated temperature, and combined letters for the combinations of factors.

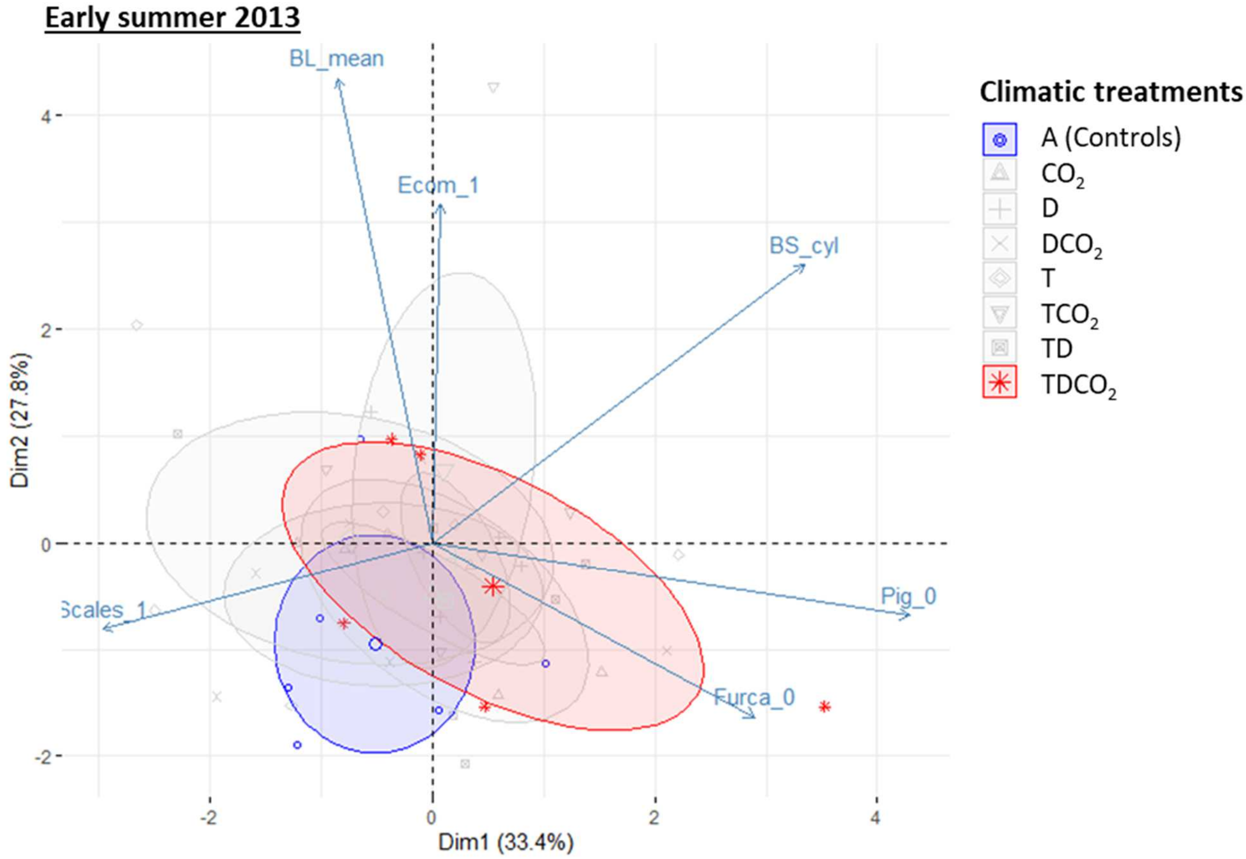

Figure 2 – Functional composition of collembolan communities based on 6 traits in Early Summer 2013 in CLIMAITE. Principal Component Analysis (PCA) on 240 communities (first 2 axes are shown representing a total of 61.2% of the total variance) from which only the Early Summer 2013 ones are selected, each community being characterized by 6 Community-Weighted Mean (CWM) trait values. 1 dot represents 1 community. Communities are grouped by climatic treatment (dots colour and shape) with confidence ellipses at the 0.95 level; arrows represent the traits. We particularly highlighted the 'Controls' (A) and 'Temperature x Drought x CO_2' ($TDCO_2$) treatments.

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