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1 **Climate change does not alter land-use effects on soil fauna communities**

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20

21 **ABSTRACT**

22 Soil organisms are important drivers of the functioning of terrestrial ecosystems and
23 co-determine how these ecosystems respond to human-induced changes in climate and land
24 use. In the present study, we assessed the interacting effects of these two global change
25 drivers on soil faunal communities. We carried out an experimental field study within the
26 framework of the Global Change Experimental Facility (GCEF) manipulating (1) two
27 climatic conditions (ambient vs. future) and (2) five land-use regimes (with two croplands:
28 conventional farming and organic farming; and three grasslands: intensively-used meadow,
29 extensively-used meadow and extensively-used pasture). The future climate treatment is
30 characterized by a slight increase of soil temperature ($\sim 0.5^{\circ}\text{C}$), whereas precipitation was
31 strongly decreased during the summer (by $\sim 20\%$) but moderately increased during spring and
32 autumn (by $\sim 10\%$). Soil fauna was sampled in two consecutive years in spring and autumn.
33 Overall, future climate tended to have negative effects on soil fauna communities. For specific
34 taxa, the detrimental effects of climate change were only evident for Isotomidae (Collembola)
35 and Chilopoda. In general, soil faunal composition differed strongly between grasslands and
36 croplands, with a higher number of macrofauna taxa and generally higher abundances of
37 meso- and macrofauna in grasslands. However, land-use intensity within these land-use types
38 had no further effect. Likewise, there were negligible interactive effects of climate and land
39 use, and short-term effects of projected climate change on the community compositions of
40 soil fauna were found to be more subtle than land-use effects. Land-use effects on soil fauna
41 are therefore equally strong under ambient and future climatic conditions.

42

43 **Keywords:**

44 Community composition; GCEF; intensive land use; global change; soil animals

45

46 **1. Introduction**

47 Soil biota fulfill different functional roles and drive many essential ecosystem processes
48 (Menta, 2012). The soil mesofauna comprises important secondary decomposer organisms
49 (e.g., Collembola and Oribatida) that provide the basis for soil fertility and nutrient
50 availability by mineralizing organic matters and thereby supporting the growth of microbes
51 and plants (Wang et al., 2017; Wickings and Grandy, 2011). Simultaneously, soil fauna can
52 modify the community composition of microbes and thus affect early stages of litter
53 decomposition and other microbial processes (Coleman and Wall, 2015; García-Palacios et al.,
54 2013). Similarly, soil macrofauna profoundly enhances litter fragmentation and soil
55 aggregation, and indirectly promotes water and nutrient infiltration as well as gaseous
56 emissions (Ayuke et al., 2011; Lavelle et al., 2001). Given these critical ecosystem functions,
57 soil fauna are gradually becoming a key research frontier in the context of global change
58 (Coyle et al., 2017).

59 Some soil fauna groups (e.g., Collembolans) are often used as bioindicators to evaluate soil
60 quality since they are quite sensitive to environmental changes, which is reflected by shifts in
61 their abundance and community composition (Lavelle et al., 2006; Lindberg et al., 2002).
62 Worldwide, climate change has become a main topic for soil ecological research (Eisenhauer

63 et al., 2017), and the functions provided by soil fauna have been found to be
64 climate-dependent (García-Palacios et al., 2013; Wall et al., 2008). Future climate models
65 predict a general increase in temperature with rising greenhouse gas emissions, lower
66 precipitation, especially in summer, and more extreme weather events, like droughts, in many
67 parts of the world (IPCC, 2014). Climate change has highly variable effects on soil faunal
68 communities with differences in the direction as well as magnitude of effects depending on
69 local conditions and taxonomic groups (Blankinship et al., 2011; Coyle et al., 2017; Wu et al.,
70 2014). Furthermore, a recent study demonstrated that different climate change drivers
71 interactively influence the functioning of soil faunal communities, as warming had negative
72 effects on the feeding activity of soil detritivores only in combination with reduced
73 precipitation (Thakur et al., 2018), which is a common scenario in many climate change
74 models. Hence, future climatic conditions may impair key soil processes (e.g., decomposition)
75 by decreasing the activity of detritivores (Yin et al., 2019).

76 Climate and land-use changes have been ranked as the biggest threats to global biodiversity
77 (Sala et al., 2000). Moreover, land-use change potentially leads to feedback effects (de
78 Chazal and Rounsevell, 2009). Soil faunal feeding activity and soil food webs have been
79 shown to be particularly vulnerable to land-use change (Tao et al., 2016; Tsiafouli et al.,
80 2015). Current land-use change is mainly driven by two ongoing processes: first, a
81 conversion of land-use types, usually from complex natural or semi-natural systems to
82 simplified agricultural systems; and second, land-use intensification within certain land-use
83 types (McLaughlin and Mineau, 1995). Both factors may significantly influence the diversity,

84 abundance, and community composition of soil fauna (Baker, 1998; Postma-Blaauw et al.,
85 2010) with potential consequences for ecosystem functions like primary production
86 (Cardinale et al., 2004). There are increasing concerns regarding the sustainability of
87 simplified farming systems (Bardgett and Van Der Putten, 2014; Wall et al., 2015) and how
88 they will respond to climate change. Generally, soil food webs in grasslands are more
89 resistant and adaptable to drought compared to croplands (De Vries et al., 2012). This
90 indicates that responses of soil biota to climate change can be modulated by different
91 land-use types. Given the potentially strong influence of climate and land use, it is surprising
92 that so far little effort has been made to investigate the potential interaction between climate
93 and land use on soil fauna communities (de Chazal and Rounsevell, 2009). Here, we address
94 this gap by studying soil meso- and macrofauna in a large-scale field experiment crossing two
95 climate scenarios (ambient vs. future) with five different land-use regimes (with the two
96 land-use types croplands and grasslands differing in management intensity). Our aim is to
97 answer the following question: What are the effects of climate change on the diversity,
98 abundance, and community composition of soil fauna and how are they altered by land-use
99 type (croplands vs. grasslands) and management intensity?

100

101 **2. Materials and Methods**

102 *2.1. Field site*

103 The study was conducted in 2015 and 2016 at the Global Change Experimental Facility
104 (GCEF), which is located at the field research station of the Helmholtz-Centre for

105 Environmental Research in Bad Lauchstädt, Saxony-Anhalt, Germany (51° 23' 30N, 11° 52'
106 49E, 116 m a.s.l.). This experimental platform was established on a former arable field with the
107 last crop (oat) on all subplots in 2013, and it is characterized by a low mean annual rainfall
108 (498 mm) and a mean temperature of 8.9°C. The soil of the study site is Chernozem. This
109 highly fertile soil type is typically developed upon carbonatic loess substrate under
110 summer-dry climatic conditions and characterized by a high content of humus (in Bad
111 Lauchstädt 2%) down to a depth of more than 40 cm, a high water storage capacity (31.2%) and
112 storage density (1.35 g/cm³). Furthermore, high nutrient contents (like N, P and K) together
113 with a soil pH of ~ 7.0 lead to favorable soil conditions for flora and fauna (Altermann et al.,
114 2005).

115 *2.2. Experimental set-up*

116 The GCEF has been established on a former arable field which was homogenously cultivated
117 for decades and comprises 10 mainplots (80 m x 24 m) with each mainplot consisting of 5
118 subplots (each 16 m x 24 m). The minimum distance between the mainplots is 25 m. The five
119 subplots per mainplot (in total 50) are randomly assigned to one of the five land-use regimes:
120 (1) conventional farming, (2) organic farming, (3) intensively used meadows, (4) extensively
121 used meadows and (5) extensively used pastures with sheep grazing (for detailed description
122 see Table S1). All land-use regimes were established by seeding in 2013. Half of the
123 mainplots are subjected to an ambient climate scenario, the other half to a future climate
124 scenario. This results in a split-split-plot design with climate as mainplot factor and land use
125 as subplot factor (five replicates per climate × land use combination).

126 All subplots are equipped with steel framework elements with a total height of 5.50 m
127 allowing the use of agricultural machines. Within the mainplots subjected to future climate,
128 all subplots are equipped with plastic tarpaulins serving as roofs and side panels on the longer
129 sides of the subplots which are automatically closed from sundown to sunrise to increase
130 night temperatures. Further, rain sensors allow for the modulation of water supply by opening
131 or closing the roofs and an irrigation system, fed by a large water reservoir, was installed as
132 potential additional water source. To avoid possible side effects of the construction itself,
133 steel frameworks were also established on all subplots within mainplots with ambient climate
134 treatment. Subplots within the mainplots are separated from each other by translucent plastic
135 blinds ranging from 50 cm belowground to 50 cm aboveground.

136 The future climate treatment is based on climatic conditions predicted for Central Germany in
137 the period from 2070 to 2100. It resembles a consensus scenario derived from 12 climate
138 simulations based on four different emission scenarios using three established regional
139 climate models: COSMO-CLM (Rockel et al., 2008), REMO (Jacob and Podzun, 1997) and
140 RCAO (Döscher et al., 2002). Whilst the mean temperature was projected to increase over all
141 seasons of the year by 1 to 2°C, the amount of precipitation was predicted to strongly
142 decrease in summer and slightly increase during the rest of the year. For this, mean values of
143 the 12 projections were calculated resulting in a precipitation change of about +9% in spring
144 (March – May) as well as in autumn (September – November) and about -18% in summer
145 (June – August). For this, every week and after stronger rain events, we added the amount of
146 water to reach ~110% of total rain under ambient conditions to the subplots with future

147 climate in spring and autumn. In summer, the rain sensor together with the irrigation system
148 was used to adjust precipitation on the subplots with future climate to ~80% of ambient
149 rainfall. In 2015, precipitation was increased by 9.3% and 9.2% in spring and autumn,
150 respectively, and reduced by 21% in summer on the subplots with future climate. In 2016,
151 precipitation was increased by 13.6% and 9.2 % in spring and autumn, respectively, and
152 decreased by 19.7% in summer (Fig. S1A). To apply the temperature treatment on future
153 climate mainplots, roofs and side panels were closed during 80% of the total night time from
154 February 15th to December 11th in 2015 and from March 22nd to November 29th in 2016.
155 Roofs and side panels are also used to apply a passive nighttime warming to the subplots
156 (Beier et al., 2004), in case of strong frosts and high wind speed. The roof phases were from
157 February 15th to December 11th in 2015 and from March 22nd to November 29th in 2016. This
158 night closing resulted in an increase of the daily mean of air temperature close to the ground
159 (5 cm height) by 0.55°C across the roof phases, in a depth of 1 cm by 0.62°C, and in a depth
160 of 15 cm by about 0.50°C. Near-surface soil temperatures in a depth of 1 cm showed a certain
161 dependency on land-use regime with a trend toward higher temperatures in the grasslands
162 (Fig. S2A). The mean increase of daily soil temperature due to roof closing in the night
163 varied among the land-use regimes between 0.20°C and 0.43°C (Fig. S2B). Mean soil water
164 content mainly followed the ambient rain pattern and was affected by the precipitation
165 treatment, but showed no obvious differences between land-use regimes (Fig. S1B-F).
166 Croplands and intensively used meadows were established on the respective subplots in
167 summer/autumn of 2013. Plants for the extensively used meadows and pastures were

168 repeatedly sown during spring and autumn of 2014. The temperature treatment started in
169 April 2014 in all land-use regimes; however, to homogenize moisture conditions during the
170 establishment of seedlings of grassland plants, roofs stayed open during rain. The
171 manipulation of precipitation started in July 2014 for all land-use regimes. A more detailed
172 description of the facility and the concept of the project can be found in Schädler et al.
173 (2019).

174 *2.3. Collection and identification of soil fauna*

175 Soil fauna samples were taken twice per year in spring and autumn of 2015 and 2016. Thus,
176 the first sampling was done one year after the initiation of the climate treatment. On each
177 sampling date, three soil core samples (Ø 6 cm, 5 cm depth) were taken per subplot to extract
178 mesofauna (mostly Collembola and Acari) using a Macfadyen high-gradient extractor
179 (Macfadyen, 1961). Collembolans were determined to family level and Acari to order level
180 using a VHX-Digital microscope. Macrofauna was sampled with two soil cores (Ø 16 cm, 5
181 cm depth) per subplot and extracted through a 10 days gradual increase in temperature using
182 a Kempson extraction method (Kempson et al., 1963). Soil macrofauna was determined to
183 family level (Staphylinidae, Carabidae and Formicidae), order level (Diptera, Araneae,
184 Isopoda, Haplotaxida, Julida and Psocoptera) or class level (Chilopoda, Araneae, Symphyla
185 and Gastropoda), respectively.

186 *2.4. Statistical analysis*

187 The datasets of soil meso- and macrofauna were based on the mean values per sampling date
188 and per subplot. Number of taxa (diversity), total abundance, Pielou's evenness, and the

189 abundances of specific taxa were calculated and then analyzed using a repeated-measures
190 split-plot general linear mixed models with type III sum of squares in SAS (University
191 Edition v9.4). Count data was analyzed assuming Poisson-distributed residuals with log-link
192 function. There was no indication for overdispersion of data, and assuming alternative
193 distributions (including negative binomial) resulted in inferior model fit (assessed via Akaike
194 Information Criterion). The same analyses were applied to data on the abundances of single
195 taxa which could be found in at least half of the samples. Post hoc Tukey's HSD tests were
196 carried out to reveal significant differences among the respective levels within factors.

197 To assess a possible general trend of climate treatment across all taxa of soil fauna, we
198 calculated *Cohen's d* as effect size of climate effect for all taxa (Lakens, 2013) and the 95%
199 confidence intervals to test for significant deviation from zero. The effect of land use was not
200 examined using this approach since there is no possibility to define differences across 5
201 different levels as negative or positive effects.

202 To analyze the relationships between meso- and macrofaunal community composition and the
203 two experimental factors (climate, 2 levels and land use, 5 levels; both categorical),
204 redundancy analyses - RDA (Rao, 1964; van den Wollenberg, 1977) using standardized
205 abundance data were carried out using R 2.1.4.2., package *vegan* (Oksanen et al., 2015). We
206 checked for linear relationships in the data sets (Euclidean metric; prerequisite for this
207 method) by conducting detrended correspondence analyses (DCA) and identifying the
208 respective longest gradient. As these were always below 3, the use of linear methods is
209 appropriate (Lepš and Šmilauer, 2003). Significance of ordination axes and environmental

210 variables were tested using Monte Carlo permutation tests (999 permutations). Only land-use
211 types showed significant correlations with the community composition of meso- and
212 macrofauna; so, we used one-way permutational multivariate analysis of variance -
213 PERMANOVA (Anderson, 2001) based on abundance data and Bray–Curtis distances to test
214 for significant differences in meso- and macrofaunal community compositions between
215 different land-use regimes (overall and pairwise comparisons). Statistical significances were
216 based on 999 permutations. Bonferroni-corrected P values were used because more than two
217 groups were compared. Each pair of land-use regimes showing significant differences in their
218 meso- and/or macrofaunal community composition in the PERMANOVA was further
219 analyzed using Similarity Percentages - SIMPER (Clarke, 1993). This enabled us to identify
220 the respective soil fauna taxa, which mainly generated the dissimilarity patterns between two
221 land-use types (croplands and grasslands). PERMANOVA and SIMPER analyses were
222 conducted with the program “PAST” (Hammer et al., 2001).

223

224 **3. Results**

225 *3.1. Climate and land-use effects on ecological indices of meso- and macrofauna*

226 There was a general trend towards more macrofauna taxa and higher abundances in the
227 grasslands compared to the croplands, and the number of taxa and total abundance of meso-
228 and macrofauna tended to be lower under future climate, though the difference from ambient
229 climate was not significant (Table 1, 2; Fig. 1A, B). Land-use treatments significantly
230 affected the number of macrofauna taxa (Table 2) as well as the total abundances of meso-

231 and macrofauna (Table 1, 2), but the specific pattern and the magnitude differed between
232 sampling dates (land use \times date interaction, Table 1, 2). In general, the number of macrofauna
233 taxa and total abundances of meso- and macrofauna were higher in grasslands than in
234 croplands, and this pattern was especially pronounced in autumn (especially in autumn 2016),
235 when the abundances of both, meso- and macrofauna as well as the number of macrofauna
236 taxa were significantly higher in the three grassland sites compared to the croplands (Fig.
237 1C-E). Further, there were no significant climate and land-use effects on Pielou's evenness of
238 meso- and macrofauna (Table 1, 2). Also, we did not find any significant interactive effects of
239 climate and land use on these ecological indices (number of taxa, total abundance and
240 Pielou's evenness) of meso- and macrofauna Table 1, 2).

241 *3.2. Climate and land-use effects on specific groups of meso- and macrofauna*

242 The most abundant mesofaunal groups were Collembola and Acari, with Collembolans
243 accounting for one quarter of the total abundance of mesofauna. Therein, Isotomidae was the
244 dominant family, which made up ~70% of the total Collembola abundance. Under future
245 climate, the abundances of Collembola as well as the Collembolan family Entomobryidae
246 were marginally significantly lower compared to ambient climate (Table 1). The same pattern
247 was found for Isotomidae (Table 1; Fig. 2A). However, the other Collembolan families,
248 including Katiannidae, Sminthurididae, Onychiuridae, and Hypogastruridae, were not
249 significantly affected by the climate treatment (Table 1).

250 There were significant interacting effects of climate and date on Entomobryidae, which was
251 mostly caused by the high abundance in autumn 2016, where their abundance was

252 significantly higher under ambient compared to future climate (Table1, Fig. 2B). This might
253 indicate an increasing influence of climate treatment with time; however, we could not find
254 this pattern in other groups of Collembola. There was a general significant effect of land-use
255 type on the total abundance of Collembola and the abundances of specific Collembolan
256 families with higher individual numbers in grasslands compared to croplands (Fig. 2C-D).
257 This effect was especially strong for total Collembola in the first and last sampling (Fig. 2F),
258 whereas for Isotomidae in the first sampling (Fig. 2G) and for Katiannidae in last sampling
259 (Fig. 2H; significant land use \times date interaction, Table 1).

260 Acari made up nearly three quarters of the total abundance of mesofauna, of which Oribatida
261 was the most dominant group accounting for more than 70% of total Acari abundance.
262 However, we could not find any significant climate effect neither on the total abundance nor
263 on specific groups of Acari (Oribatida, Mesostigmata and Prostigmata; Table 1). In contrast,
264 we found significantly higher abundances of total Acari and the groups Oribatida,
265 Mesostigmata and Prostigmata in grasslands compared to croplands (Table 1; Fig. 3A-D). For
266 Oribatida, these land-use effects were especially strong in the last sampling (Fig. 3E;
267 significant land use \times date interaction, Table 1).

268 Nearly all taxa of macrofauna did not respond significantly to climate change, except for
269 Chilopoda (Table 2), where future climate significantly decreased their abundance (Fig. S3A),
270 and this effect was most pronounced in autumn 2016 (Table S3B). The responses of single
271 macrofauna taxa to land use were found to differ in magnitude and direction. More
272 specifically, land-use treatments significantly affected the abundances of total Staphylinidae

273 (adults and larvae), total Carabidae (adults and larvae), Diptera pupae, Chilopoda, Hemiptera,
274 Araneae, Diplura, Isopoda and Formicidae (Table 2). All these macrofauna taxa showed
275 generally higher abundances in grasslands compared to croplands (Fig. S4A-L). Total
276 Staphylinidae (adults and larvae), Chilopoda, Diplura, Isotoda and Formicidae tended to be
277 more abundant in extensively used meadows than in intensively used meadows and
278 extensively used pastures, whilst the abundance of Carabidae (adults and larvae), Diptera
279 pupae and Araneae decreased from extensively-used pastures over extensively-used meadows
280 to intensively-used meadows. Additionally, the land-use effects on abundances of
281 Staphylinidae (adults and larvae), Carabidae (adults and larvae), Chilopoda, Isopoda and
282 Halpotaxida, differed according to the sampling dates, with stronger effects in autumn than in
283 spring (Fig. S4M-N; e.g., Staphylinidae and Carabidae adults). Even if there was no
284 significant response of the majority of fauna groups to the climate treatment according to the
285 GLMM, there was a general negative response across all taxa to climate change (Table S2,
286 mean *Cohen's d* = - 0.45, 95% confidence interval: lower limit = - 0.80, upper limit = - 0.10).

287 *3.3. Climate and land-use effects on community composition of meso- and macrofauna*

288 Land-use treatments significantly affected the community composition of soil meso- and
289 macrofauna, while there was no significant climate effect (Fig. 4A, B). The climate effect was
290 therefore excluded from the analyses. For mesofauna, 20.76% of the total variance in the data
291 set was explained by the five constrained RDA axes (Table S2). RDA 1 significantly
292 explained 62.47% of this variance (Fig. 4A; Table S3; Table S4) and represented mostly the
293 intensively used meadows (Table S5—highest absolute value at RDA 1). Katiannidae got the

294 highest species score (Table S6). The RDA 2 accounted for 30.14 % of explained variance
295 (Fig. 4A; Table S3, Table S4), and represented mostly the extensively used meadows (Table
296 S5—highest absolute value at RDA 2), and Sminthurididae got the highest species score
297 (Table S6).

298 For macrofauna, 21.35% of the total variance in the data set was explained by the five
299 constrained RDA axes. The RDA 1 significantly explained 66.47% of this variance (Fig. 4B;
300 Table S3, Table S4) and represented mostly the organic farming (Table S4—highest absolute
301 value at RDA 1), and adult Carabidae got the highest species score (Table S6). The RDA 2
302 accounted for 14.41% of the explained variance (Fig. 4B; Table S3, Table S4), and
303 represented mostly the intensively used meadows (Table S6—highest absolute value at RDA
304 2), and Diptera larvae got the highest species score (Table S6).

305 The results from PERMANOVA showed that the significant land-use effect on the
306 community compositions of meso- and macrofauna were driven by land-use type (croplands
307 vs. grasslands) and not by land-use management intensity within the same land-use type
308 (Table S7). SIMPER analysis confirmed that the community compositions of meso- and
309 macrofauna were moderately to strongly different between croplands and grasslands. The
310 overall dissimilarity ranging from 47.83% (mesofauna, conventional farming vs. extensively
311 used pastures) to 94.75% (macrofauna, organic farming vs. extensively used meadows).
312 Detailed information on percent dissimilarity and top 5 taxa of soil meso- and macrofauna
313 that contributed the most to the observed difference in the communities between croplands
314 and grasslands are shown in Table S8.

315

316 **4. Discussion**

317 *4.1. Climate effects on soil fauna*

318 Climate change may alter the activity of soil biota (fauna and microbes) by changing soil
319 microclimate, and thereby ecosystem functions, such as litter decomposition (Allison et al.,
320 2013; Yin et al., 2019). In separate analyses, the number of taxa, evenness and the abundance
321 of fauna in total as well as most taxa showed no significant responses, while we found a
322 decrease in Collembolan abundance under future climatic conditions. This result is in
323 accordance with Makkonen et al. (2011) who found Collembola to be vulnerable to soil
324 desiccation under future climate. As warming exacerbates the effects of drought (Thakur et al.,
325 2018; Vestergård et al., 2015), these drought periods, in particular, are likely to be the main
326 driving force behind the decline of Collembola rather than the temperature increase itself
327 (Hodkinson et al., 1998). Larger-sized epedaphic Collembola are generally more
328 drought-tolerant and may better survive under future climatic conditions than the more
329 hydrophilic, smaller-sized euedaphic species (Makkonen et al., 2011). In contrast, we found
330 that the future climate treatment only tended to decrease the abundances of larger-sized
331 Collembola (i.e., Isotomidae and Enotomobyidae), whereas the smaller-sized Collembola (i.e.,
332 Katiannidae, Sminthurididae, Onychiuridae and Hypogastruridae) were less affected. Hence,
333 epedaphic Collembola with larger body size were more susceptible to our climate treatment
334 than epedaphic Collembola with smaller body size or euedaphic families. Our results are
335 basically in line with those of Jucevica and Melecis (2006), who demonstrated that climate

336 change-induced drought negatively and profoundly affected litter-dwelling Collembola,
337 especially epedaphic species, because the soil surface is more vulnerable to environmental
338 fluctuations compared to deeper soil layers.

339 Besides Collembola, Acari are frequently used as bioindicators for environmental
340 assessments (Behan-Pelletier, 2003). Similar to Collembolans, drought can decrease the
341 species richness and abundance of Acari. Especially vulnerable are species of the order
342 Oribatida (Lindberg et al., 2002), which was one of the most dominant groups in our study,
343 accounting for around three quarters of total Acari abundance (followed by Mesostigmata and
344 Prostigmata). However, our results showed that future climatic conditions had no significant
345 effects neither on Oribatida nor on Mesostigmata or Prostigmata. In line with our findings,
346 Acari were reported to be less drought-sensitive than Collembola (Vestergård et al., 2015),
347 whilst soil mesofauna may be generally unaffected even by long-term manipulations of
348 climate (Holmstrup et al., 2013). However, Holmstrup et al. (2013) also suggest that annual
349 drought events can alter the community structure of Collembola without detectable effects on
350 the Acari community. Thus, our study adds to the body of evidence that Acari might be less
351 sensitive to changes in climatic conditions.

352 Further, most macrofauna taxa showed no response to climate change in the present study,
353 except for Chilopoda, whose abundance decreased under future climatic conditions. Whilst
354 this might be a direct effect of drought, it is also plausible that this predatory group suffers
355 from the climate change-induced decline in Collembola density, i.e., from bottom-up induced
356 changes in the soil food web (Crowther and Grossart, 2015). A non-random loss of top

357 predators in soil communities has been found under drought conditions and warming (Lindo
358 et al., 2012), leading to corresponding trophic cascade prey release (Staddon et al., 2010).
359 Future studies should address how biotic interactions and the balance of bottom-up versus
360 top-down forces shifts in soil food webs in a changing world. We are aware that several
361 groups of macrofauna (e.g., Diptera, Coleoptera) may have a higher mobility and can move
362 among the experimental plots. Any effects of experimental treatments can therefore be
363 considered as conservative measures of the real effects. However, we could not observe
364 generally weaker effects of climate change on macrofauna compared to mesofauna in this
365 study.

366 Soil fauna is known to be strongly dependent on soil moisture (Coleman et al., 2004),
367 therefore, the absence of stronger effects of the precipitation changes on most of soil fauna
368 groups in our experiment were surprising and in contrast to several other published studies
369 (Blankinship et al., 2011; Kardol et al., 2011; Lindberg and Bengtsson, 2005). Eisenhauer et
370 al. (2012) argued that in some cases fauna in the upper soil layers might have the capacity to
371 adapt to drought events and may therefore be less vulnerable. Moreover, soil fauna may move
372 to deeper soil layers during drought phases. Since we sampled soil fauna during the activity
373 peaks in spring and autumn (which receive in contrast to the summer slightly more
374 precipitation in the future climate treatment), we might have missed this specific effect of the
375 stronger summer drought. Further, it might be speculated that one year of climate
376 manipulation before the first sampling might be rather short to provoke changes in the
377 abundance of soil fauna. However, generation times mainly range between a few days and a

378 few months across the studied taxa (Table S9), which should allow several generations per
379 year and therefore noticeable changes of population densities. Moreover, we could not find
380 weaker climate effects on macrofauna with generally longer generation times. Nevertheless, it
381 can be expected that the climate manipulation will cause accumulative changes in the biotic
382 and abiotic environment with potentially stronger effects after several years.

383 In our experiment, the temperature increase in soil caused by roof closing during the night is
384 about the same or may slightly exceed the increment of air temperatures near the soil surface.
385 This somewhat surprising result can be explained by a reduced vegetation cover in this
386 treatment as a consequence of the changed climate and thereby an increased exposure of the
387 soil surface to direct insolation (Schädler et al., 2019). Night warming therefore increases soil
388 temperature directly and indirectly via changes in the vegetation cover, which has to be
389 considered as a realistic scenario rather than an artifact. This is also the case for other
390 environmental variables which are directly or indirectly linked to the manipulated climate.
391 For instance, we could demonstrate a longer frost-free period and an increase of growing
392 degree days on plots with future climate due to the temperature manipulation (Schädler et al.,
393 2019), and both phenomena are important components of future climatic scenarios (Maracchi
394 et al., 2005). In the case of relative air humidity, we found lower values on future climate
395 plots even during the night, which is counterintuitive to the expected results of roof closing.
396 Again, the realistic effect of a reduced vegetation cover is overriding the possible artifact of
397 experimental manipulation in this case. Related to this, differences of effects of climate
398 treatment between land-use regimes can also be assigned to mediating effects of the

399 corresponding vegetation structure and cover. The proportion of bare soil as well as height
400 and density of vegetation determine the level of temperature increase by night roofing in
401 microhabitats in the vegetation and below the soil surface. This adds to the potentially
402 interacting effects of climate and land use in real ecosystems. In sum, even a climatic
403 condition with a rather small increase of the mean daily temperature has been shown to
404 directly and indirectly affect soil fauna and also associated soil processes in this experiment
405 (Yin et al., 2019). This should be kept in mind when critical thresholds of temperature
406 increase and potential consequences are discussed (e.g., the “two degrees goal”, Rogelj et al.,
407 2016).

408 *4.2. Climate-independent land-use effects on soil fauna*

409 The observed strong effects of land-use regimes on the soil fauna with lower abundance,
410 lower number of taxa and changed composition in croplands compared to grasslands are in
411 accordance with previous studies (Barrios et al., 2005; Foley et al., 2005; Muchane et al.,
412 2012; Schmidt et al., 2015). Detrimental effects in croplands were shown to include clearing
413 of native vegetation and the disturbance of the soil upper horizon, application of
414 agrochemicals, mono-cropping, exposure to desiccation, limited access to food sources, and
415 habitat modifications (Alvarez et al., 2001; Baker, 1998; Muchane et al., 2012). The
416 responses of Collembolan families to land use differed in direction and magnitude. In line
417 with a previous study (Cluzeau et al., 2012), the dominant family Isotomidae has been shown
418 to be rather insensitive to land use, although significant land-use effects were found on total
419 Collembola.

420 Our results suggest that land-use conversion from grasslands to croplands is an important
421 driver of abundances of all orders of Acari, but not management intensity within the two
422 land-use types. In part, these results are in line with those of Minor and Cianciolo (2007),
423 who show that land-use types along an increasing intensity gradient negatively affected
424 Oribatida but not Mesostigmata. Overall, we found Acari to be more sensitive to the changes
425 of land use compared to Collembola. Accordingly, Acari are often regarded as good
426 bioindicator for assessing the consequences of land-use change (Gulvik, 2007).

427 Further, most of the macrofaunal groups in this study (Coleoptera, Diplura, Isopoda and
428 Formicidae) were more abundant in grasslands compared to croplands. Several previous
429 studies showed that frequent disturbances due to intensive agricultural practices in croplands
430 are detrimental to the macrofauna community in the soil, while the conditions in meadows
431 and pastures can support high levels of diversity and abundance of these organisms (Barrios
432 et al., 2005; Brévault et al., 2007; Muchane et al., 2012; Pauli et al., 2011; Tsiafouli et al.,
433 2015). Furthermore, land-use effects on soil biota may also be mediated through indirect
434 effects on microclimatic conditions. The soil water content showed no substantial differences
435 between the land-use regimes in our study. However, the tendency of higher soil temperatures
436 in the grasslands (Fig. S2) might positively affect soil fauna abundance. Microclimatic effects
437 of land management can therefore be suggested to superimpose the effects of minor and
438 moderate changes of ambient temperatures.

439 Most soil fauna groups showed strong variations between sampling dates which often
440 interacted with land-use type. The mesofauna showed the highest abundances in spring 2016

441 and autumn 2016, mainly driven by Collembola. We can only speculate about the reasons for
442 these variations, but they might be due to shifts in activity patterns in response to climatic
443 differences. Macrofauna showed a distinct maximum at the last sampling date, which might
444 be the result of the ongoing colonization of the former arable site.

445 The findings of De Vries et al. (2012) indicate that extensive land management buffers the
446 effects of climate change on microbial soil food-webs. However, this could not be confirmed
447 by our study on soil fauna, since no significant interaction effects between land-use regime
448 and climate change were found on the abundance and community composition of soil fauna.
449 Comparable studies are needed in the future to assess the generality of these findings.

450

451 **5. Conclusions**

452 Our study indicates that the effects of a predicted climate change scenario on soil fauna
453 communities are minor, even though we found a negative overall effect on the abundances
454 across all investigated taxa. Especially, abundances of few key taxa (e.g., Isotomidae and
455 Chilopoda) decreased under the future climate scenario. Notably, these minor climate change
456 effects were consistent across the five common land-use types in the region. Generally, meso-
457 and macrofauna were more abundant in grasslands than in croplands. This might be caused
458 by direct effects of management (e.g., disturbances, plant diversity), but also by indirect
459 effects via a changed microclimate in soil. Within these land-use types, however, land-use
460 intensity had minor effects. Taken together, these results suggest that land-use effects on soil
461 fauna communities are equally strong under current and future climate conditions.

462

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476

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Table 1. Mesofauna responses to climate, land use, date and their interactions. Results (*F-values*) of the split-plot generalized linear mixed model (type III sum of squares) with repeated measures on number of taxa, total abundance, Pielou's evenness of mesofauna, as well as the abundances of Collembola groups and Acari groups. *F-values* with * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Abbreviations: Coll: Collembola; Isot: Isotomidae; Ento: Entomobryidae; Kati: Katiannidae; Smin: Sminthurididae; Hypo: Hypogastruridae; Onyc: Onychiuridae; Acar: Acari; Orib: Oribatida; Pros: Prostigmata; Meso: Mesostigmata.

Independent variable	<i>Df</i>	Number of taxa	Total abundan	Pielou's evenness	Coll	Isot	Ento	Kati	Smin	Onyc	Hypo	Acar	Orib	Meso	Pros
Climate (C)	1,8	2.57	2.37	0.09	5.2 ⁺	10.67*	4.64 ⁺	0.06	0.07	0.99	0.02	0	0.03	0	1.91
Land use (L)	4,32	0.78	11.6***	0.29	2.69*	1.2	4.48**	1.75	4.75**	1.49	0.64	8.95***	6.28***	5.74**	3.89*
Date (D)	3,24	4.86**	8.04***	0	27.89***	42.68***	15.65***	6.94**	10.33***	5.36**	2.89	10.22***	12.07***	7.2**	96.98***
C × L	4,32	0.43	0.63	0.02	1.4	0.29	0.55	1.08	0.37	0.17	0.41	0.35	0.52	0.28	0.35
C × D	3,24	0.07	0.74	0.05	0.18	0.32	3.39*	1	0.71	0.21	0.31	1.9	1.74	0.31	2.95
L × D	12,96	1.14	3.12***	0.02	5.51***	4.13***	1.56	2.65**	3.5***	1.51	2.01*	1.64	1.89*	0.98	3.23***
C × L × D	12,96	0.13	0.64	0.01	0.32	0.54	1.14	1.19	0.55	0.98	0.54	1.32	1.19	0.7	0.74

Table 2. Macrofauna responses to climate, land use, date and their interactions. Results (*F*-values) of the split-plot generalized linear mixed model (type III sum of squares) with repeated measures to analyze the effects on number of taxa, total abundance, Pielou's evenness of macrofauna, as well as the abundances of selected macrofauna taxa. *F*-values with * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Abbreviation: Stap: Staphylinidae; Stap_A: Staphylinidae adult; Stap_L: Staphylinidae larvae; Cara: Carabididae; Cara_A: Carabididae adult; Cara_L: Carabididae larvae; Dipt: Diptera; Dipt_A: Diptera adult; Dipt_P: Diptera pupae; Dipt_L: Diptera larvae; Chil: Chilopoda; Aran: Araneae; Dipl: Diplura; Isop: Isopoda; Form: Formicidae; Symp: Symphyla; Gast: Gastropoda; Hapl: Haplotaxida; Juli: Julida; Psoc: Psocoptera.

Independent variable	<i>Df</i>	Number of taxa	Total abundance	Pielou's evenness	Stap	Stap_A	Stap_L	Cara	Cara_A	Cara_L	Dipt	Dipt_A	Dipt_P
Climate (C)	1,8	0.06	0.32	0.11	0.7	0.5	0.38	2.47	1.05	1.72	0.66	0.04	0.11
Land use (L)	4,32	17.89***	34.45***	0.26	12.34***	8.35***	7.21***	12.58***	10.31***	4**	2.37	0.62	3.79*
Date (D)	3,24	5.88**	8.9***	0.32	5.56*	3.91*	17.2***	3.6*	10.2***	14.39***	6.11**	13.17***	13.28***
C × L	4,32	0.9	0.89	0.01	1.32	0.87	2.22	0.54	0.66	0.21	0.59	0.56	1.36
C × D	3,24	2.06	1.28	0.02	0.43	0.46	0.37	0.63	0.43	1.72	0.74	0.96	0.96
L × D	12,96	3.12***	4.83***	0.03	3.7***	3.31***	6.59***	1.41	1.92*	2*	1.72	0.84	1.65
C × L × D	12,96	1.35	1.25	0.02	0.98	0.71	1.62	1.12	1.13	0.71	1.23	0.51	0.66
		Dipt_L	Chil	Aran	Dipl	Isop	Form	Symp	Gast	Hapl	Juli	Psoc	
Climate (C)	1,8	0.91	5.59*	0.12	0.1	0.42	0.01	2.97	2.4	2.08	0.51	0.05	
Land use (L)	4,32	2.09	3.59*	6.16***	2.91*	3.42*	4.95**	1.43	0.6	0.52	1.6	1.31	
Date (D)	3,24	2.47	9.8***	8.11***	6.45**	6.24**	3.29*	8.17***	5.37**	2.88	1.58	2.42	
C × L	4,32	0.85	0.91	0.99	0.43	0.82	0.12	2.27	0.51	1.98	1.05	0.95	
C × D	3,24	1.75	3.3*	0.27	0.12	1.21	0.89	2.55	1.84	0.89	1.18	1.11	
L × D	12,96	1.62	2.58**	1.74	1.79	2.71**	1.54	1.7	0.43	2.57**	0.94	0.88	
C × L × D	12,96	1.51	0.7	0.63	1.11	1.85	0.96	1.67	0.74	1.6	0.88	1.08	

Figure legends

Fig. 1. **A:** Effects of climate on number of taxa of meso- and macrofauna. **B:** Effects of climate on total abundance of meso- and macrofauna. **C:** Effects of land use \times date interaction on the number of macrofauna taxa. **D:** Effects of land use \times date interaction on the total abundance of mesofauna. **E:** Effects of land use \times date interaction on the total abundance of macrofauna.

Notes: Values as Mean + SE, and all significant differences were revealed by one-way ANOVA with Tukey's Post-hoc-test (*the same as below*). **A-B:** n.s. represents non-significant differences between ambient and future climate treatments. **G-E:** Different lowercase letters represent significant differences among land-use regimes in the same date. Land-use regimes are abbreviated (*the same as below*) as CF for conventional farming, OF for organic farming, IM for intensively used meadows, EM for extensively used meadows and EP for extensively used pastures.

Fig. 2. **A:** Effects of climate on the abundances of Collembolan groups (Collembola, Isotomidae and Entomobryidae). **B:** Effects of climate \times date interaction on the abundance of Entomobryidae. **C:** Effects of land use on Collembola abundance. **D:** Effects of land use on Entomobryidae abundance. **E:** Effects of land use on Sminthurididae abundance. **F:** Effects of land use \times date interaction on Collembola abundance. **G:** Effects of land use \times date interaction on Isotomidae abundance. **H:** Effects of land use \times date interaction on Katiannidae abundance.

Notes: **A-B:** Significance levels between ambient and future treatments are given as +

for $P < 0.1$ and * for $P < 0.05$. Different lowercase letters represent significant differences among different dates in the same climate treatment. **C-E**: Different lowercase letters represent significant differences among different land-use regimes. **F-H**: Different lowercase letters represent significant differences among land-use regimes in the same date. For abbreviations of land-use regimes see Fig. 1.

Fig. 3. A: Effects of land use on Acari abundance. **B:** Effects of land use on Oribatida abundance. **C:** Effects of land use on Mesostigmata abundance. **D:** Effects of land use on Prostigmata abundance (Mean + SE). **E:** Effects of land use \times date interaction on Oribatida abundance.

Notes: A-D: Different lowercase letters represent significant differences among different land-use regimes. **E:** Different lowercase letters represent significant differences among land-use regimes in the same date. For abbreviations of land-use regimes see Fig. 1.

Fig. 4. A: Effects of climate and land use on community composition of mesofauna. **B:** Effects of climate and land use on community composition macrofauna.

Notes: Results based on redundancy analyses (RDA), and arrows refer to two climate treatments (Ambient and Future), and five land-use regimes (for abbreviations see Fig. 1). Abbreviations for soil fauna groups (in alphabetical sequence): Aran: Araneae, Cara_A: Carabididae adult, Cara_L: Carabididae larvae, Chil: Chilopoda, Dipl: Diplura, Dipt_A: Diptera adult, Dipt_L: Diptera larvae, Dipt_P: Diptera pupae, Ento:

Entomobryidae, Form: Formicidae, Gast: Gastropoda, Hapl: Haplotaxida, Hemi:
Hemiptera, Hypo: Hypogastruridae, Isop: Isopoda, Isot: Isotomidae, Juli: Julida, Kati:
Katiannidae, Meso: Mesostigmata, Onyc: Onychiuridae, Orib: Oribatida, Pros:
Prostigmata, Psoc: Psocoptera, Smin: Sminthurididae, Stap_A: Staphylinidae adult,
Stap_L: Staphylinidae larvae and Symp: Symphyla.

Fig. 1

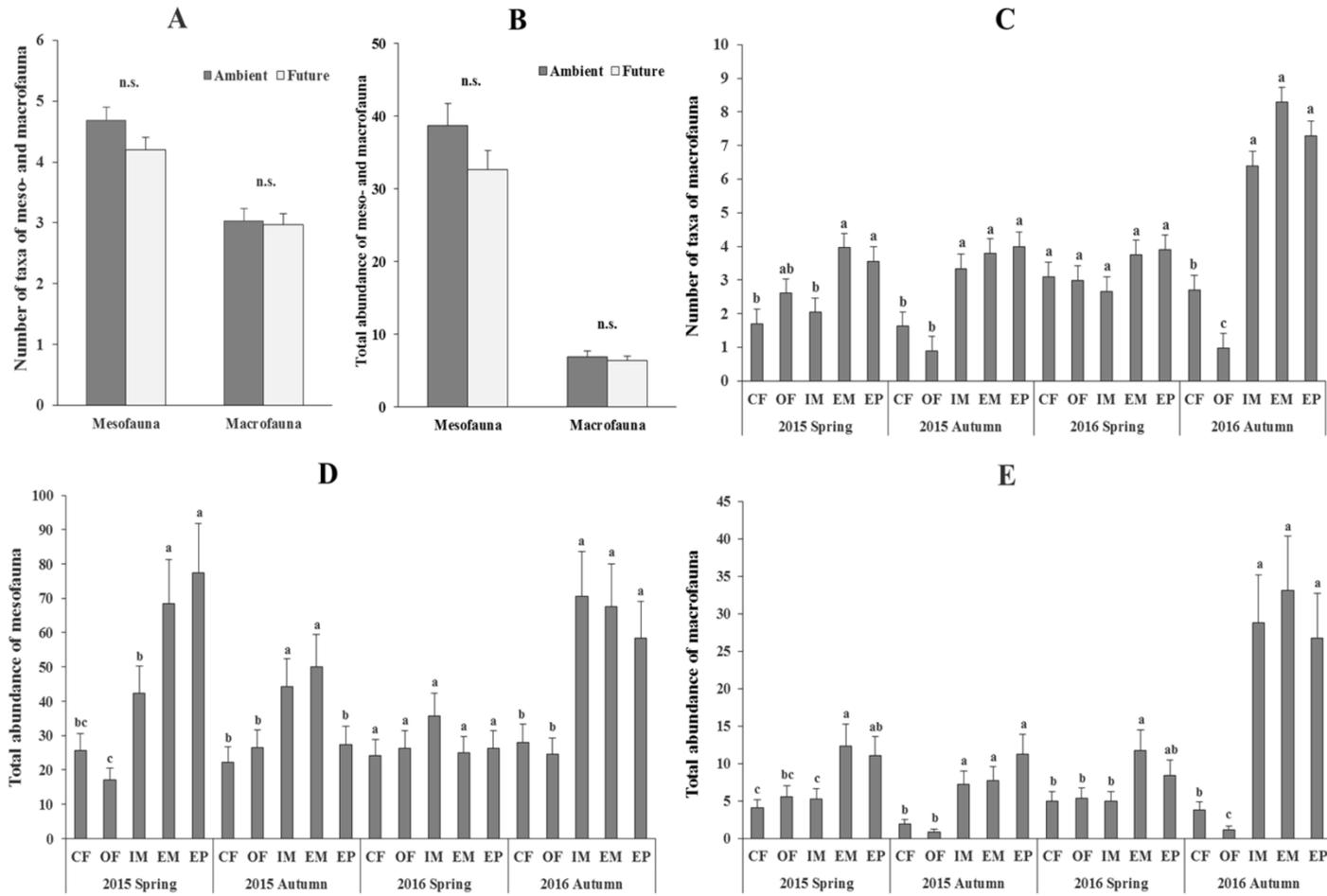


Fig. 2

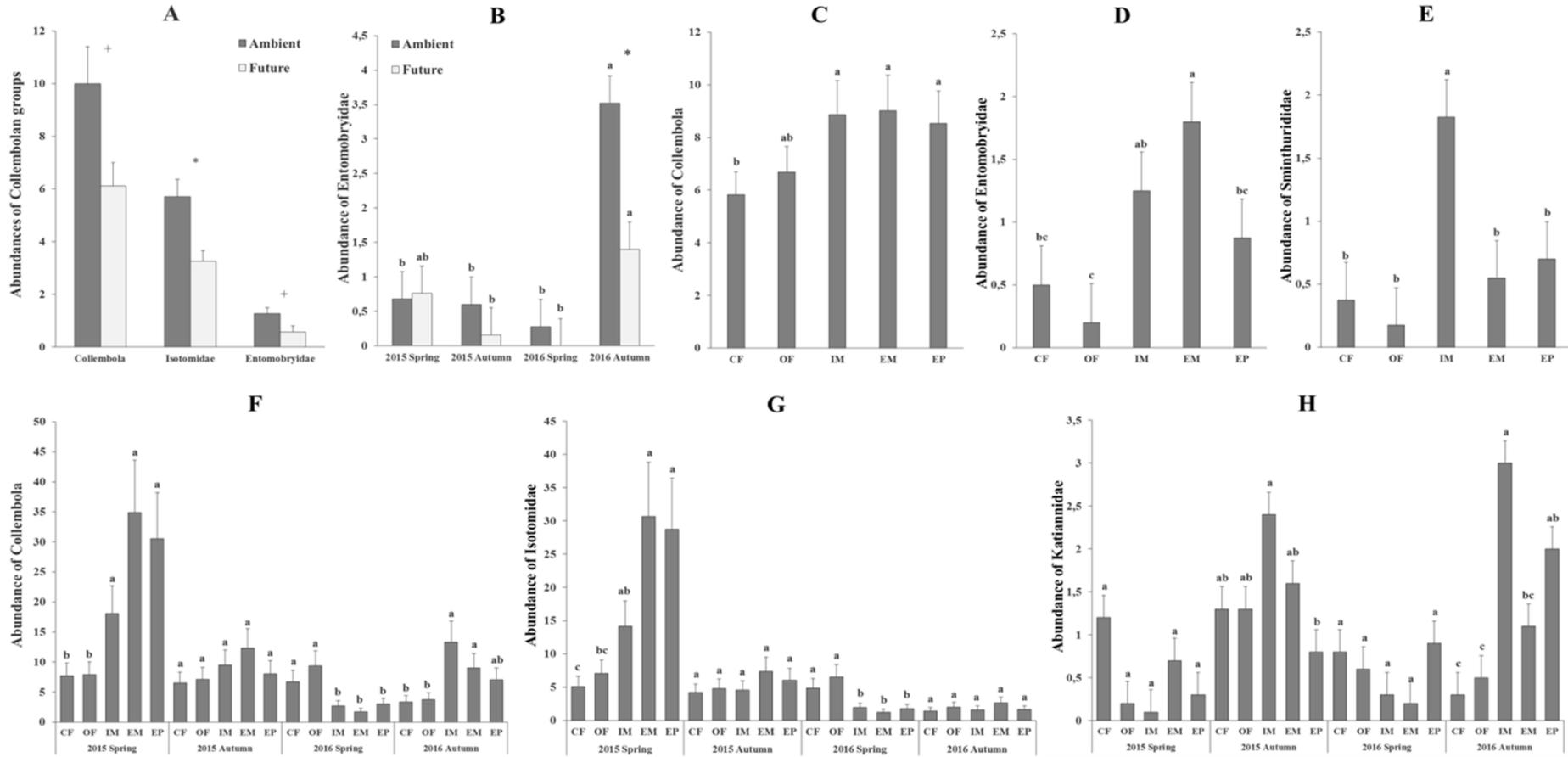


Fig. 3

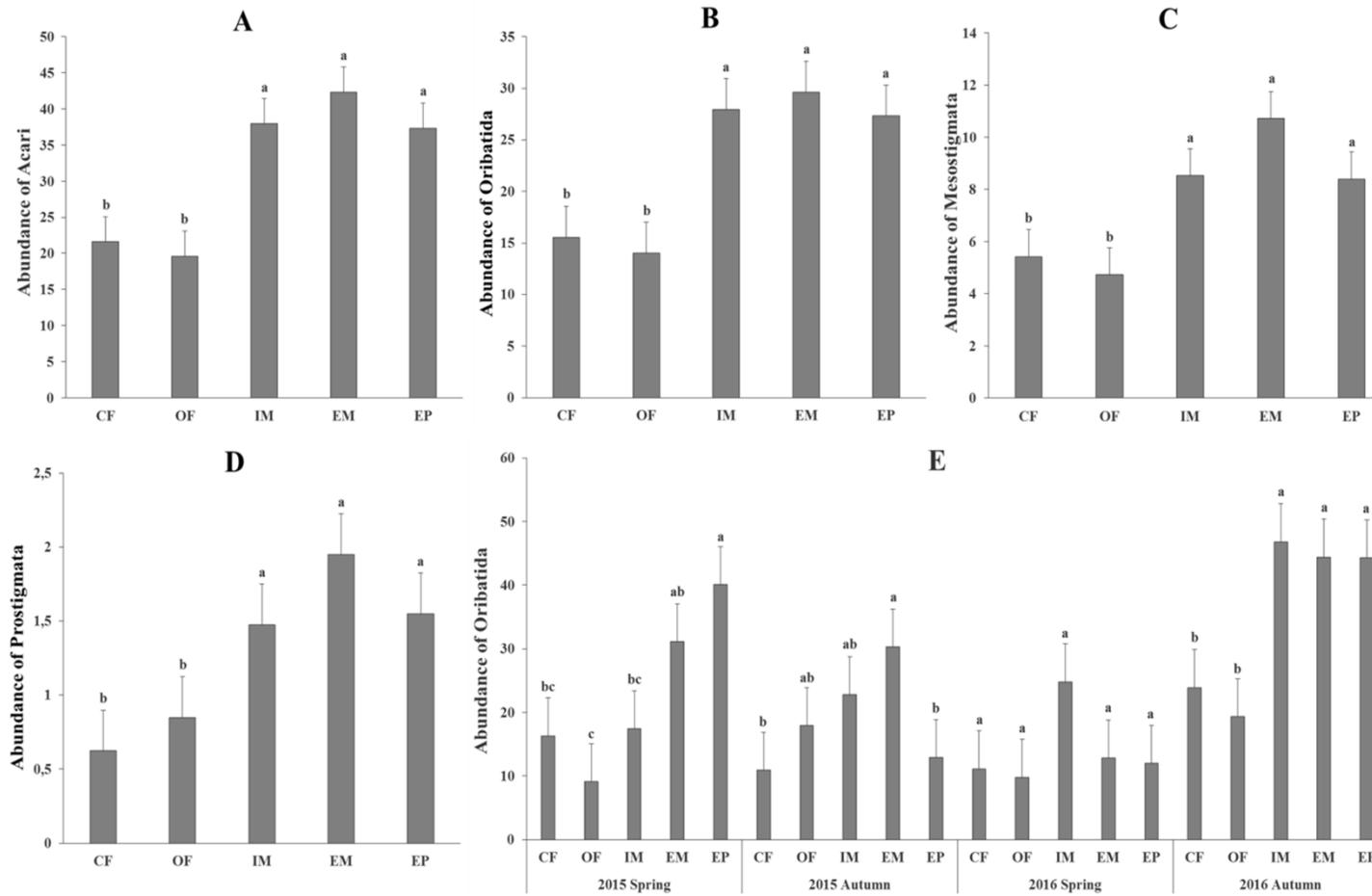


Fig. 4

