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## Communities of Collembola show functional resilience in a long-term field experiment simulating climate change

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1 **Title:**

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3 **Communities of Collembola show functional**  
4 **resilience in a long-term field experiment**  
5 **simulating climate change**

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22

## 23 **Abstract**

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

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

## 46 **Highlights**

- 47 1. In an 8-year field experiment we increased temperature, atmospheric CO<sub>2</sub> and drought  
48 duration
- 49 2. Collembolan communities were sampled under different climatic treatments and controls
- 50 3. Their short-term, mid-term and long-term functional responses were scrutinised
- 51 4. Only minor effects of climate change on collembolan traits were observed
- 52 5. Collembola appear functionally resilient to climate change of moderate intensity

## 53 **1. Introduction**

54 The world is currently experiencing a series of global changes due to human activities. One of  
55 these is climate change, which is expected to occur at a rapid rate over the 21<sup>st</sup> century. The  
56 increasing concentration of CO<sub>2</sub> in the atmosphere is causing rising temperatures and increased  
57 variation in precipitation patterns, including extended periods of summer drought (IPCC, 2018).  
58 These environmental factors – and their interactions (Rillig et al., 2019) – are expected to have  
59 an impact both on soil organisms and the physico-chemical properties of soil, potentially  
60 threatening soil ecosystem functioning. As soil ecosystems provide numerous ecosystem  
61 services, in the context of climate change, research into these systems is urgent (Wall & Six, 2015).

62 Soil invertebrates and Collembola in particular contribute to several ecological functions in soil,  
63 such as organic matter decomposition, microbial activity regulation, soil structure, etc. (Hopkin,  
64 1997; Lavelle et al., 2006) and this contribution is climate dependent (Wall et al., 2008). Yet the  
65 impacts of commonly projected climatic scenarios based on temperature, drought or CO<sub>2</sub> on soil  
66 biota in general may differ (Blankinship et al., 2011; Meehan et al., 2020). The links between  
67 organisms and ecosystem functioning are increasingly explored by studying functional traits  
68 (Violle et al., 2007). Such trait-based studies have been widely used in plant ecology, notably to  
69 explore trait–climate relationships in a changing world (Wieczynski et al., 2019). A growing body  
70 of evidence shows that functional diversity helps to understand how terrestrial ecosystems –  
71 including soil fauna – respond to climate change at a community level (Bardgett & van der Putten,  
72 2014). To date, the complexity of the links between soil fauna and soil ecosystem functioning has  
73 been little studied in a climate change context (Wolters et al., 2000). However, trait-based  
74 approaches are becoming more common in soil fauna studies (Pey et al., 2014) given the current  
75 need for relevant descriptive data concerning soil invertebrates (Phillips et al., 2017) and the  
76 ability of species traits to explain soil functioning in complement to taxonomic indicators  
77 (Heemsbergen, 2004). In the present study, we aim to investigate the links between collembolan  
78 communities – bioindicators within soil fauna – and climate change using a trait-based approach.

79 Elevated temperature may have (i) direct positive effects on soil fauna, by bringing species closer  
80 to their performance optimum, especially at high latitudes (Deutsch et al., 2008), as well as (ii)  
81 indirect positive effects, notably on food supply: for decomposers through increased plant growth  
82 (Dietzen et al., 2019; Rustad et al., 2001) and for grazers through changes in the fungi:bacteria  
83 ratio (Haugwitz et al., 2014). Elevated atmospheric CO<sub>2</sub> may also have indirect positive effects, by  
84 contributing to an increase in plant litter C:N ratios, net primary production (Pendall et al., 2004)  
85 and plant biomass (Wang et al., 2012), and thus of food supply available for decomposers. C:N  
86 ratio was thus positively affecting collembolan communities' diversity in heathland after 2 years  
87 of elevated CO<sub>2</sub> condition (Holmstrup et al., 2017). Moreover, an increase in both temperature  
88 and CO<sub>2</sub> might potentially reinforce one another (Bradford et al., 2016). In contrast, extended  
89 summer droughts are expected to have negative effects on soil fauna, as the precipitation regime  
90 is considered to have a greater general impact on soil biota than temperature and CO<sub>2</sub>  
91 (Blankinship et al., 2011). Drought is also expected to impact community assembly processes in  
92 Collembola since these animals express a moisture preference gradient at a species level from  
93 drought tolerant to drought sensitive species. The species' abundances are thus expected to vary  
94 with soil moisture when facing a drought event e.g. during the summer season (Verhoef & Selm,  
95 1983). These effects might be lethal, or they may lead to non-lethal adaptations, such as triggering  
96 resistance mechanisms in these organisms (Holmstrup & Bayley, 2013) or behavioural avoidance  
97 responses (Tsiafouli et al., 2005).

98 Communities of Collembola are known to respond along several gradients, such as land use  
99 (Joimel et al., 2017) or their vertical position in the soil profile (Cortet & Poinso-Balaguer, 1998).  
100 Furthermore, in the face of temperature and/or moisture stress, some collembolans are able to  
101 form climate-specific resistance stages through so-called ecomorphosis (Cassagnau, 1974). Trait-  
102 environment relationships have been studied in Collembola on a range of scales, from local  
103 (Santorufu et al., 2015) to large areas (Salmon et al., 2014). These relationships can be explored  
104 through single-trait (Garnier et al., 2004) and multi-traits (Mouillot et al., 2013) metrics. In a

105 context of climate change, it is thus relevant to explore the impacts of increasing temperatures,  
106 CO<sub>2</sub> and drought on Collembola traits in soils.

107 To test for the effects of different climatic parameters on the functional composition and structure  
108 of collembolan communities, we used data from the CLIMAITE experiment in Denmark, which  
109 has been simulating realistic climate change modifications in a semi-natural ecosystem  
110 (Mikkelsen et al., 2008). In this experiment, all combinations of three climatic parameters –  
111 elevated temperature, elevated atmospheric CO<sub>2</sub> and extended summer drought – were tested.  
112 Their consequences on soil biodiversity were measured over a period of eight years, in order to  
113 track the temporal dynamics of soil biodiversity responses. However, hypothesizing the trait-  
114 environment relationships in such a dynamic and complex system can be a challenge since  
115 multiple possible effects and interactions between such effects are to be expected in a full-  
116 factorial experiment. For simplicity, we therefore stated the following hypotheses on the  
117 relationships between traits and environment:

118 (1) We expected elevated CO<sub>2</sub> to enhance the availability of organic matter in soils leading to  
119 larger collembolan body size.

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

## 127 **2. Materials & methods**

### 128 **2.1 Experimental site and climatic treatments**

129 The CLIMAITE experiment is extensively described by Mikkelsen et al. (2008). The experimental  
130 site is located in Brandbjerg, Denmark (55°53' N, 11°58' E) on a hilly, nutrient-poor sandy  
131 substrate. It consists of heathland and grassland dominated by the grass *Deschampsia flexuosa* L.  
132 and the dwarf shrub *Calluna vulgaris* Hull, 1808. Long-term annual mean precipitation and air  
133 temperature (1961–90) for the area was 613 mm and 8.0°C, respectively (www.dmi.dk in  
134 Mikkelsen et al., 2008), while the mean data from the site's meteorological station during the  
135 study period (2006–13) showed mean annual precipitation and air temperature of 648 mm and  
136 9.7°C (Larsen et al., 2019). An experimental design using automated curtains allowed the control  
137 of three climatic parameters: elevated temperature (aiming for +2°C), elevated atmospheric  
138 concentration of CO<sub>2</sub> (aiming for 510 ppm) and reduced soil moisture (aiming to simulate a more  
139 intense summer drought). The effect of the temperature and drought conditions are presented in  
140 Annex 1. These climatic modifications were consistent with the expected climate in 2075 in  
141 Denmark at the time the experiment was designed (IPCC, 2001). The experiment started in  
142 October 2005. A full-factorial design was used, allowing each parameter to be tested alone (T:  
143 elevated temperature, D: extended drought period, CO<sub>2</sub>: elevated CO<sub>2</sub>) and in each combination  
144 (TD for 'Temperature x Drought', and the following DCO<sub>2</sub>, TCO<sub>2</sub>, TDCO<sub>2</sub>), resulting in 7 climatic  
145 treatments in addition to control plots (A: ambient controls). Each of these climatic treatments  
146 and the controls were replicated 6 times on a total of 48 plots. The efficacy of treatments have  
147 been documented in several studies (Holmstrup et al., 2015; Vestergård et al., 2015): the actual  
148 increased air concentration of CO<sub>2</sub> was very close to the target of 510 ppm, and the extended  
149 drought (3–4 weeks) resulted in a water content of 4–5 vol%. However, the average soil  
150 temperature in warmed plots was not more than 0.5–1°C.



## 151 **2.2 Collembola abundance data**

152 Collembola were sampled at different phases of the experiment: after **short-term** exposure  
153 (October 2006), after **medium-term** exposure (October 2007), and after **long-term** exposure  
154 (2012–13). For the latter, there were three sampling dates: August 2012 (summer, after the  
155 'Drought' treatment); April 2013 (mid-spring, before the 'Drought'); June 2013 (early summer,  
156 just at the end of the 'Drought'), resulting in a total of five sampled temporal phases. In total, our  
157 data gathers 240 communities (5 temporal phases \* [7 treatments + 1 control] \* 6 replicates).

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

## 170 **2.3 Collembola trait data**

171 Trait data was extracted at species level from the open-access BETSI database  
172 (<https://portail.betsi.cnrs.fr>). We first selected trait values from Scandinavian sources, then  
173 completed the dataset with Gisin (1960) and Zimdars (1994 and 'Synopses') values, as  
174 recommended by Bonfanti et al. (2018). Computation of several literature sources – thus trait  
175 values – per trait per species, were made possible by using a fuzzy coding procedure: splitting  
176 traits into binary attributes coded in percentage (except for body length, continuous value in mm)

177 as described in Hedde et al. (2012). Five morphological traits were used from this dataset  
178 (pigmentation, furca, body shape, scales, body size). **Absence of pigmentation** and **absence of a**  
179 **furca** are both sensitive traits that reveal a species' preference for the vertical position in the soil  
180 habitat: pigmentation, when present, is a protection against sunlight and indicative of a  
181 hemiedaphic or epiedaphic life form. A furca, when present and developed, confers high  
182 immediate motility through springing (e.g. to avoid danger). **Body shape** might be partly linked  
183 to the species' vertical position in the soil, so we also considered that it reflects the sensitivity of  
184 a species to desiccation. Cylindrical body shapes have a higher surface-to-volume ratio than  
185 spherical body shapes, relatively increasing their risk of desiccation (Kaersgaard et al., 2004). The  
186 **presence of scales** is expected to strengthen the cuticular impermeability of a species and can  
187 generally be considered to protect against evaporative water loss. We selected **body size** as a  
188 general performance trait. We considered that body size is notably linked to energy transfers in  
189 soil ecosystems – Collembola being both a very abundant group of microbial feeders and a very  
190 abundant pool of prey for taxa of higher trophic levels. Additionally, we also considered the ability  
191 of a species to display **ecomorphosis** as a feature of interest, here used as a trait in further  
192 analysis. This strategy allows an individual to switch into specific resistance stages triggered by  
193 stressful environmental conditions, notably temperature increase and drought during the  
194 summer season. The data on ecomorphosis ability was obtained from Bonfanti (2021). A  
195 summary of these traits and their links to our hypotheses is given in Table 1. Species trait values  
196 used in the analysis are listed in raw data files.

## 197 **2.4 Statistical analysis**

### 198 2.4.1 Communities' functional composition and structure

199 Based on these six traits, we investigated: (i) the functional composition of a community and (ii)  
200 its functional structure. To do this, we calculated the community-weighted mean (CWM) metric  
201 (Garnier et al., 2004) as follows:  $CWM_{j,y} = \frac{\sum_{k=1}^{n_j} A_{k,j} \cdot z_k}{n_j}$ , where  $n_j$  is the number of species  
202 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

203 species k. To visualize the multidimensional response of communities' functional composition to  
204 time and climatic treatments factors, we built a functional space using a Principal Component  
205 Analysis (PCA) ran on the 240 communities (lines), described by their six CWM trait values as  
206 quantitative variables (columns), from which we display the two first axes. Additionally, to  
207 visualize how n species (e.g., the experimental site species pool from one temporal phase) are  
208 located within the same trait space, we ran a PCA on these n species (lines), described by their six  
209 trait values as quantitative variables (columns), from which we display the two first axes.

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

#### 216 2.4.2 Effects of climatic parameters on community metrics

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

224 Then the main effects of the three modified climatic parameters ('Temperature', 'Drought' or  
225 'CO<sub>2</sub>') were characterized with a standardized effect size mean difference:  $\theta = \frac{\mu_1 - \mu_0}{\sigma}$ , where  $\mu_1$   
226 is the mean CWM value in plots containing a modified climatic parameter, and  $\mu_0$  the mean CWM  
227 value in plots used as controls (i.e. not subject to this modified climatic parameter), and  $\sigma$  is the  
228 standard deviation of the whole CWM value series for each climatic parameter.

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

## 233 3. Results

### 234 3.1 Effects on community functional composition

#### 235 3.1.2 Pairwise comparisons of climatic treatments

236 The mean CWM trait values per climatic treatment for every temporal phase are presented in  
237 Table 2, and the detailed CWM trait values in Annex 2. All the statistical tests outputs used to  
238 conclude on the effects of climatic treatments on CWM values are detailed in Annex 3. After **short-**  
239 **term** exposure, we generally observed no effect of treatments on mean trait values (Figure 1). In  
240 this temporal phase, on average, the absence of pigmentation varied from 30–55%, cylindrical  
241 body shape from 54–72%, the presence of ecomorphosis from 1–7%, the presence of scales from  
242 13–20%, the absence of furca from 33–47%, and body length from 0.83–0.99 mm. We noted a  
243 significant difference in the presence of ecomorphosis, with ‘Temperature’ treatment exhibiting  
244 higher values than ‘Temperature x Drought’ treatment (Anova  $\chi^2=21.6$ ;  $df=8$ ;  $p<0.01$ ).

245 After **medium-term** exposure, we observed no effect of treatments on trait values. In this  
246 temporal phase, on average, the absence of pigmentation varied from 40–62%, cylindrical body  
247 shape from 72–91%, the presence of ecomorphosis from 4–18%, the presence of scales from 0–  
248 7%, the absence of furca from 32–55%, and body length from 0.96–1.39 mm.

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

256 Finally, after long-term exposure, the multidimensional response of the communities’ functional  
257 composition to climatic treatments shows no clear pattern and especially no difference between

258 the Controls (A) and the full factorial climatic simulation treatment ('Temperature x Drought x  
259 CO<sub>2</sub>', TDCO<sub>2</sub>) as shown by the large overlap of the ellipses on PCA in Figure 2. This absence of  
260 response pattern can also be observed at all the other temporal phases (Annex 4).

### 261 3.1.1 Main effects of climatic parameters

262 The main effects of each climatic parameter on CWM trait values and for each temporal phase are  
263 presented in Annex 5. We show only the cases for which a significant effect ( $p < 0.05$ ) was found  
264 and for which no interaction effect was found. Of the 90 main effects tested (3 parameters \* 6  
265 traits \* 5 temporal phases), seven were significant. After medium-term exposure, elevated CO<sub>2</sub>  
266 led to a higher presence of cylindrical body shape. After long-term exposure, each modified  
267 climatic parameter led to a higher presence of cylindrical body shape, while extended drought led  
268 to a higher absence of pigmentation, and elevated CO<sub>2</sub> led to a higher presence of ecomorphosis  
269 and of scales.

## 270 3.2 Effects on community functional structure

271 We generally observed no effect of the climatic treatments on functional diversity indices, either  
272 after short-term, medium-term or long-term exposure (Table 2). After short-term exposure and  
273 for all treatments, functional richness varied from 0.06 to 0.83, functional evenness from 0.15 to  
274 0.85 and functional divergence from 0.52 to 0.99. After medium-term exposure and for all  
275 treatments, functional richness varied from 0.02 to 0.95, functional evenness from 0.08 to 0.97  
276 and functional divergence from 0.34 to 0.96. After long-term exposure and for all treatments,  
277 functional richness varied from 0.00 to 0.85, functional evenness from 0.10 to 0.97 and functional  
278 divergence from 0.42 to 0.99. We did note a significant difference in functional divergence in  
279 spring 2013, with 'Drought' treatment exhibiting higher values than 'Temperature x CO<sub>2</sub>'  
280 treatment (Anova  $\chi^2 = 1148.6$ ;  $df = 8$ ;  $p < 0.001$ ). A high intra-treatments variability of scores is  
281 observed.

282

## 283 **4. Discussion**

284 Generally, the results did not indicate any marked effect of the climatic treatments on the chosen  
285 community metrics, in contrast to what we had expected. While our hypotheses were based on  
286 independent climatic parameters, climatic treatments resulting from combinations of factors  
287 were more complex to postulate. Nonetheless, we expected an elevated temperature combined  
288 with an extended drought to be even more stressful, as elevated temperatures increase  
289 evaporation and thus reduce moisture in soils. However, such an additive effect was not observed.  
290 The full factorial climatic simulation treatment ('Temperature x Drought x CO<sub>2</sub>') allowed us to  
291 explore to what extent a combination of both stressful and stimulating factors would result in a  
292 balanced situation. This simulation of a future climate scenario showed no effect on community  
293 functional structure or composition – whether this is due to balance is hard to determine.

### 294 **4.1 Almost no effect on functional structure and composition**

295 According to our first hypothesis, we expected higher body size values resulting from CO<sub>2</sub>  
296 elevation. Conversely, our second hypothesis expected lower functional diversity values resulting  
297 from physiological constraints caused by drought.

298 In fact, few significant main effects of climatic parameters were observed and, of these, all were  
299 positive, meaning that they led to higher CWM values for every concerned trait. These significant  
300 effects were found only in three temporal phases and for four traits. Cylindrical body shape was  
301 slightly favoured by each of the climatic parameters and thus cannot be interpreted according to  
302 our hypotheses. Absence of pigmentation was slightly favoured by extended drought, which may  
303 indicate that euedaphic species might be more tolerant to this stress in the observed conditions,  
304 or that species confined to deeper soil layers are less exposed to drought, which may support our  
305 second hypothesis. But resistance traits such as the presence of ecomorphosis and the presence  
306 of scales were favoured by elevated CO<sub>2</sub>, which goes against our first hypothesis, which expected  
307 this to be more a stimulating than a stressful factor. The two traits (presence of scales and  
308 ecomorphosis) that exhibited moderate effect sizes from climatic parameters (0.5–1 sd) also had

309 very low CWM values (0–5%); in all other cases, the effect sizes were low. In general, the main  
310 effects were marginal considering the number of tests, and no clear pattern could be seen.

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

322 Any significant differences that did exist between the effect of climatic treatments in CWM trait  
323 values went against our hypotheses, especially the second hypothesis. For example, we observed  
324 that the presence of ecomorphosis was highest in 'Temperature' (T) plots and lowest in  
325 'Temperature x Drought' (TD) plots, in autumn 2006. At this period, two species were able to  
326 display ecomorphosis: *Folsomia quadrioculata* (Tullberg, 1871) and *Isotomurus palustris* (Müller,  
327 1776) (raw data). Looking at the relative abundance of these species (raw data), the latter was  
328 only present in control plots (moreover, at a very low density), while *F. quadrioculata* was present  
329 in all treatments. Thus, the ecomorphosis was mainly explained by fluctuations in  
330 *F. quadrioculata* density, which was highest in T plots – ca. 7% – while it was only 0.7% in TD  
331 plots. We should note that we have a slight doubt concerning the proportion of ecomorphosis due  
332 to *I. palustris* abundance: in the dataset, we inferred this species as a proxy for collected  
333 *Isotomurus* individuals (raw data), but the literature mentions a *palustris*-complex (Potapov,  
334 2001), and the status of different forms remains unclear. However, the neotype was described



335 from individuals collected in Denmark, which reduces the misidentification risk about this  
336 Holarctic species in our study (Carapelli et al., 2001).

337 We also observed, in spring 2013, that the absence of furca was highest in 'Drought' (D) plots and  
338 lowest in 'Temperature x CO<sub>2</sub>' (TCO<sub>2</sub>) plots. Looking at species relative abundance (raw data),  
339 *Isotomiella minor* Schäffer, 1896 was particularly abundant in TCO<sub>2</sub> plots, and this species has a  
340 furca. At this period, its relative abundance reached an average of ca. 70% in TCO<sub>2</sub> plots.  
341 Conversely, its relative abundance was lower in D plots, where the communities were dominated  
342 mainly by *Mesaphorura macrochaeta* Rusek, 1976; this species does not have a furca and reached  
343 an average ca. 51% of relative abundance in these plots.

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

351 Following the same trend, community functional structure, through functional diversity indices  
352 calculations, mostly did not allow us to detect any effect of climatic treatments in this study. The  
353 effect found on functional divergence (FDiv) in spring 2013 followed the previously described  
354 pattern ('Drought' vs 'Temperature x CO<sub>2</sub>' plots). This can again be explained by looking at species  
355 dominance, FDiv being sensitive to relative abundance. In the spring 2013 trait space (Annex 6)  
356 based on our six traits, we can see that *I. minor*, dominating in TCO<sub>2</sub> plots with a low FDiv value,  
357 is located in the centre. Thus, switching community dominance to *M. macrochaeta* (in D plots)  
358 results in a wider FDiv volume since the latter species is located more externally in the trait space  
359 (see e.g. Mouillot et al., 2013). Furthermore, in CLIMAITE communities at any sampling date, the  
360 most abundant species were in most cases either *I. minor*, *M. macrochaeta* or *Parisotoma notabilis*

361 (Schäffer, 1896). They may represent a slight gradient of euedaphic life habits, observed on axis-  
362 1 in Annex 6, as they differ in terms of pigmentation, furca and body length (raw data).

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

## 373 **4.2 Comparison with similar studies**

374 In another field experiment with a similar design conducted on an old-field grassland, the effects  
375 of climatic parameters on Collembola after long-term exposure were contrasted (Kardol et al.,  
376 2011). While functional traits were not studied, taxonomic responses revealed low impacts of  
377 climatic treatments even at a higher magnitude (e.g. warming of ca. +3°C) than in the CLIMAITE  
378 experiment. Collembola abundance tended to decrease with a reduction in precipitation, while  
379 the low effects of elevated temperature and CO<sub>2</sub> were probably indirect, i.e. mediated through  
380 availability of water in the soil. However, the authors mention shifts in community composition,  
381 which we did not observe in our experiment, and that might have driven changes in CWM trait  
382 values, which remains to be tested. Kardol et al. (2011) also mentioned high within-treatments  
383 variation in microarthropods responses, possibly blurring discrepancies in communities'  
384 responses across different treatments.

385 A more recent field experiment showed that collembolan community functional diversity is  
386 sensitive to elevated temperature (Holmstrup et al., 2018). However, the magnitude of the

387 maximum temperature increase was much larger (up to +10°C) than in our study and was due to  
388 geothermal activity. Moreover, this effect was observed after 6 years but was not detected after  
389 50 years, suggesting the high functional resilience of Collembola in a long-time horizon. Finally,  
390 the authors mention a negative correlation between temperature and CWM body size, thus  
391 illustrating metabolic scaling rules that result in smaller species being favoured at higher  
392 temperatures due to higher individual and population growth rates (Brown et al., 2004).

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

399 Lastly, we note that CLIMAITE community abundance was consistent with that found in the  
400 literature. Collembola mean density per plot ranged mostly from  $2 \cdot 10^3$  to  $9 \cdot 10^3$  ind./m<sup>2</sup> (raw  
401 data), which is slightly lower than the mean 10 to  $12 \cdot 10^3$  ind./m<sup>2</sup> found in French grasslands  
402 (Joimel et al., 2017), while maximum density values were the same (ca.  $40 \cdot 10^3$  ind./m<sup>2</sup> in both  
403 cases).

#### 404 **4.3 Why were so few effects observed in our study?**

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

##### 409 **4.3.1 High community stochasticity**

410 Our results showed high amplitude in functional diversity indices values, which may be due to  
411 high variability in community structure and composition within the climatic treatments and may  
412 explain the lack of difference in comparisons between the different treatments. The local

413 stochasticity in community composition mentioned by Kardol et al. (2011) should be considered  
414 regarding the relative body size of our biological model compared to the scale of the experimental  
415 design. Theory has predicted how sampling scale can influence the relative importance of  
416 environmental factors (such as those in our hypotheses) versus neutral factors (Chase, 2014). We  
417 based our hypotheses on the effect of environmental (i.e. niche) factors while, in fact, collembolan  
418 communities may be assembled under mainly neutral (i.e. stochastic) factors, thus hindering  
419 responses between different conditions. This assumption of high stochasticity has been observed  
420 for collembolan species at a small scale (Van Der Wurff et al., 2003), and more generally for  
421 mesofauna species in soils on a 12-ha experimental site (Zinger et al., 2018), and is also consistent  
422 with the fine-scale and meso-scale horizontal distribution of soil mesofauna described by Berg  
423 (2012). In other words, while our experiment tried to intentionally shift the macro-scale  
424 ecological preferences of species by modifying the ambient climatic conditions, we observed them  
425 at an experimental scale in which communities are too stochastically assembled to detect  
426 significant discrepancies.

#### 427 4.3.2 Climatic intensity modifications that were too low given the organisms' thermal 428 tolerance

429 Another possible explanation for our results could be the moderate intensity (although consistent  
430 with e.g. Barreto et al., 2021) of climatic changes applied in the experiment (Blankinship et al.,  
431 2011), with the consequence that the individuals were not stressed to any significant degree, and  
432 the ecological preferences of species were not threatened. A similar subtlety in the effects of  
433 temperature elevation on collembolan traits was observed even following an 'extreme' event of  
434 +4°C during 17 days (Krab et al., 2013).

435 If we look at the thermal tolerance of soil animals, it has been observed that terrestrial  
436 ectotherms' warmer distribution range boundaries do not indicate their maximum heat tolerance  
437 (Sunday et al., 2012), and that soil ectotherms in northern European latitudes (CLIMAITE site: ca.  
438 55°N) exhibit the broadest thermal tolerance (Deutsch et al., 2008). These species are thus

439 currently living in climates that are cooler than their optimum and are consequently not  
440 threatened by moderate warming; in fact, this probably has a stimulating effect. The same  
441 assumption may apply to other climatic parameters as well, if the relative changes are too small  
442 to trigger a threat to local species and/or populations. Indeed, the three species dominating  
443 CLIMAITE communities (*I. minor*, *M. macrochaeta* and *P. notabilis*) are known to be eurytopic,  
444 meaning they are commonly found across several European regions, and especially in northern  
445 Europe (Dunger & Schlitt, 2011; Potapov, 2001), in different biomes and climates. They are thus  
446 likely to have a wide climatic tolerance range and to exhibit wide phenotypic plasticity.

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

#### 461 **4.4 Perspectives: how to track changes in soil biodiversity?**

##### 462 4.4.1 On the difficulty to build proper hypotheses

463 The links between climatic parameters and collembolan traits at the community level and on a  
464 field study were difficult to hypothesize on. Notably, the links between body size and temperature

465 are complex. Assuming a correlation between temperature and latitude, Bonfanti et al. (2018)  
466 showed that mean body size between several collembolan populations (intraspecific trait  
467 variability) peaked in northern Europe, but the observed geographical gradient was limited to  
468 55–60°N. In contrast, Ulrich & Fiera (2010) showed that species body size (interspecific trait  
469 variability) peaked around 45°N, with an observed gradient going up to 80°N. Moreover the  
470 duration of exposure to elevated temperatures may also play a role in community assembly  
471 processes (Rezende et al., 2014). Thus, interpreting a temperature elevation as a “moving south”  
472 gradient for local Danish species initially around 55° N we can imagine that: (i) after short  
473 exposures, intraspecific trait variability would play a greater role – the community dealing with  
474 species already present at the experimental start – resulting in a reduced body size and thus  
475 following ‘downsizing’ hypotheses (Lindo, 2015); whereas (ii) after long exposures, species out  
476 of their thermal niche could be replaced, making interspecific trait variability play a greater role,  
477 which would result in an elevated body size. It is also possible to consider a direct physiological  
478 effect of temperature on the development of individuals. In cold environment, although they are  
479 adapted, individuals’ development may be still limited by low temperatures, a temperature  
480 elevation resulting in a faster growth (Birkemoe & Leinaas, 2000). We thus question the  
481 opportunity to involve in our analysis more traits – e.g., linked to physiology – and/or individual  
482 measurements of trait values.

#### 483 4.4.2 Searching for sensitive and functionally important traits

484 As mentioned, the climate modifications in our study may not have been sufficient to move  
485 species out of their tolerance range, and probably moved them closer to their performance  
486 optimum. Nor did we observe negative effects from the ‘Drought’ treatment, although this factor  
487 was expected to induce physiological constraints on the organisms. Even in stressful temperature  
488 conditions, desiccation has been shown to be even more threatening, such as in termites and  
489 other soil ectotherms (Woon et al., 2019). The ecomorphosis trait did not reveal any response to  
490 drought (except for those we inferred to a ‘foundation effect’). So which traits would be good  
491 indicators of effects related to climate change? Bahrndorff et al. (2006) showed that in a eurytopic

492 species (*O. cincta*) intraspecific trait variability is observable in climatic stress-related traits, and  
493 mentioned the genetic adaptation of populations. Over an approximately 2000-km north-to-  
494 south European gradient, latitudinal clines were shown in traits related to resistance to high and  
495 low temperatures, desiccation, water loss rate, water pool and body size between populations.  
496 Individuals from the most northern and southern populations had the highest desiccation  
497 resistance. This pattern had been previously observed (Poinsot-Balaguer, 1990), suggesting that  
498 hydric stress, occurring in low or high temperature climates, induces convergent long-term  
499 physiological adaptations. It also suggests that northern European populations, such as the ones  
500 in CLIMAITE, may be adapted to cold conditions and thus have a high drought tolerance (Block,  
501 1996; Holmstrup, 2014). This argument adds support to our explanation that the climatic  
502 modification in our study was too moderate to induce stress on the animals, which remained in  
503 the core of their climatic tolerance range and/or ecological preference. However, moderate  
504 changes in temperature may lead to other examples of sublethal reactions in collembolan  
505 individuals, such as body and membrane fatty acid composition (van Dooremalen & Ellers, 2010).  
506 In that study, storage lipids became more saturated over time during warm acclimation, while  
507 they became more unsaturated during cold acclimation. These reactions to cold were also in line  
508 with reactions to drought acclimation (Holmstrup et al., 2002). Other studies have found that  
509 Collembola can significantly acclimate to moderate drought stress and thus consistently elevate  
510 their survival rate when subject to acute drought stress (Sjursen et al., 2001). Hence, acclimation  
511 can improve the climatic stress tolerance of populations, and thus the resilience of communities,  
512 in a climate change context in which periods of drought are expected to increase in length and  
513 intensity.

#### 514 4.4.3 Enhancing precision through measuring intraspecific trait variation

515 While we used trait values collected from the literature to make comparisons within our data,  
516 measurements of trait responses in the context of sub-lethal reactions led us to consider local  
517 intraspecific trait variability (ITV). Other evidence has shown that ITV may alter our perception  
518 of climate impacts on thermal tolerance in ectotherms (Herrando-Pérez et al., 2019). More

519 generally, ITV has recently been observed in Collembola at biogeographical scales (Bonfanti et al.,  
520 2018) in a performance trait, namely body size. In other organisms, it has also been observed at  
521 regional or local scales, and it can account for a non-negligible part of the total trait variation in  
522 communities along ecological gradients (Siefert et al., 2015). We speculate as to what extent ITV  
523 may have helped in our CLIMAITE experiment to detect fine-scale changes in Collembola  
524 morphology, physiology and performance, as a growing body of research considers ITV an  
525 important facet to be taken into account in community ecological dynamics (Raffard et al., 2019).  
526 This opens up a potential interest in measuring individual traits – within the local population – in  
527 these communities, as it has recently been standardized in soils by Moretti et al. (2016), although  
528 the degree of precision is under discussion (Griffiths et al., 2016). For such abundant animals as  
529 Collembola, acquiring individual (and thus ITV) data would represent an extensive effort in such  
530 a large sampling experiment as CLIMAITE; the feasibility of these practices is currently being  
531 evaluated for several morphological traits (Raymond-Léonard et al., 2019).



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## 543 **Data accessibility**

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

549

## 550 **Supplementary materials**

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

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

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

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

558 Annex 5 presents the main effect of 'Temperature', 'Drought' and 'CO<sub>2</sub>' modified parameters on  
559 CWM trait values in the communities.

560 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<sub>2</sub> and extended drought on Collembola at a community level.*

<b>Species features</b>	<b>Status</b>	<b>Links to the hypotheses</b>	<b>Abbreviations used</b>
<b>Body shape</b>	MPPB traits (Pey et al., 2014); Euedaphic life habit indicators (Martins da Silva et al., 2016)	“Cylindrical” confers susceptibility to Drought	BS_cyl
<b>Furca</b>		“Absence” favoured by Drought	Furca_0
<b>Pigmentation</b>		“Absence” favoured by Drought	Pig_0
<b>Scales</b>		“Presence” favoured by Drought	Scales_1
<b>Body size</b>	Performance trait (Pey et al., 2014)	Promoted by elevated temperature & CO <sub>2</sub>	Body length
<b>Ecomorphosis</b>	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<sub>2</sub> = elevated CO<sub>2</sub>, and combined letters for the combinations of factors. Functional composition presents the average  $\pm$  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
<b>Functional composition (mean <math>\pm</math> sd)</b>					
Pig_0	41 $\pm$ 19	50 $\pm$ 25	53 $\pm$ 21	68 $\pm$ 19	46 $\pm$ 21
BS_cyl	63 $\pm$ 17	81 $\pm$ 20	87 $\pm$ 10	89 $\pm$ 10	77 $\pm$ 17
Ecom_1	<b>2 <math>\pm</math> 4</b>	8 $\pm$ 11	0 $\pm$ 1	0 $\pm$ 1	1 $\pm$ 5
	<b>T (a), TD (b), all other (ab)</b>				
Scales_1	17 $\pm$ 12	3 $\pm$ 6	5 $\pm$ 9	1 $\pm$ 2	5 $\pm$ 7
Furca_0	39 $\pm$ 20	46 $\pm$ 23	23 $\pm$ 16	<b>35 <math>\pm</math> 24</b>	39 $\pm$ 23
	<b>D (a), TCO<sub>2</sub> (b), all other (ab)</b>				
Body length	0.90 $\pm$ 0.16	1.08 $\pm$ 0.31	1.21 $\pm$ 0.36	0.99 $\pm$ 0.16	0.98 $\pm$ 0.25
<b>Functional structure (mean <math>\pm</math> sd)</b>					
FRic	0.42 $\pm$ 0.19	0.53 $\pm$ 0.24	0.21 $\pm$ 0.12	0.13 $\pm$ 0.11	0.31 $\pm$ 0.14
FEve	0.49 $\pm$ 0.16	0.59 $\pm$ 0.16	0.61 $\pm$ 0.11	0.49 $\pm$ 0.13	0.64 $\pm$ 0.15
FDiv	0.80 $\pm$ 0.12	0.76 $\pm$ 0.14	0.80 $\pm$ 0.12	<b>0.74 <math>\pm</math> 0.12</b>	0.75 $\pm$ 0.11
	<b>D (a), TCO<sub>2</sub> (b), all other (ab)</b>				

# Figures

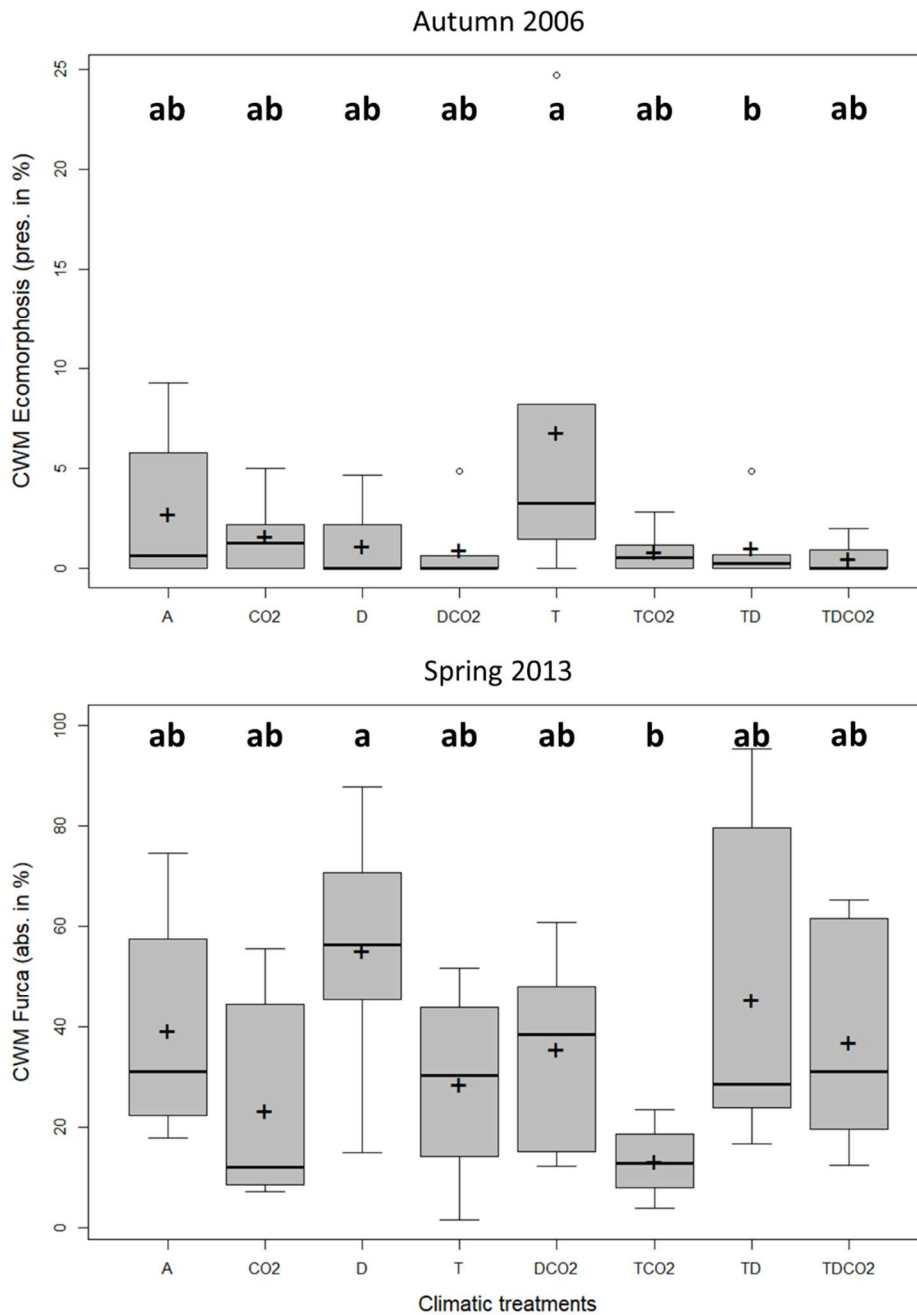


Figure 1 – Effect of climatic treatments on CWM trait values: (top) presence of ecomorphosis (Autumn 2006) and (bottom) absence of furca (Spring 2013) in collembolan communities. CWM trait values are presented in boxplots, with the bold line indicating the median and the plus sign the mean. Lowercase 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, CO<sub>2</sub> = elevated CO<sub>2</sub>, D = extended summer drought, T = elevated temperature, and combined letters for the combinations of factors.

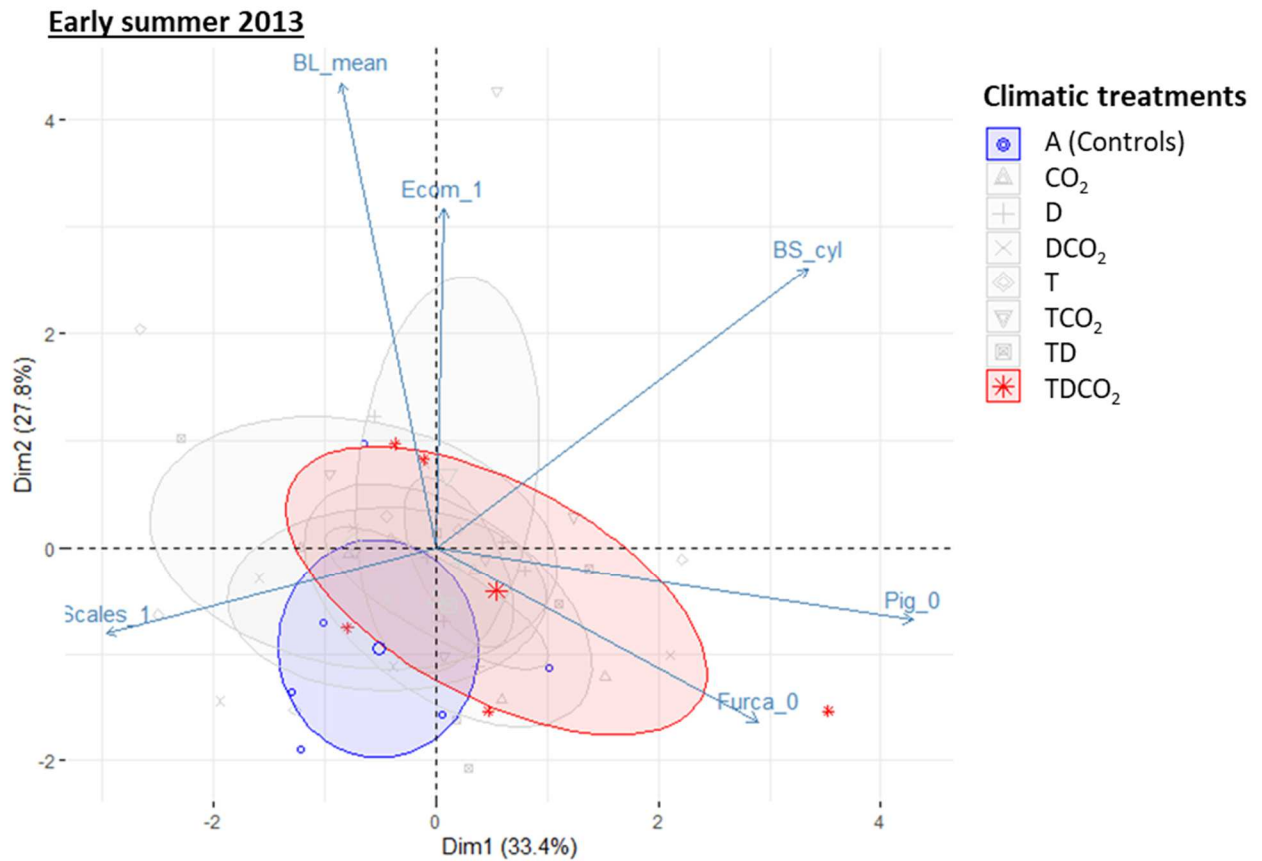


Figure 2 – Functional composition of collembolan communities based on 6 traits in Early Summer 2013 in CLIMATE. Principal Component Analysis (PCA) on 240 communities (first 2 axes are shown representing a total of 61.2% of the total variance) from which only the Early Summer 2013 ones are selected, each 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<sub>2</sub>' (TDCO<sub>2</sub>) treatments.

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