This is the preprint of the contribution published as:

Yin, R., Gruss, I., Eisenhauer, N., Kardol, P., Thakur, M.P., Schmidt, A., Xu, Z., Siebert, J.,
Zhang, C., Wu, G.-L., Schädler, M. (2019):
Land use modulates the effects of climate change on density but not community composition of Collembola
Soil Biol. Biochem. 138, art. 107598

The publisher's version is available at:

http://dx.doi.org/10.1016/j.soilbio.2019.107598

- 1 Article type: Research Article
- 2 Title: Land use modulates the effects of climate change on density but not community
- 3 composition of Collembola
- 4 Running head: Land use-modulated climate effects on Collembola density
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29

30 Abstract

Collembola are highly abundant and diverse soil animals and play key roles in litter 31 32 decomposition and nutrient cycling. Given their functional significance, it is important to understand their responses to human-induced global changes, such as climate change and land-33 use intensification. Here, we utilized an experimental field study, to test the interactive effects of 34 climate (ambient vs. future) and land use (five land-use regimes, from extensively-used meadow 35 to conventional farming) on three eco-morphological life forms of Collembola: epedaphic, 36 hemiedaphic, and euedaphic species. We found that the effects of climate change on Collembola 37 density were modulated by land use, and that the responses of different life forms to climate \times 38 land use interaction differed in magnitude and/or direction. The densities of total and 39 40 hemiedaphic Collembola significantly decreased under organic farming and marginally increased in grasslands under future climatic conditions, whereas epedaphic Collembola tended to decrease 41 their density with climate change in grasslands. In contrast, the density of euedaphic Collembola 42 43 significantly increased with climate change in intensively-used grasslands. Further, we found that grasslands (especially extensively-used meadow) support the most abundant Collembola 44 communities, with high species richness but low evenness. Multivariate analyses revealed 45 46 independent effects of climate change and land-use intensification on Collembola community

47 composition. Together, our findings indicate that the effects of climate change on Collembola 48 communities depend on their life forms and land-use types. Surface-dwelling Collembola are 49 more vulnerable to land use and climate change than those living in deeper soil layers. This may 50 slow down the process of soil-surface litter decomposition in a changing world.

51

52 Key words

Future climate; intensive land use; invertebrate decomposers; global change; life forms; soil
biodiversity

55

56 1. Introduction

Climate change and land-use intensification are two of the most pervasive global 57 environmental changes, which are threatening the biodiversity and functioning of terrestrial 58 ecosystems (Sala et al., 2000). However, the impacts of these global changes and their potential 59 interactions are mostly studied for aboveground communities, and we still know less about the 60 responses of below-ground communities (Bokhorst et al., 2012). Soil fauna communities are 61 remarkably abundant and diverse. They play crucial roles in soils, which regulate multiple 62 63 ecosystem functions and determine how these ecosystems respond to global changes, such as climate and land use (Bardgett and Van Der Putten, 2014). Among them, Collembola are one of 64 the most abundant invertebrate decomposer groups in almost all terrestrial ecosystems, with 65 66 densities often reaching thousands of individuals per square meter (Hopkin, 1997). They greatly contribute to litter decomposition through fragmentation or via stimulating microbial activity by 67 grazing (Hanlon, 1981). Moreover, Collembola often occupy a key position in soil food webs, as 68 69 they are not only consumers of microorganisms (Thakur and Geisen, 2019; Turnbull and Lindo,

2015), but also prey of predators, such as centipedes and predatory mites (Turnbull and Lindo,
2015; Yin et al., 2019b). Due to their high sensitivity to environmental changes, Collembola are
often used as indicators to assess environmental degradation and soil quality (Frampton, 1997;
Hågvar and Klanderud, 2009).

The dynamics and assemblage of Collembola communities are closely related to 74 environmental conditions (Chernova and Kuznetsova, 2000; Makkonen et al., 2011). Kardol et 75 al. (2011) found that the density and species richness of Collembola were positively related to 76 soil moisture content and were negatively related to soil temperature (due to warming-related 77 78 reductions in soil moisture content). Therefore, both warming and desiccation can negatively affect Collembola communities (particularly euedaphic species, Krab et al., 2010). Different 79 species are likely to differ in response to these environmental factors (McGeoch et al., 2006), 80 which could alter their community structure (Bokhorst et al., 2008; Pollierer and Scheu, 2017). 81 Again, temperature and moisture have also been shown to explain most of the variation in 82 community composition of soil microarthropods (Kardol et al., 2011) and their activity (Thakur 83 et al., 2018). However, many previous studies investigated the effects of temperature and 84 moisture separately on Collembola communities. Though, in most regions, future climate is 85 86 characterized by the combination of higher temperatures and altered precipitation patterns (Dale et al., 2001; IPCC, 2018). Therefore, studies are urgently needed to explore their combined 87 effects under realistic climate scenarios (Korell et al., 2019). . Besides, the changes in land-use 88 type and management intensity are also considered as primary factors determining Collembola 89 community composition (Hopkin, 1997; Lavelle, 1997). Understanding these effects of global 90 changes on Collembola is thus essential to develop and implement effective measures to 91 92 conserve their community and ecosystem functioning (Sousa et al., 2006).

93 Collembola species occupy distinct spatial habitats within the soil (Rusek, 1998), and are accordingly grouped into three main life forms (Hopkin, 1997). First, species dwelling on the 94 surface of the soil are epedaphic Collembola with relatively large body size and fast dispersal 95 ability. Second, species dwelling in the soil are euclaphic Collembola with relatively small body 96 size and low dispersal ability, and third, species showing intermediate characteristic between 97 epedaphic and euedaphic species are called hemiedaphic Collembola. These life forms of 98 Collembola exert distinct roles in the soil. For example, epedaphic species tend to initiate the 99 earlier stages of decomposition (with higher litter C to N ratios), while euclaphic species (by 100 101 dwelling in the deeper layers of the organic soil horizon with lower soil C to N ratios) become active during the later stages of decomposition (Krab et al., 2010). Moreover, different life forms 102 may differ in their responses to climate change and land-use intensification, which may 103 104 subsequently result in shifts in the structure of Collembola communities (Auclerc et al., 2009), and thereby the functioning of ecosystems (Briones et al. 2009). However, it is still poorly 105 known how global change drivers affect different life forms of Collembola. 106

107 Temperature differences determined by soil layers are indicative for the thermal niches of soil organisms living therein (Liefting and Ellers, 2008). Euedaphic species occupy comparatively 108 stable environments, therefore they have been shown to be more negatively affected by 109 fluctuating temperature regimes and extreme weather events compared to hemiedaphic and 110 epedaphic species (Bokhorst et al., 2012; Holmstrup et al., 2018). Tsiafouli et al. (2005) showed 111 112 that the desiccation intolerance of Collembola was related to their body size, cutaneous respiration, and relatively thin exoskeleton. Therefore, Collembola with smaller body size, such 113 as euclaphic species, have higher surface area to volume ratios and are particularly vulnerable to 114 115 desiccation (Krab et al., 2010). Additionally, different life forms of Collembola may differ in 116 response to intensive land use (Pollierer and Scheu, 2017), but until now, there is no consensus 117 on potential differences. For example, Ponge et al. (2006) suggested that euclaphic species, due to their limited active dispersal, may suffer more from land-use intensification, compared to 118 119 hemiedaphic and epedaphic species. By contrast, Ellers et al. (2018) showed stronger effects of intensive land use on epedaphic than euedaphic Collembola. Furthermore, land-use types 120 characterized by higher plant diversity can favor Collembola communities (Querner et al., 2018), 121 but these effects might differ among Collembola life forms with more pronounced effects on 122 soil-dwelling species than on epedaphic species (Eisenhauer et al., 2011). 123

Given that both climate change and land-use intensification can negatively influence 124 Collembola communities and may differentially influence specific life forms of Collembola, it is 125 plausible that climate-change effects are dependent on land-use type and/or management 126 127 intensity (Walter et al., 2013; Yin et al., 2019a). In fact, land-use effects can further cause shifts in microclimate (i.e., temperature and moisture), which may modulate climate-change effects on 128 soil organisms (Petersen, 2011). Intensive land use, often with low biodiversity, may intensify 129 130 detrimental climate-change effects. By contrast, extensive land use, with relatively high biodiversity, may buffer these detrimental effects, since systems with high diversity often have 131 132 higher resistance to combat adverse environmental conditions (de Mazancourt et al., 2013; Goldenberg et al., 2018; Siebert et al., 2019). Therefore, exploring the potential interactive 133 effects of climate and land use is crucial to predict how Collembola communities and their 134 135 functions may be influenced and could be maintained under future conditions.

Here, we utilized the Global Change Experimental Facility (GCEF; Schädler et al., 2019) to
investigate the single and interactive effects of climate change and land-use intensification on
Collembola communities. In this experimental platform, a future climate scenario for Central

139 Germany in the years of 2070 - 2100 is simulated by increased air and soil temperatures (+0.6°C 140 vs. ambient) and altered precipitation (-20% in summer and +10% in spring/autumn vs. ambient). In addition, five land-use regimes with two croplands (conventional farming and organic farming) 141 142 and three grasslands (intensively-used meadow, extensively-used meadow and extensively-used pasture) were set up. The aim of this study was to explore the effects of climate change on the 143 density, species richness, and community composition of Collembola, and how these effects are 144 altered by land-use type (croplands vs. grasslands) and management intensity. We tested four 145 hypotheses: (1) climate change will decrease the densities and species richness of Collembola 146 147 communities, especially for euclaphic (soil-dwelling) species; whereas epedaphic (surfacedwelling) and hemiedaphic (intermediate between epedaphic and euedaphic) species may be 148 influenced to a lower extent. (2) Grasslands and extensively-managed fields will have higher 149 150 densities and species richness of Collembola than croplands and intensively-managed fields. More specifically, epedaphic Collembola species will be more vulnerable to land-use 151 intensification than euedaphic Collembola. (3) Climate-change effects on the densities and 152 153 species richness of Collembola communities will be modulated by land-use type/management intensity. Specifically, the detrimental climate-change effects will be intensified in croplands 154 155 and/or under intensive management, with the most pronounced effects on epedaphic and hemiedaphic Collembola; whereas detrimental climate-change effects will be modest in 156 grasslands and/or under extensive management, with the most pronounced effects for euedaphic 157 158 Collembola. (4) Interactive effects of climate and land use will alter the community composition of Collembola, as driven by the distinct responses of Collembola species with different life forms. 159 Investigating how Collembola communities respond to the interactive effects of climate change 160

161 and land-use intensification will allow us to better predict the responses of soil communities and

the processes they drive (i.e., litter decomposition and nutrient cycling) to global change.

163

164 2. Materials and Methods

165 *Study site*

The study site is located at the field research station of the Helmholtz-Centre for 166 Environmental Research (UFZ) in Bad Lauchstädt, Saxony-Anhalt, Germany (51° 23' 30N, 11° 167 52' 49E, 116 m a.s.l.), which was a former arable land (with the last crop cultivation in 2011). 168 The soil type of this study site belongs to Haplic Chernozem, which is based upon carbonic loess 169 substrate. The humus layer reaches down to a soil depth of more than 40 cm. Within the upper 15 170 cm, the soil is characterized by high concentrations of total carbon (1.71% - 2.09%) and total 171 nitrogen (0.15% - 0.18%), as well as high water storage density (1.35 g/cm^3) (WRB, 2007), 172 which provides a habitat with generally favorable conditions for soil organisms with a neutral pH 173 (~ 7.0) and low susceptibility to drought (Altermann et al., 2005). 174

175

176 Experimental set-up

The Global Change Experimental Facility (GCEF, Schädler et al., 2019) was established in 2013 as an experimental platform for ecologists to investigate the interacting effects of climate and land use on multiple ecosystem processes. The two experimental treatments were implemented using a split-plot design with climate as main-plot factor (n = 10) and land use as sub-plot factor (n = 50). Specifically, each of the ten main-plots was divided into five sub-plots (16 m \times 24 m), resulting in 50 sub-plots in total (Fig. S1a). Half of the main-plots are subjected to ambient climate conditions, while the other half main-plots are subjected to future climateconditions (Fig. S1b).

The climate treatments were first applied in 2014 (initiating the temperature treatment in 185 spring; and initiating precipitation treatment in summer). The main-plots with future climate 186 have steel construction (5 m height) with an irrigation system as well as mobile roofs and side 187 panels that can be closed via rain sensors/timers. The main-plots with ambient climate also have 188 steel constructions to control for potential side effects of the infrastructure, i.e., microclimatic 189 effects. The climate treatments were chosen based on a consensus scenario across several 190 191 dynamic models for Central Germany for 2070-2100, which include higher inter-annual rainfall variability with longer drought periods over summer and increased precipitation in spring and 192 fall (Jacob & Podzun, 1997, Rockel et al., 2008). The mean projection across the different 193 194 scenarios is an increase of mean temperature across all seasons by around ~1°C. For precipitation, mean values of the 12 projections resulted in an experimental treatment consisting 195 of a $\sim 9\%$ increase in spring (March – May) and autumn (September – November) and a $\sim 21\%$ 196 197 decrease in summer (June – August).

For our future climate treatment, shelters were automatically closed from sundown to sunrise 198 199 to increase night temperature (Beier et al., 2004). During our experiment, the roofs were active from 22nd March to 29th November in 2016. The night closing during these periods increased 200 the mean daily air temperature at 5 cm-height by 0.55°C, as well as the mean daily soil 201 temperature in 1 cm- and 15 cm-depth by 0.62°C and 0.50°C, respectively. With the irrigation 202 system we added around $\sim 110\%$ of ambient rainfall to the main-plots with future climate in 203 spring and autumn. Additionally, the rain sensors associated with the irrigation system were used 204 205 to control precipitation on the main-plots with future climate to ~80% of ambient rainfall in summer (from May to August). As a result, precipitation was increased by 9.2% to 13.6% in
spring and autumn and decreased by 19.7% to 21.0% in summer in 2016.

Within each main-plot, the five sub-plots were randomly assigned to one of the five land-use 208 209 regimes: (1) conventional farming (CF, cropland), (2) organic farming (OF, cropland), (3) intensively-used meadow (IM, grassland), (4) extensively-used meadow (EM, grassland), and (5) 210 extensively-used pasture with sheep grazing (EP, grassland; Fig. S1c). Before the establishment 211 of the land-use treatments, oat was planted in 2013 to homogenize the plots. Each land-use 212 treatment represents a common local management type that entails multiple aspects of above-213 214 ground vegetation diversity and composition, management intervals, and fertilization (Schädler et al., 2019). In brief, under conventional farming a typical crop rotation (winter rape-winter 215 wheat-winter barley) was established while allowing the use of the usual mineral fertilizers and 216 217 pesticides whereas under organic farming fertilization is exclusively realized by replacing rape by legumes (alternating alfalfa and white clover) and most pesticides are not allowed. The 218 intensively used grassland was established from a seed mixture of 4 forage grasses and is 219 220 moderately fertilized and mown four times per year. The extensively used grasslands are established from a mixture of about 60 grassland species from different local populations and are 221 222 mown two times per year (meadows) or grazed by sheep three times per year (pastures). While the two extensively-used grasslands contained 53.1 ± 2.0 plant species per 9 m², the intensively-223 used grassland had 10.1 ± 3.6 plant species per 9 m² (mean \pm SD for 2015-2017). The land-use 224 225 treatments were established in autumn 2013 and spring 2014 (extensively used grasslands) by sowing. To avoid edge effects, a buffer zone of 4.5 m at the northern and southern sides and 2 m 226 at the eastern and western sides of the subplots is generally excluded from any measurements. 227

For further details on experimental design and the plant species pools and sowing densities seeSchädler et al. (2019).

230

231 Collembola sampling, extraction, and identification

To investigate Collembola communities, two soil cores (Ø 16 cm, 5 cm length) were taken at 232 a distance of more than 2.5 meters along a 15 m x 0.6 m transect from each sub-plot (Fig. S1d) in 233 October 2016. Within 10 days, Collembola were extracted from the soil cores using a Kempson 234 heat extractor by gradually increasing the temperature. The extracted Collembola were preserved 235 in ethanol (70%) and identified to species level and classified into three life-form groups, 236 epedaphic, hemiedaphic, and euedaphic (specific species with basic description see Table S1, 237 Dunger and Schlitt, 2011; Fjellberg, 2007; Hopkin, 1997, 2007, Pomorski, 1998; Potatov, 2001) 238 239 using a VHX-Digital Microscope (Japan).

240

241 Statistical analysis

Individual numbers (abundance), density, and species richness were determined for each subplot. We further calculated the diversity indices, i.e., Shannon-Wiener diversity (H'), Pielou's evenness (J'), and Simpson dominance (c).

245 Shannon-Wiener diversity:

$$H' = \sum_{i=1}^{N} Pi \ln Pi$$

246 Pielou's evenness:

 $J' = H' / \ln N$

247 Simpson dominance:

248

where *N* represents total number of species and $Pi = n_i/N$ represents the relative ratio on abundance of the *i*th species (*n_i*) to total abundance (*N*).

All response variables were analyzed in relation to climate and land use using a split-plot 251 generalized linear mixed models (GLMM) with Type III sum of squares (PROC MIXED, SAS 252 253 University Edition v9.4). The effects of climate (two levels) were analyzed at the main-plot level, and the effects of land use (5 levels) and its interaction with climate were tested at the sub-plot 254 255 level. Count data were analyzed assuming Poisson-distributed residuals with the log-link 256 function. There was no indication of overdispersion of data, and assuming alternative distributions (including negative binomial) resulted in inferior model fit (assessed via Akaike 257 Information Criterion). When the ANOVAs indicated significant treatment effects, post-hoc 258 Tukey's HSD tests were conducted to test for differences among the respective levels within 259 factors. 260

261 To analyze the relationships between Collembola community composition and the two experimental factors (climate, 2 levels and land use, 5 categories), redundancy analyses-RDA 262 (Rao, 1964; van den Wollenberg, 1977) with permutation tests (permutation number: 999) were 263 264 carried out using abundance data (R 2.1.4.2. package vegan, Oksanen et al., 2015). We checked for linear relationships in the data sets (Euclidean metric; prerequisite for this method) by 265 266 detrended correspondence analyses (DCA) and identifying the respective longest gradient. As 267 these were always lower than 3, the use of linear methods was considered appropriate (Lepš and Šmilauer, 2003). Additionally, we used scores of RDA axis 1 as a proxy for 'community' 268 269 composition'. Pairwise Pearson's correlation was tested between the community composition of 270 Collembola and the densities and species richness of total, epedaphic, hemiedaphic, and

271 euedaphic Collembola.

272

273 **3. Results**

274 Population density

Overall, the densities of Collembola communities were significantly influenced by land use 275 (Table 1a; Fig. 1). Specifically, the density of total Collembola significantly decreased from the 276 extensively-used meadow to conventional farming, with generally higher densities in grasslands 277 (EM > IM > EP) compared to croplands (OF > CF; Fig. 1a). Epedaphic Collembola followed the 278 279 same pattern as total Collembola (Fig. 1b). In contrast, hemiedaphic Collembola showed a slightly different pattern, with highest densities in intensively- and extensively-used meadows, 280 followed by organic croplands and extensively-used pasture and lowest densities under 281 conventional farming (Fig. 1c). Euedaphic Collembola responded differently between croplands 282 (CF > OF), and differently among grasslands (meadows > EP) (Table 1a; Fig. 1d) but with lower 283 overall differences. 284

Moreover, these land-use effects were modulated by climate, with a significant interaction 285 effect on densities of Collembola communities (Table 1a). Future climate significantly decreased 286 287 (by 56%) the density of total Collembola under organic farming, while future climate tented to increase the density of total Collembola in grasslands (Fig. 2a). The responses of different life 288 forms of Collembola to these interactive effects varied in direction and magnitude (Fig. 2b-d). 289 290 The density of epedaphic Collembola had no consistent significant effects of climate (Fig. 2b). The density of hemiedaphic Collembola was significantly decreased (by 77%) in organic farming, 291 but tended to increase in grasslands under future climatic conditions (Fig. 2c). By contrast, the 292 density of euedaphic Collembola increased significantly with climate change in intensively-used 293

meadows and extensively-used pastures (Fig. 2d). Additionally, the responses of individual species of epedaphic, hemiedaphic, and euedaphic Collembola to the effects of climate and land use were highly variable (Tables S2-4).

297

298 Species richness

Land-use regime significantly affected the Collembola species richness, whereas climate 299 change did not (Table 1b). Total Collembola species richness was highest in intensively- and 300 extensively-used meadows, followed by extensively-used pasture, and the two types of croplands 301 (Fig. 3a). The responses of the different life forms of Collembola to these land-use effects were 302 different in magnitude, although similar in direction. Specifically, the species richness of 303 epedaphic Collembola was found to be significant higher in the three types of grasslands than in 304 the croplands (Fig. 2b). The species richness of hemiedaphic Collembola was significantly 305 higher in the extensively-used meadow than in the two croplands and extensively-used pasture 306 (Fig. 2c). The species richness of euedaphic Collembola was not significantly affected by land 307 308 use (Table 1b; Fig. 2d).

309

310 *Diversity indices*

Pielou's evenness of Collembola was significantly affected by land use but not by climate, with substantially higher evenness in the two croplands compared to the three grasslands (Table 1c; Fig. 4). No significant climate and land-use effect on Simpson dominance and Shannon-Wiener diversity was found (Table 1c).

315

316 *Community composition*

317 Climate change and land use significantly and independently affected the community composition of Collembola, no interaction effects were detected (Table 2). About 20% of the 318 total variance in the data set was explained by the five constrained RDA axes (Table S5). Therein, 319 320 the first RDA axis explained ~49% of the variance (Table 2, 3; Fig. 5), among which the extensively-used meadow explained mostly (Table S6), and Isotoma viridis had the highest 321 species score (Table S7). The second RDA axis accounted for ~24% of the variance (Table 2; Fig. 322 5), among which the intensively-used meadow explained mostly (Table S6), and *Sminthurus* 323 *niger* had the highest species score (Table S7). 324

In addition, the community composition of Collembola (= RDA axis 1) was significantly correlated with the densities and species richness of total, epedaphic, and hemiedaphic Collembola, but not the density and species richness of euedaphic Collembola (Fig. S2).

328

329 **4. Discussion**

In this study, we tested the interactive effects of climate change and land use on the 330 responses of Collembola communities. We found that (1) climate change alone did not 331 significantly decrease the densities and species richness of Collembola communities; (2) land-332 use type significantly influenced Collembola communities, generally with higher densities and 333 species richness in grasslands than in croplands; (3) climate-change effects on densities of 334 Collembola communities varied among land-use regimes and among the three life forms, as 335 indicated by significant interactive effects of the two global change drivers; and (4) effects of 336 climate change and land-use intensification on Collembola community composition were 337 independent from each other. Moreover, shifts in community composition of Collembola were 338 339 significantly correlated with the shifts in densities and species richness of epedaphic and

hemiedaphic Collembola but not euedaphic Collembola. Together, we showed that different Collembola life forms vary in responses to changing environmental conditions, and species more associated to the soil surface may be more vulnerable to these changes than species living deeper in the soil. This is likely to slow down the litter decomposition at soil surface under intensive land use and future climate conditions.

345

346 Weak effects of climate change on the structure of Collembola communities

Previous studies have shown negative effects of climate change on Collembola (Kardol et al., 347 348 2011; Krab et al., 2013; Makkonen et al., 2011; Petersen et al., 2011; Sjursen et al., 2005; Xu et al., 2012). However, contrary to our first hypothesis, we did not find any main effects of climate 349 change on the densities and species richness of Collembola communities. The weak effects of 350 351 climate change in our study could be related to the season of fauna sampling (i.e., autumn), when the climate manipulation consists of elevated temperature and higher precipitation. These 352 climatic conditions may have counteracted potential effects of previous summer drought. This 353 354 assumption is supported by Hodkinson et al. (1998), who showed that desiccation (rather than increased temperature) may drive declines of Collembola communities especially in the dry 355 356 season (i.e., summer). Moreover, our previous study showed that soil fauna-driven litter decomposition decreased in summer, but not in other seasons (Yin et al., 2019a). Therefore, the 357 climate-change effects on Collembola communities may vary among seasons, and more studies 358 are needed with multiple samplings across the year and during several years for understanding 359 seasonal variations in soil invertebrate animals (Eisenhauer et al., 2018; Siebert et al., 2019). 360 This would reveal if intra-annual effects of changed precipitation and temperature patterns would 361 362 result in neutral long-term climate-change effects.

364 Significant land-use effects on the structure of Collembola communities

Our findings largely support our second hypothesis that grasslands and extensively-managed 365 fields will have higher densities and species richness of Collembola than croplands and 366 intensively-managed fields, and that epedaphic Collembola species will be more vulnerable to 367 land-use intensification than euedaphic Collembola. Specifically, we found that the density of 368 total Collembola in grasslands can reach up to 5,000 ind.m⁻², which was several times higher 369 than the total Collembola density in croplands (conventional farming had especially low values 370 of density with less than 1,000 ind.m⁻²). This finding is supported by Sousa et al. (2006), who 371 found that the densities of Collembola were significantly higher in grasslands (meadows and 372 pastures) than in croplands across Europe. Additionally, we also found that the species richness 373 374 of total Collembola was significantly higher in the three grasslands (15±4) compared to the two croplands (7.3 ± 3.1) . This result is in line with several previous studies (Alvarez et al., 2000; 375 Heisler and Kaiser, 1995; Sousa et al., 2006), which indicated that land use with lower plant 376 377 species richness and/or more frequent disturbances related to intensive management may cause a decrease in Collembola species richness. In further support of our second hypothesis, we also 378 found that the effects of land use on Collembola were stronger for epedaphic species than for the 379 other life forms. This finding suggests that epedaphic species may be particularly vulnerable to 380 intensive land use, as they are more directly affected by changes in soil surface conditions such 381 as differences in vegetation composition (Querner et al., 2018). 382

383

384 Land use-modulated climate effects on densities of Collembola communities

385 In support of our third hypothesis, climate-change effects were modulated by land-use type/intensity, particularly for Collembola densities. More specifically, our results showed that 386 future climate decreased the density of total Collembola in croplands, especially in the organic 387 farming treatment; while it tended to increase the total density in the three grasslands. This 388 finding is somehow supported by some other studies (Isbell et al., 2017; Oliver et al., 2016), 389 which suggest that intensive land use may aggravate climate-change effects on insect diversity 390 and agroecosystems functioning due to higher disturbance and lower above- and below-ground 391 biodiversity. Accordingly, detrimental climate-change effects could be intensified in croplands. 392 393 Furthermore, the densities of different life forms varied in response to the interactive effects of climate and land use. More specifically, we found that epedaphic Collembola were not affected 394 by the interaction of both factors. By contrast, the density of hemiedaphic Collembola 395 significantly decreased with climate change in organic farming, whereas the density of euedaphic 396 Collembola significantly increased in intensively-used grasslands. These results give us a new 397 perspective that highly variable effects of climate change on Collembola communities depend on 398 399 their life form and land-use type. Moreover, these findings partly support the other part of our third hypothesis, postulating that detrimental climate-change effects would be intensified by 400 401 croplands and/or intensive management, with the most pronounced responses for epedaphic and hemiedaphic Collembola; whereas detrimental climate-change effects would be alleviated by 402 grasslands and/or extensive management, with the most pronounced responses for euclaphic 403 404 Collembola.

405

406 Independent effects of climate and land use on community composition of Collembola

407 In contrast to our fourth hypothesis, we did not find any interactive effects of climate and land use on the community composition of Collembola. However, we found significant but 408 independent effects of climate change and land-use intensification. Specifically, croplands could 409 410 lead to a less diverse community assemblage by particularly affecting soil surface-dwelling species. By contrast, ambient climate and grasslands (especially extensively-used meadow) 411 supported a more diverse Collembola community. Together, these findings indicate rather 412 consistent climate-change effects on Collembola species across land-use regimes. The 413 independent climate and land-use effects on Collembola community composition are supported 414 by an unpublished study in our experiment, where we demonstrated that climate change and 415 land-use intensification independently decreased the total biomass of soil microarthropods due to 416 i) climate change-induced reduction of their mean body size, and ii) land use-induced decreases 417 of their densities. A better understanding of global change effects on the community composition 418 of Collembola may help to predict how soil ecosystems will function in a changing world (Yin et 419 al., 2019a). 420

421

422 **5.** Conclusion

We conclude that climate change and land-use type conversion from grasslands to croplands could negatively affect Collembola communities by decreasing their density and diversity. Moreover, our findings reveal that different global-change drivers can vary in their effects on Collembola communities through differential responses of Collembola life forms. These varying responses of life forms may alter the soil ecosystem services they provide. For example, soil surface-litter decomposition, which is driven by soil surface-dwelling Collembola, may slow down in a changing world. Accordingly, future studies should focus on i) analyzing soil communities at different soil depths, ii) exploring their functional trait responses, and iii) assessing the soil processes at the corresponding soil depths. This can, for instance, be done by measuring soil enzymes and microbial communities and/or placing root litterbags and other organic substrates at different soil depths. For that, Collembola life-form groups and their traits can be ideal for further exploration and in explaining soil ecological functions and processes in a changing world.

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437 Conflicts of interest

438 The authors declare no conflict of interest.

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440 Acknowledgments

We thank the anonymous reviewers for their valuable comments on our manuscript. We 441 thank the Helmholtz Association, Federal Ministry of Education and Research, the State Ministry 442 of Science and Economy of Saxony-Anhalt and the State Ministry for Higher Education, 443 Research and the Arts Saxony to fund the Global Change Experimental Facility (GCEF) project. 444 We acknowledge the funding from National Natural Science Foundation of China (NSFC 445 41722107, 41977063 to G.L.W.), China Scholarship Council (CSC No. 201406910015 to R.Y.), 446 and German Research Foundation (TH 2307/1-1 to M.P.T.). This project also received support 447 from the European Research Council under the European Union's Horizon 2020 research and 448 449 innovation program (grant agreement No. 677232 to N.E.). Further support came from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the 450 DFG (FZT 118). We also thank the staffs of the Bad Lauchstädt Experimental Research Station 451 452 (especially Ines Merbach and Konrad Kirsch) for their hard work in maintaining the plots and

- 453 infrastructures of the GCEF, and Dr. Stefan Klotz, Prof. Dr. Francois Buscot and Dr. Thomas454 Reitz for their roles in setting up the GCEF.
- 455

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Table 1. Results (F-values) of split-plot generalized linear mixed models (type III sum of squares) testing the effects of climate, land use, and their interaction on (a) density and (b) species richness of total, epedaphic, hemiedaphic, and euedaphic Collembola, as well as (c) diversity indices (Pielou's evenness, Simpson dominance and Shannon-wiener diversity) of Collembola communities. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

Efforts	Df	a) Density				
Effects	Dj	Total Collembola	Epedaphic Collembola	Hemiedaphic Collembo	bla Euedaphic Collembola	
Climate (C)	1,8	0.26	0.05	0.54	0.15	
Land use (L)	4,32	495.2***	280.74***	126.37***	3.21*	
$\mathbf{C} \times \mathbf{L}$	4,32	12.28***	3.17*	26.65***	19.66***	
Effects	Df		b)	Species richness		
Effects	Df	Total Collembola	Epedaphic Collembola	Hemiedaphic Collembo	ola Euedaphic Collembola	
Climate (C)	1,8	0.93	0.08	1.03	0.33	
Land use (L)	4,32	15.69***	18.61***	2.77*	0.22	
$\mathbf{C} \times \mathbf{L}$	4,32	0.81	0.8	0.47	0.57	
Effects	Df		c)	Diversity indices		
Effects	Df	Shannon-wiene	er diversity Pie	elou's evenness	Simpson dominance	
Climate (C)	1,8	0.33		0.00	2.01	
Land use (L)	4,32	0.98		5.69**	0.6	
$\mathbf{C} \times \mathbf{L}$	4,32	1.93		0.03	1.15	

Table 2. ANOVA table of permutation tests for the effects of climate, land use, and their
interaction on community composition of Collembola, as well as the five RDA axes. Significant
effects are indicated in bold font. Var: the constraining variance.

	Df	Var	<i>F</i> -value	<i>P</i> -value
Climate effects	1	1.34	2.05	0.009
Land-use effects	4	5.87	2.44	0.001
Climate \times land use interaction	4	178.4	0.56	0.903
RDA 1	1	3.55	5.43	0.001
RDA 2	1	1.73	2.64	0.012
RDA 3	1	1.03	1.58	0.308
RDA 4	1	0.5	0.76	0.976
RDA 5	1	0.41	0.63	0.893

660 Figure legends

Fig. 1. Effects of land use on densities of (a) total, (b) edaphic, (c) hemiedaphic and (d) euedaphic Collembola. Boxplots show the median (horizontal line), the mean (red dot), first and third quartile (rectangle), $1.5 \times$ interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes by Post hoc Tukey's HSD tests at *P* < 0.05. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture (by sheep grazing).

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Fig. 2. Interactive effects of climate and land use on densities of (a) total, (b) edaphic, (c) 669 hemiedaphic, and (d) euedaphic Collembola. Boxplots show the median (horizontal line), the 670 671 mean (red dot), first and third quartile (rectangle), $1.5 \times$ interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters and capital letters represent significant 672 differences between land-use regimes under ambient and future climate scenarios, respectively 673 674 identified by Post hoc Tukey's HSD tests at P < 0.05. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-675 676 used meadow; EP = extensively-used pasture (by sheep grazing).

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Fig. 3. Effects of land use on the species richness of (a) total, (b) edaphic, (c) hemiedaphic and (d) euedaphic Collembola. Boxplots show the median (horizontal line), the mean (red dot), first and third quartile (rectangle), $1.5 \times$ interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes identified by Post hoc Tukey's HSD tests at *P* < 0.05. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used
meadow; EP = extensively-used pasture (by sheep grazing).

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Fig. 4. Effects of land use on evenness of Collembola communities. Boxplots show the median (horizontal line), the mean (red dot), first and third quartile (rectangle), $1.5 \times$ interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes by Post hoc Tukey's HSD tests at *P* < 0.05. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture (by sheep grazing).

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Fig. 5. Species-treatment plot resulting from redundancy analyses (RDA) of Collembola 693 community composition. About 20% of the total variance in the data set was explained by the 694 five constrained RDA axes. Therein RDA axis 1 and 2 explained ~49% and ~24% of this 695 variance representatively. Treatments included are climate (Ambient and Future) and land-use 696 697 regimes (CF, OF, IM, EM and EP). Epedaphic species are in black, Hemiedaphic species in red, and Euclaphic species in blue. Abbreviations for land-use regimes: CF = conventional farming; 698 699 OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP =extensively-used 700 pasture (by sheep grazing), and for Collembolan species: Bra_par=Brachystomella parvula, Cer_sp=Ceratophysella sp., Des_mul=Desoria multisetis, 701 702 Des_oli=Desoria olivacea, *Des_tigr=Desoria* tigrina, Des_vio=Desoria violacea, Deu_sp=Deuteraphorura sp., Ent_nic=Entomobrya nicoletti, Fol_ang=Folsomides angularis, 703 704 *Fol_par=Folsomides* parvulus., *Fol_sp=Folsomia* Fri_mir=Friesea mirabilis, sp., 705 Iso ang=Isotoma anglicana, Iso vir=Isotoma viridis, Iso min=Isotomiella minor,

Iso_pro=Isotomodes productus, Lep_cya=Lepidocyrtus cyaneus, 706 *Lep_lig=Lepidocytus Lep_par=Lepidocyrtus* paradoxus, 707 lignorum, *Lep_vio=Lepidocyrtus* violacea, Mes_sp=Mesaphorura sp., Orc_vill=Orchesella villosa, Par_not= Parisotoma notabilis, 708 709 Par_sp=Paratullbergia sp., Pro_mini=Proisotoma minima, Pro_minu=Proisotoma minuta, *Pro_sp=Protaphorura sp., Pse_alb=Pseudosinella alba, Pse_imm=Pseudosinella immaculata,* 710 Sin_cur=Sinella curviseta, Smi_ele=Sminthurinus elegans, Smi_nig=Sminthurus niger, 711 712 Smi_par=Sminthurides parvulus, Smi_vir=Sminthurinus viridis, Sph_pum=Sphaeridia pumilis, *Ste_sp= Stenaphorura sp., Wil_bus=Willowsia buski.* 713

715 Fig. 1.



717 Fig. 2.



719 Fig. 3.



721 Fig. 4.



723 Fig. 5.



1 Supplementary materials

- 2 Table S1. Basic information on family and life form of all observed Collembola species in the
- 3 different land-use types (CF, OF, IM, EM, EP) and climate treatments (ambient, future).
- 4 Abbreviations: CF = conventional farming; OF = organic farming; IM = intensive-used meadow;
- 5 EM = extensive-used meadow; EP = extensive-used pasture.

Species	Family	Life form	Occurrence		
			Ambient climate	Future climate	
Brachystomella parvula (Schäffer, 1896)	Brachystomellidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Desoria multisetis (Carpenter & Phillips, 1922)	Isotomidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Desoria olivacea (Tullberg, 1871)	Isotomidae	Epedaphic	OF	-	
Desoria violacea (Tullberg, 1877)	Isotomidae	Epedaphic	CF, IM, EP	OF, IM, EM, EP	
Entomobrya nicoletti (Nicolet, 1847)	Entomobryidae	Epedaphic	IM	IM, EM, EP	
Isotoma anglicana (Lubbock, 1862)	Isotomidae	Epedaphic	EM, IM, EP	EM, IM, EP	
Isotoma viridis (Handschin, 1942)	Isotomidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Lepidocyrtus cyaneus (Tullberg, 1871)	Entomobryidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Lepidocytus lignorum (Fabricius, 1775)	Entomobryidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Lepidocyrtus paradoxus (Uzel, 1891)	Entomobryidae	Epedaphic	-	EP	
Lepidocyrtus violacea (Salmom, 1949)	Entomobryidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Orchesella villosa (Geoffroy, 1764)	Entomobryidae	Epedaphic	CF, OF, EM	CF, OF, EM, EP	
Sminthurinus elegans (Fitch, 1862)	Katiannidae	Epedaphic	CF, OF, EM, EP	CF, OF, EM	
Sminthurus niger (Lubbock, 1867)	Katiannidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Sminthurides parvulus (Krausbauer, 1898)	Katiannidae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Sminthurinus viridis (Linnaeus, 1758)	Katiannidae	Epedaphic	OF	CF, EM	
Sphaeridia pumilis (Krausbauer, 1898)	Sminthurididae	Epedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Willowsia buski (Lubbock, 1869)	Entomobryidae	Epedaphic	OF, EM, EP	CF, OF, EM	
Ceratophysella sp., (Ceratophysella Börner, 1932)	Hypogastruridae	Hemiedaphic	IM	CF	
Desoria tigrina (Nicolet, 1842)	Isotomidae	Hemiedaphic	IM	-	
Folsomides parvulus (Folsomides Stach, 1922)	Isotomidae	Hemiedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Folsomia sp., (Folsomides Stach, 1922)	Isotomidae	Hemiedaphic	OF, IM	-	
Friesea mirabilis (Frieseinae Massoud, 1967)	Neanuridae	Hemiedaphic	CF	OF, IM, EM	
Isotomiella minor (Schäffer, 1896)	Isotomidae	Hemiedaphic	EM	IM, EM, EP	
Isotomodes productus (Axelson, 1906)	Isotomidae	Hemiedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Parisotoma notabilis (Schäffer, 1896)	Isotomidae	Hemiedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Proisotoma minuta (Tullberg, 1871)	Isotomidae	Hemiedaphic	CF, OF, IM, EM	CF, OF, IM, EM	
Proisotoma minima (Absolon, 1901)	Isotomidae	Hemiedaphic	CF, OF, IM, EM	CF, OF, IM, EM	
Pseudosinella alba (Packard, 1873)	Entomobryidae	Hemiedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Pseudosinella immaculate (Lie-Pettersen, 1896)	Entomobryidae	Hemiedaphic	OF, IM, EM, EP	IM, EM	
Sinella curviseta (Brook, 1882)	Entomobryidae	Hemiedaphic	CF, IM, EM	-	
Deuteraphorura sp., (Deuteraphorura Absolon, 1901)	Onychiuridae	Euedaphic	CF, OF, EP	CF, OF, IM, EM, EP	
Mesaphorura sp., (Mesaphorura Börner, 1901)	Onychiuridae	Euedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Paratullbergia sp., (Paratullbergia Womersley, 1930)	Onychiuridae	Euedaphic	EM	-	
Protaphorura sp., (Protaphorura Absolon, 1901)	Onychiuridae	Euedaphic	CF, OF, IM, EM, EP	CF, OF, IM, EM, EP	
Stenaphorura sp. (Stenaphorura Absolon, 1900)	Onychiuridae	Euedaphic	CF	CF	

6	Table S2. Results (F-values) of the split-plot generalized linear mixed model (type III sum of squares) testing the effects climate, land
7	use and their interaction on densities of observed epedaphic Collembola species. $^+ = P < 0.1$, $* = P < 0.05$, $** = P < 0.01$, $*** = $
8	0.001. Abbreviations for Collembolan species: Bra_par=Brachystomella parvula, Des_mul=Desoria multisetis, Des_oli=Desoria
9	olivacea, Des_vio=Desoria violacea, Ent_nic=Entomobrya nicoletti, Iso_ang=Isotoma anglicana, Iso_vir=Isotoma viridis,
10	Lep_lig=Lepidocytus lignorum, Lep_par=Lepidocyrtus paradoxus, Lep_vio=Lepidocyrtus violacea, Orc_vill=Orchesella villosa,
11	Smi_ele=Sminthurinus elegans, Smi_nig=Sminthurus niger, Smi_par=Sminthurides parvulus, Smi_vir=Sminthurinus viridis,
12	Sph_pum=Sphaeridia pumilis, Wil_bus=Willowsia buski.

Effects	Df	Bra_par	Des_mul	Des_oli	Des_vio	Ent_nic	Iso_ang	Iso_vir	Lep_cya	Lep_lig
Climate (C)	1,8	0.63	0.15	1	7.83	1	9.68*	0.92	1.65	0.04
Land use (L)	4,32	1.98	6.34**	1	4.29**	1.07	4.72**	30.57***	4.54**	80.9***
$\mathbf{C} \times \mathbf{L}$	4,32	0.45	1.92	1	4.34**	0.48	4.48**	0.95	1.15	16.14***
		Lep_par	Lep_vio	Orc_vill	Smi_ele	Smi_nig	Smi_par	Smi_vir	Sph_pum	Wil_bus
Climate (C)	1,8	Lep_par 1	Lep_vio 1.3	Orc_vill 4 ⁺	<i>Smi_ele</i> 7.21*	Smi_nig 1.85	Smi_par 2.19	Smi_vir 3.6^+	<i>Sph_pum</i> 0.42	<i>Wil_bus</i> 7.04*
Climate (C) Land use (L)	1,8 4,32	<i>Lep_par</i> 1 1	<i>Lep_vio</i> 1.3 111.79***	<i>Orc_vill</i> 4 ⁺ 3.79*	<i>Smi_ele</i> 7.21* 2.64 ⁺	Smi_nig 1.85 10.67***	<i>Smi_par</i> 2.19 2.91*	Smi_vir 3.6 ⁺ 1.6	<i>Sph_pum</i> 0.42 74.9***	Wil_bus 7.04* 2.04

Table S3. Results (F-values) of the split-plot generalized linear mixed model (type III sum of squares) testing the effects climate, land 14 use and their interaction on densities of observed hemiedaphic Collembola species. $^+ = P < 0.1$, * = P < 0.05, ** = P < 0.01, *** = P < 0.01, ***15 0.001. Abbreviations for Collembolan species: Cer_sp=Ceratophysella sp., Des_tigr=Desoria tigrina, Fol_par=Folsomides 16 17 parvulus., Fol_sp=Folsomia sp., Fri_mir=Friesea mirabilis, Iso_min=Isotomiella minor, Iso_pro=Isotomodes productus, Par_not= minima, *Pro_minu=Proisotoma minuta,* Pse_alb=Pseudosinella notabilis, *Pro_mini=Proisotoma* alba, 18 Parisotoma Pse_imm=Pseudosinella immaculata, Sin_cur=Sinella curviseta. 19

Effects	Df	Cer_sp	Des_tig	Fol_par	Fol_sp	Fri_mir	Iso_min	Iso_pro
Climate (C)	1,8	1.45	2.67	4.54^{+}	1.2	0.81	1.45	0.03
Land use (L)	4,32	2.14^{+}	2.67^{+}	11.78***	0.95	0.6	.091	0.21
$\mathbf{C} \times \mathbf{L}$	4,32	2.59	2.67^{+}	13.14***	0.95	1.05	0.91	0.35
		Par_not	Pro_mini	Pro_minu	Pse_alb	Pse_imm	Sin_cur	
Climate (C)	1,8	0	0.44	0.95	0.05	1.22	2.25	
Land use (L)	4,32	99.03***	1.26	1.09	25.48***	0.64	0.55	

Table S4. Results (*F*-values) of the split-plot generalized linear mixed model (type III sum of squares) testing the effects climate, land use and their interaction on densities of observed
euedaphic Collembola species. ⁺ = P < 0.1, * = P < 0.05, ** = P < 0.01, *** = P < 0.001.
Abbreviations for Collembolan species: *Deu_sp=Deuteraphorura sp.*, *Mes_sp=Mesaphorura sp.*, *Par_sp=Paratullbergia sp.*, *Pro_mini=Proisotoma minima*, *Pro_minu=Proisotoma minuta*, *Pro_sp=Protaphorura sp.*, *Ste_sp= Stenaphorura sp.*

Effects	Df	Deu_sp	Mes_sp	Par_sp	Pro_sp	Ste_sp
Climate (C)	1,8	0.86	0.51	1	0.05	0.4
Land use (L)	4,32	2.41^{+}	4.39**	1	5.82**	3.6*
$\mathbf{C} \times \mathbf{L}$	4,32	0.9	15.37***	1	1.15	0.81

- 28 Table S5. Eigenvalues, proportion explained cumulative proportion, accumulated constrained
- 29 (Acc.) eigenvalues, Acc. proportion explained variation and Acc. cumulative proportion of the

	RDA 1	RDA 2	RDA 3	RDA 4	RDA 5	
Eigenvalue	3.55	1.73	1.03	0.5	0.41	
Proportion explained (%)	9.86	4.8	2.9	1.4	1.1	
Cumulative Proportion (%)	9.86	14.66	17.52	18.9	20.04	
Acc. eigenvalue	3.55	1.73	1.03	0.5	0.41	
Acc. proportion explained (%)	49.22	23.94	14.31	6.86	5.68	
Acc. cumulative Proportion (%)	49.22	73.15	87.46	94.32	100	

30 five RDA axes based on the community analyses of Collembolan abundances.

Treatment	RDA 1	RDA 2
Ambient	-0.13	-0.6285
Future	0.13	0.6285
CF	1.11	-0.2104
OF	0.96	-0.1141
IM	-0.66	1.191
EM	-1.26	-0.8661
EP	-0.15	0.00

32 Table S6. Centroids for factor constraints of the first two RDA axes. Highest absolute values in

33 RDA 1 and RDA 2 are indicated in bold font.

Table S7. Species scores of Collembolan species for the first two RDA axes. Highest absolute 35 values in RDA 1 and RDA 2 are indicated in bold font. Abbreviations for Collembolan species: 36 Bra_par=Brachystomella parvula, Des_mul=Desoria multisetis, Des_oli=Desoria olivacea, 37 Des_vio=Desoria violacea, Ent_nic=Entomobrya nicoletti, Iso_ang=Isotoma anglicana, 38 *Iso_vir=Isotoma viridis, Lep_lig=Lepidocytus lignorum, Lep_par=Lepidocytus paradoxus,* 39 *Orc_vill=Orchesella villosa, Smi_ele=Sminthurinus elegans, Smi_nig=Sminthurus niger,* 40 Smi_par=Sminthurides parvulus, Smi_vir=Sminthurinus viridis, Sph_pum=Sphaeridia pumilis, 41 Wil_bus=Willowsia buski. 42

Variables	RDA 1	RDA 2	Variables	RDA 1	RDA 2
Bra_par	-0.28	0.1	Lep_vio	-0.63	-0.31
Cer_sp	-0.10	0.15	Mes_sp	-0.2	0.15
Des_mul	-0.61	0.04	Orc_vill	-0.39	0.01
Des_oli	-0.03	0.03	Par_not	-0.36	0.14
Des_tig	-0.16	0.16	Par_sp	-0.21	-0.25
Des_vio	-0.42	-0.42	Pro_mini	0.02	-0.02
Deu_sp	0.35	-0.17	Pro_minu	-0.07	-0.3
Ent_nic	-0.32	-0.12	Pro_sp	-0.19	-0.31
Fol_par	0.11	-0.07	Pse_alb	-0.33	0.23
Fol_sp	0.15	-0.12	Pse_imm	-0.21	-0.02
Fri_mir	-0.11	-0.02	Sin_cur	-0.08	-0.18
Iso_ang	-0.47	-0.33	Smi_ele	-0.41	0.24
Iso_min	-0.25	0.2	Smi_nig	-0.46	0.53
Iso_pro	0.09	0.03	Smi_par	-0.32	0.42
Iso_vir	-0.68	-0.21	Smi_vir	-0.25	0.34
Lep_cya	-0.46	-0.32	Sph_pum	-0.43	0.39
Lep_lig	-0.51	-0.26	Ste_sp	0.33	0.00
Lep_par	-0.21	-0.25	Wil_bus	-0.38	0.21







Fig. S1. Global Change Experimental Facility (GCEF). (a) Aerial image of GCEF set-up with 50 44 sub-plots in Bad Lauchstädt, Germany. Picture: Tricklabor/Service Drone, copyrights: UFZ. (b) 45 Climate treatments as main-plot factor with two levels, ambient climate (as control) vs. future 46 47 climate. Picture: Andrè Künzelmann, copyrights: UFZ. (c) Land-use treatments as sub-plot factor with five land-use regimes. (d) Soil fauna sampling transect (15 m \times 0.6 m, highlight yellow 48 line) in the middle of each sub-plot. two soil cores (Ø 16 cm, 5 cm length) were taken with the 49 50 interval more than 2.5 meters along the transect. Abbreviations: CF = conventional farming; OF = organic farming; IM = intensive-used meadow; EM = extensive-used meadow; EP = extensive-51 used pasture. 52



Fig. S2. Scatter plots indicating the degree of correlation between the community composition of Collembola, as well as the densities and species richness of total, epedaphic, hemiedaphic, and euedaphic Collemola. Variables (below diagonal) and pairwise Pearson's correlation r values (above diagonal) are shown. Statistically significant correlation coefficients are indicated as following: *P < 0.05, **P < 0.01 and ***P < 0.001.