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Title

# **Trait-mediated responses to aridity and experimental drought by springtail communities across Europe**

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**AUTHOR CONTRIBUTIONS:** G.P., L.M. and J.P. designed the study. H.P., S.S., J-F.P., M.A., B.E., C.B., I.K.S., A.T., P. de A., D.L., E. K-L., G. K-D., M.E. and M.B. conducted field or laboratory work and/or contributed data. M.F., L.M. and G.P. analyzed the data. M.F. and G.P. wrote the first draft of the manuscript, with substantial inputs from J.P., and all authors contributed to revisions.

**Data availability:** The raw data supporting the results of this study will be available at a public repository upon the acceptance of the manuscript.

# Trait-mediated responses to aridity and experimental drought by springtail communities across Europe

## Abstract

1. The capacity to forecast the effects of climate change on biodiversity largely rely on identifying traits capturing mechanistic relationships with the environment through standardized field experiments distributed across relevant spatial scales. The effects of short-term experimental manipulations on local communities, however, may overlap with regional climate gradients that have been operating during longer time periods, though to the best of our knowledge, there are no studies simultaneously assessing such long-term macroecological drivers with climate manipulations.

2. We analyzed this hypothesis with springtails (subclass Collembola), a principal group of soil fauna, in a standardized climate manipulation experiment conducted across six European countries encompassing broad climate gradients. We crossed community data (near 20K specimens classified into 102 species) with 22 eco-morphological traits and reconstructed their phylogenetic relationships to track the evolution of adaptations to live at different soil depths, which is key to cope with dryness. We then applied joint species distribution models to investigate the combined effect of the regional aridity gradient with the local experimental treatment (drought and warming) over the assembly of springtail communities and tested for significant trait-environment relationships mediating their community-level responses.

3. Our results show: (1) a convergent evolution in all three major collembolan lineages of species adapted to inhabit at different soil strata; (2) a clear signature of aridity selecting traits of more epigeic species at a biogeographic scale, and (3) the association of short-term experimental drought with traits related to more edaphic life-forms.

4. The hemiedaphic condition is the plesiomorphic state for Collembola while the adaptations for an epigeic life would have been secondarily gained. Epigeic springtails are more resistant to drought but also have a higher dispersal capacity that allows them to seek more favorable micro-habitats after experiencing drier conditions. The observed relative edaphization of the springtail communities after short-term experimental drought may thus be a transient community response.

31 5. The disparity between macroecological trends and fast community-level responses  
32 after climate manipulations highlights the need of simultaneously assessing long-term  
33 and short-term drivers at broad spatial scales to adequately interpret trait-environment  
34 relationships and better forecast biodiversity responses to climate change.

35 **Keywords:** climate change, collembola, functional biogeography, joint species  
36 distribution models, shrublands, soil fauna

## 37 **1. Introduction**

38 Global biodiversity patterns are undergoing rapid shifts driven by on-going climate  
39 change (Blowes et al., 2019). Our capacity to forecast such biodiversity responses rely,  
40 however, on detailed knowledge of the processes behind species' population rates and  
41 the corresponding community reorganizations. Ecological theory predicts that a  
42 continued stress will filter out the species with the most vulnerable combinations of  
43 traits leading to changes on the functional structure of communities (Mouillot et al.,  
44 2013). This selection process may be either the result of the new abiotic conditions  
45 impairing the population growth of some species (strict environmental filtering) or the  
46 outcome of a reduced competitive performance under the new environmental conditions  
47 (Cadotte & Tucker, 2017). Traits, defined as any morphological, physiological,  
48 behavioural or phenological feature measurable at an individual level with impacts on  
49 species fitness via their effect on growth, reproduction and survival, are thus posited as  
50 the common currency for functional biogeography (McGill et al., 2006; Violle et al.,  
51 2014). Because trait selection generally precedes diversity loss, it is therefore  
52 fundamental to detect those traits capturing mechanistic relationships with stress factors  
53 such as climate change if we are to anticipate shifts on species composition and  
54 ultimately on ecosystem functioning (Berg et al., 2010; Haddad et al., 2008).

55 Coordinated and distributed multisite field experiments of climate manipulation are  
56 among the best tools available to infer these trait-environment relationships at relevant  
57 spatial scales under a scenario of rapid climate change (Halbritter et al., 2020). The  
58 effects of short-term experimental manipulations on local communities, however,  
59 overlap with regional climate gradients that have been operating during longer time  
60 periods which may lead to divergent ecosystem responses across such gradients that  
61 hinder our interpretations (Reinsch et al., 2017). This dependency of observed  
62 ecological patterns on multiple processes operating across a hierarchy of space-time  
63 scales is a classic issue in functional biogeography that strongly affects our predictive  
64 ability because general inferences and extrapolations are too often bogged down in local  
65 contingencies (Levin, 1992; Mouquet et al., 2015). Thus, for the development of the so-  
66 called predictive ecology, a key is to incorporate this complexity when assessing the  
67 performance of the analytical methods available in the macroecological toolkit  
68 (Mouquet et al., 2015).

69 Despite the growing concern over the impact of climate change on biodiversity, there  
70 has been a disproportionate focus on aboveground communities disregarding the key  
71 role of soil fauna on ecosystem functioning (Bardgett & Putten, 2014; Filser et al.,  
72 2016; Guerra et al., 2021). Among this neglected soil biodiversity there are the  
73 springtails (subclass Collembola), an abundant and diverse group of small arthropods  
74 whose communities show fast reductions in taxonomic, phylogenetic and functional  
75 richness due to drought, and additionally, are also a good proxy of ecosystem functions  
76 like litter decomposition (Peguero et al., 2019). Springtails present a diverse array of  
77 adaptations related to dwelling in specific soil layers (Figure 1). Smaller collembolan  
78 species with unpigmented bodies, shorter appendages, reduced sensory organs and  
79 mostly parthenogenetic reproduction are associated with more edaphic habitats  
80 (Chahartaghi et al., 2006; Salmon et al., 2014), while larger species with pigmented  
81 bodies, longer appendages, sexual reproduction and conspicuous mechanic and light  
82 receptors such as trichobothria and ocelli respectively, are typical from epigeic  
83 environments (Salmon et al., 2014). The species inhabiting the upper soil horizons have  
84 a greater drought resistance thanks to a lower cuticular permeability that allow them to  
85 resist desiccation (Kærsgaard et al., 2004). On the other hand, living deeper in the soil  
86 profile implies a lower exposure to variability in temperature and soil moisture, and  
87 additionally, soil-dwelling species also present biochemical, physiological and  
88 behavioral mechanisms to cope with drought (Holmstrup et al., 2001). Accordingly, a  
89 multi-site replicated experiment suggested that increasingly drier conditions may  
90 eventually favor edaphic over epigeic springtail species after short-term climate  
91 manipulations (Petersen, 2011). Even though, this relative edaphization may show  
92 idiosyncratic responses to short-term climate manipulations since in single-site studies  
93 at sub-arctic latitudes epigeic species seem to be favored by experimental warming  
94 (Bokhorst et al., 2012; Makkonen et al., 2011). Hence, potentially divergent community  
95 responses across large spatial scales may hamper our ability to detect general trends,  
96 and in particular to identify those traits behind the current climate-induced community  
97 reorganizations. This may be even more difficult if broad climate constraints have had  
98 time to differentially shape springtail assemblages across such environmental gradients,  
99 although this macroecological dimension, to the best of our knowledge, has never been  
100 included in studies assessing soil fauna responses to climate change.

101 The present study unfolds from a standardized climate manipulation experiment  
102 replicated across six natural shrublands encompassing the broad gradients of  
103 temperature and precipitation present in Europe (Beier et al., 2004). Here, we  
104 investigated the simultaneous effect of short-term experimental climate treatments (i.e.,  
105 drought and warming) and the regional long-term climate gradient synthesized in the  
106 aridity index, an indicator based on mean annual temperature and precipitation, over the  
107 composition and trait distribution of springtail communities. First, we harnessed data  
108 from a comprehensive sampling of near 20 thousand springtail specimens sorted out in  
109 102 species (Petersen, 2011) and then we crossed it with 22 eco-morphological  
110 springtail traits (Salmon et al., 2014) to track across the springtail phylogeny the  
111 evolution of the suite of adaptations to inhabit in specific soil layers (Table 1). Finally,  
112 we leveraged this community data to build joint species distribution models (JSDM) to  
113 test for significant associations between traits with climate manipulation treatments and  
114 aridity that could be mediating the assembly of collembolan communities. We  
115 specifically addressed the following hypotheses and predictions: (i) the adaptations that  
116 allow springtails to thrive at different layers of the soil matrix will show a pattern of  
117 repeated convergent evolution across the main lineages of Collembola; (ii) the long-  
118 term environmental forcing of the large-scale climatic gradient present across Europe  
119 has driven a selection of drought-tolerant springtail species with increasing aridity; (iii)  
120 the experimental short-term increase in local dryness and warming will be a major  
121 disturbance driving fast responses that eventually favor more edaphic springtail  
122 assemblages.

## 123 **2. Materials and Methods**

### 124 **2.1 Study sites and climatic manipulations**

125 The six shrublands studied comprised most of the European climatic regions (Figure S1  
126 and Table S1). Mean annual precipitation (MAP) at the sites ranged from 544 to 1,263  
127 mm, and mean annual temperature (MAT) ranged from 7.4 to 16.1 °C. The major types  
128 of shrublands present in the study area were: Atlantic heathland (UK, United Kingdom;  
129 NL, The Netherlands; DK, Denmark), continental forest steppe (HU, Hungary), and  
130 Mediterranean garrigue (SP, Spain; IT, Italy). In each study site, nine 20-m<sup>2</sup> plots were  
131 divided into three blocks and randomly assigned one plot at each block to a warming  
132 treatment, a drought treatment, or as a control. Warming plots were covered with  
133 reflective curtains during the night throughout the year inducing a passive night-time

134 warming, while drought plots were automatically covered by transparent polythene  
135 curtains during precipitation events that retracted as soon as rain stopped thus avoiding  
136 any warming effect (Beier et al., 2004). Manipulations of temperature and precipitation  
137 were carried out in the same way in all sites, but the timing and duration of the  
138 experimental drought were adjusted to the local climate regime (Table S2). The sites  
139 were established in 1998 (UK, NL, DK, and SP) and 2001 (HU and IT), and on average  
140 the warming treatment produced an increase of 0.5 °C of MAT and the drought  
141 treatment a 35% reduction of soil moisture (Table S2).

## 142 **2.2 Springtail sampling, phylogeny and trait information**

143 Springtails (Subclass Collembola) were sampled sequentially (IT, SP, HU, DK, NL, and  
144 UK) from April to July 2003 to equalize mean temperatures across sites. Five quadrats  
145 of 1.25 m<sup>2</sup> representative of the most dominant plant species were chosen in each plot.  
146 Springtails were sampled from plants and soil surface by suctioning with an adapted  
147 vacuum cleaner connected to a fauna trap. Specimens dropped were also recovered by  
148 placing small polythene boxes with aqueous benzoic acid beneath the plants. Soil  
149 springtails were sampled in 10-cm deep soil cores with a surface of 25 cm<sup>2</sup> taken to the  
150 lab and put through high-gradient extraction funnels (Gjelstrup & Petersen, 1987).  
151 These procedures were slightly adapted in UK and IT due to an excess of soil moisture  
152 and stones, respectively (Petersen, 2011). Springtails were identified to species level  
153 and some dubious specimens were revised by Drs. L. Dányi, R. Jordana, and E. Mateos.  
154 A total of 19,641 springtail specimens were collected and classified into 102 species-  
155 level entities (Tables S3) and are conserved in glycerol in H. Petersen's personal  
156 collection.

157 We reconstructed the phylogenetic relationships of springtails by means of sequence  
158 data from two genes (cox1 and 28s) gathered from public repositories covering 75% of  
159 the species found in our communities (accession numbers in Table S3). We applied  
160 Maximum Likelihood and Bayesian procedures to obtain a highly-supported consensus  
161 tree that agrees with previous systematic works integrating molecular and  
162 morphological information (Yu et al., 2016). See supplementary methods and figure S2  
163 for further details.

164 Additionally, we collated data of 22 eco-morphological traits from the ColTrait database  
165 (Salmon et al., 2014) for 47 up to 64 of the species present in our study sites (Table 1

166 and Table S4). These traits encompass different dimensions of their ecological niche  
167 such as life history (e.g., reproduction strategy), dispersal ability (e.g., leg length) and  
168 biotic interactions (e.g., sensory organs and defensive structures). Besides, for each  
169 species having trait data available we calculated its Eco-Morphological Index (EMI,  
170 Parisi et al., 2005). This trait-based index provides a simple continuous metric ranging  
171 from 1 to 20 and indicates the level of adaptation of a given springtail species to a  
172 specific soil layer. Accordingly, they may be classified as atmobiotic ( $EMI < 2$ ), epigeic  
173 ( $EMI < 6$ ), hemiedaphic ( $EMI = [6-8]$ ) or edaphic ( $EMI > 8$ , Figure 1).

### 174 **2.3 Data analysis**

175 First, we investigated the evolution of the adaptations that allow springtail species to  
176 live in specific soil layers by means of the reconstruction of the ancestral EMI score  
177 across the phylogenetic tree. This was done with the function *fastAnc* of the R package  
178 *phylosig* (Revell, 2012) and assuming a Brownian-Motion model of evolution of the  
179 suite of traits associated to the EMI. We also estimated the correlation between the  
180 similarity in EMI and species' evolutionary distance (i.e. the phylogenetic signal)  
181 through Pagel's  $\lambda$ . Then, we assessed how the evolution across Collembola of the suite  
182 of traits associated with the EMI may lead to specific patterns in the phylogenetic  
183 structure of springtail assemblages in response to the drought and warming treatments.  
184 Thus, we obtained the mean neighbour taxon distance (MNTD) and the mean pairwise  
185 distance (MPD) of each springtail assemblage standardized against 999 community  
186 randomizations with the R package *picante* (Kembel et al., 2010). By accounting for  
187 both indexes we explored possible non-random patterns occurring at different  
188 phylogenetic depths since MNTD can capture changes at the tips of the phylogeny (e.g.  
189 selection of sister species sharing specific adaptations) while MPD can detect shifts in  
190 the in-depth phylogenetic structure (e.g. selection of species belonging to specific  
191 lineages with highly conserved adaptations)(Cadotte & Davies, 2016).

192 Second, we assessed the role of aridity and the experimental climate manipulations on  
193 the trait-based assembly of springtail communities across Europe. To do so, we carried  
194 out a series of generalized linear latent variable models (GLLVM), as implemented in  
195 the R package *gllvm* (Niku et al., 2019). GLLVMs are a type of JSMD that extend the  
196 basic generalized linear mixed-effects model to multivariate abundance data  
197 incorporating a small number of latent variables accompanied by species-specific factor  
198 loadings to model correlations between response variables (i.e., all species in the

199 community matrix). These latent variables have a natural interpretation as ordination  
200 axes, but have also the capacity to predict new values controlling for known  
201 environmental factors using standard model selection tools (Niku et al., 2019).  
202 Additionally, GLLVMs allow us to test for trait-environment associations and the  
203 potential effects of biotic interactions. Although the effects of the environment and  
204 biotic interactions cannot be teased apart, the inclusion of the latter are a major advance  
205 of JSDM compared with previous species distribution tools and ‘fourth corner’ models  
206 that do not include the co-variation of the abundances between all species within a  
207 series of sites or communities (Poggiato et al., 2021; Warton et al., 2015). Hence, we  
208 first built an unconstrained model (without environmental predictors) with two latent  
209 variables and a negative binomial distribution and a log link function. The selection of  
210 the best number of latent variables and distribution family followed the  
211 recommendations of Niku et al. (2019), which are based on goodness-of-fit and residual  
212 diagnostics. Afterwards, we added sequentially the aridity index and the local climate  
213 manipulation treatments as environmental constraints and performed likelihood-ratio  
214 tests (LRT) to assess the predictive improvement of these increasingly complex models,  
215 and if so, we computed the percentage of deviance explained by the best model. The  
216 aridity index of each site was calculated by means of a modified version of the inverse  
217 of the Gausson Index (iGI) as:  $iGI = 1/(MAP/(2*MAT))*100$  (Reinsch et al., 2017).  
218 This index captures the large-scale gradient of aridity currently present across Europe  
219 and that can be traced back to the beginning of the Holocene about 10,000 years ago  
220 after the last Younger Dryas cold spell came to an end (Hewitt, 1999). Finally, to see  
221 whether specific traits were selected by aridity and by the climate manipulation  
222 treatments favouring more edaphic or epigeic springtail species, we built a series of  
223 GLLVMs including or not the interaction between a given trait and these two  
224 environmental variables and tested their significance via LRT (Niku et al., 2019).

### 225 **3. Results**

226 Comparative analyses of the EMI revealed multiple independent evolutions of the  
227 collembolan traits associated to live in specific soil layers (Figure 2). In all the major  
228 lineages of subclass Collembola there are groups of species showing either an epigeic  
229 habitus (Symphleona and Entombryomorpha) or, to a lesser extent, a more edaphic  
230 habitus (Poduromorpha), apparently as a result of a convergent adaptive evolution of a  
231 distinctive suite of eco-morphological traits as depicted in Figure 1. The high and

232 significant phylogenetic signal of the EMI (Pagel's  $\lambda = 0.757$ ) pointed out, however,  
233 that once fixed phenotypic reversions in these set of traits within a clade are rare and  
234 only in a few cases sister species show contrasting soil layer preferences (e.g  
235 *Tomocerus minor* and *Oncopodura crassicornis*; TOMMIN and ONCCRAS  
236 respectively in Figure 2). The analysis of the phylogenetic structure of springtail  
237 assemblages showed that under the experimental drought there was a relative increase in  
238 phylogenetic clustering according to the MNTD, i.e. the mean distance of the more  
239 closely related species in the assemblage was smaller under drought relative to control  
240 conditions ( $P < 0.01$ ). However, the MPD showed no differences across climatic  
241 treatments ( $P = 0.37$ ), suggesting that under all experimental conditions there were  
242 rather similar phylogenetic community structure.

243 The unconstrained ordination of springtail communities displayed a clear grouping of  
244 all springtail assemblages according to the country of origin (Figure 3a). This clustered  
245 pattern captured the species turnover among our experimental sites, but additionally, the  
246 two latent variables implicitly highlighted the steep aridity gradient that pervades the  
247 European geography by grouping together the Spanish assemblages close to those from  
248 the Italian and the Hungarian sites. Accordingly, this pattern disappeared when the  
249 aridity index was included as a constraining predictor (Figure 3b), thus confirming  
250 water availability and mean annual temperature as major drivers of springtail  
251 communities across Europe. Indeed, the aridity index alone captured 70.6 % of the  
252 whole compositional variability (LRT  $P < 0.05$ ). Regarding the interaction between  
253 traits and the environment, the structuring power of aridity was stronger than that of the  
254 short-term effect of the experimental climate manipulations (Figure 4). Among the 22  
255 traits tested for trait-environment associations, 8 showed significant ( $P < 0.05$ )  
256 relationships with aridity, 6 with the experimental drought and only 3 with the warming  
257 treatment based on LRTs between equivalent models with and without the  
258 corresponding trait-environment interaction (see Table 2 for a complete list of all  
259 significant trait-environment relationships).

260 At a biogeographic scale, all traits showing significant interactions with aridity  
261 indicated a clear trend towards more epigeic springtail assemblages as mean annual  
262 temperatures increased and precipitation decreased. Indeed, species with a  
263 predominance of sexual reproduction over parthenogenesis, higher numbers of ocelli  
264 and longer furcula and antennae were positively selected by increasing aridity (Figure

265 4). On the other hand, the lower presence and abundance of pigmented species and with  
266 photoreceptors (ocelli) in the plots under the experimental drought, along with the  
267 increase of species with pseudocelli and with a greater minimum and maximum number  
268 of vesicles in this typically edaphic defensive organ pointed out to a relative  
269 edaphization of the springtail assemblages after this short-term experimental treatment.  
270 Warming only reduced the presence of species with parthenogenesis and slightly  
271 increased the minimum and maximum number of ocelli in the springtail assemblages.

## 272 **4. Discussion**

273 The capacity to forecast the effects of climate change on biodiversity largely rely on  
274 identifying those traits capturing mechanistic relationships with the environment  
275 through standardized field experiments distributed across macro-ecologically relevant  
276 spatial scales (Halbritter et al., 2020; Mouquet et al., 2015). Our results demonstrate,  
277 however, that the effects of local climate manipulations on communities of springtails  
278 overlap with the regional gradients that have been operating during longer time periods.  
279 The broad aridity gradient present across Europe promoted assemblages of species with  
280 more epigeic traits as water availability decreases and temperature increases. Despite  
281 this long-term and strong aridity driver, the effect of the drought treatment led to a  
282 relative edaphization of springtail communities. We discuss below how this disparity of  
283 community responses against short versus long-term climate restrictions result from the  
284 trait differences between epigeic and more edaphic springtails and why this also warns  
285 out that our interpretations of the trait-environment relationships behind the current  
286 biodiversity reorganizations of soil fauna may change or even be reversed as climate  
287 change continues.

### 288 **4.1 Evolutionary convergence of edaphic traits in Collembola**

289 Springtail species adapted to inhabit at specific soil strata typically share a common  
290 suite of eco-morphological traits and, to some extent, they even share a similar trophic  
291 niche irrespective of their phylogenetic affiliation (Ponge, 2000; Potapov et al., 2016;  
292 Salmon et al., 2014). Our results complement these earlier findings demonstrating that  
293 this is the result of an adaptive convergence that has repeatedly happened in the lineages  
294 of the three major Collembolan orders. The ancestral ecology of springtails has been of  
295 particular interest in light of the still unknown terrestrialization path followed by the  
296 subphylum Hexapoda (Ghilarov, 1958; van Straalen, 2021). According to our dataset,  
297 the hemiedaphic condition would be the plesiomorphic state for Collembola while the

298 adaptations for a truly epigeic life would have been secondarily gained, particularly by  
299 Entomobryomorpha and Symphyleona. This conclusion agrees with previous  
300 morphological assessments (D'Haese, 2003), thus bridging together the cladistics  
301 approach with our phylogenetic analysis.

302 The development of an epigeic habitus is associated with larger and pigmented bodies  
303 with longer appendages, sexual reproduction and more developed sensory organs, while  
304 the specialized edaphic life-form typically imply a smaller unpigmented body, shorter  
305 appendages, reduced or absent sensory organs along with the development of the ability  
306 to reproduce through parthenogenesis (Chahartaghi et al., 2006; Salmon et al., 2014).  
307 Despite the repeated convergent evolution of these traits at a broad phylogenetic scale,  
308 the transitions between epigeic and edaphic life-forms, however, are rarely reversed  
309 within a clade so that sister species usually share a similar habitus and hence soil layer  
310 preferences. A previous study at a smaller spatial scale has shown that evolutionary  
311 close species tend to co-occur due to their akin ecological preferences and competitive  
312 exclusion of sister species may be rare notwithstanding (Ponge & Salmon, 2013). This  
313 suggests that the relative phylogenetic clustering observed under the experimental  
314 drought according to the MNTD metric may mirror springtail assemblages where sister  
315 species are coexisting. The apparent discrepancy with the MPD, which points out to a  
316 lack of phylogenetic clustering due to the climate manipulations, may actually arise by  
317 the fact that in all major springtail lineages there are species relatively specialized to  
318 either an epigeic or edaphic lifestyle. Thus, the presence of species from all  
319 evolutionary lineages under all experimental treatments results in similar in-depth  
320 phylogenetic community structure and may preclude any phylogenetic imbalance in the  
321 resulting assemblages. Therefore, this adaptive convergence may explain why in  
322 Collembola phylogenetic diversity measures are less sensitive to species losses or  
323 community shifts due to warming and drought than functional richness or other trait-  
324 based diversity metrics (Peguero et al., 2019).

#### 325 **4.2 Long-term climate gradients versus short-term climate manipulations**

326 The current climate gradients present in Europe date back to around 10000 years BP and  
327 by 6000 year BP the vegetation patterns already resembled that of today (Hewitt, 1999).  
328 Here we demonstrate that the increase in aridity across Europe nowadays is coupled  
329 with springtail assemblages where species with typically epigeic traits are better  
330 represented. These positively selected traits at a macroecological scale include longer

331 furculas and antennas, well-developed light and mechanic sensory organs, and a  
332 predominance of sexual reproduction over parthenogenesis, all of them being  
333 characteristic adaptations to live in the soil surface or its uppermost horizons (Salmon et  
334 al., 2014). These atmobiotic and epigeic species have a higher resistance to drought and  
335 thermal stress than specialized soil-dwelling springtails thanks to biochemical and  
336 physiological mechanisms that include a lower cuticular permeability, the production of  
337 sugars and polyols to regulate internal osmolality and a greater plasticity in the fatty  
338 acid composition of their cellular membranes (Dooremalen et al., 2013; Kærsgaard et  
339 al., 2004). But additionally, their larger body size, longer appendages and fully  
340 functional visual organs provide these epigeic species with a greater dispersal capacity  
341 (Ojala & Huhta, 2001), which allows them to migrate to avoid adverse conditions and  
342 choose more favorable micro-habitats within their home range (Chauvat et al., 2014;  
343 Ponge et al., 2006), ultimately making them more resilient against local disturbances  
344 (Lindberg & Bengtsson, 2006; Malmström, 2012).

345 In contrast to epigeic springtails, the species adapted to live deeper in the soil profile  
346 typically migrate downwards to escape from dryness (Detsis, 2000; Hopkin, 1997). This  
347 behavioral difference may be behind the observed relative edaphization of springtail  
348 assemblages under the experimental drought. Atmobioc and epigeic species may have  
349 dispersed seeking for better patches nearby (Chauvat et al., 2014; Ojala & Huhta, 2001;  
350 Ponge et al., 2006) after experiencing between 2 up to 4 years of drought, while edaphic  
351 species were still there likely retreated below and perhaps migrating across the soil  
352 profile tracking the daily variation in moisture (Detsis, 2000; Hopkin, 1997). Indeed, the  
353 soil matrix provides a remarkable buffering capacity against environmental variation.  
354 However, the edaphic species are generally more vulnerable to desiccation and thermal  
355 stress than epigeic collembolans (Dooremalen et al., 2013; Kærsgaard et al., 2004) in  
356 spite of their biochemical and physiological adaptations (Holmstrup et al., 2001). The  
357 effectiveness of this vertical migration strategy may therefore be limited if the drought  
358 episode lasts too long. The response to the warming treatments did not lead to major  
359 changes in the functional structure of the communities. Our warming treatment was  
360 rather mild just increasing from 0.2 to 0.9 °C the MAT of the experimental plots (Table  
361 S2). Additionally, previous research suggests that the diversity and composition of  
362 springtail communities may be fairly resistant and resilient to moderate warming

363 ([Alatalo et al., 2015](#); [Holmstrup et al., 2013, 2018](#); [Peguero et al., 2019](#); [Petersen,](#)  
364 [2011](#)).

## 365 **5. Conclusions**

366 There is a solid consensus around the fact that the responses of species to withstand  
367 climate change can be grouped around two major strategies: to disperse or to adapt  
368 ([Berg et al., 2010](#); [Jump & Penuelas, 2005](#)). Springtails, and most likely all soil fauna,  
369 are no exception and when experiencing increasingly adverse environmental conditions  
370 may either ‘move or change’ ([Ponge, 2020](#)). To move implies from local dispersion up  
371 to distribution range shifts. The effectiveness of this strategy relies, however, first on  
372 the buffering capacity of the local microhabitats, and secondly on the mismatch (or not)  
373 between compositional changes of communities tracking environmental suitability and  
374 the velocity of climate change itself ([Devictor et al., 2012](#)). Dispersal estimates for  
375 collembolan species are scarce but lie in the range of few (~5) centimeters per week  
376 during the favorable season, so that springtail assemblages, at a community level, are  
377 expected to select habitats by active movement within circles up to 200 meters ([Chauvat](#)  
378 [et al., 2014](#); [Ojala & Huhta, 2001](#); [Ponge & Salmon, 2013](#); [Ponge, 2020](#)). Taking into  
379 account that birds and butterflies, which both have notably high dispersal capacities, are  
380 already experiencing climatic debts of 212 and 135 km respectively ([Devictor et al.,](#)  
381 [2012](#)), we may have serious doubts about the ability of Collembola to keep up with  
382 climate change through their active dispersal. Like other organisms such as plants that  
383 are unlikely to migrate fast enough to track the rapidly changing climate, adaptation  
384 must play an increasingly important role ([Jump & Penuelas, 2005](#); [Ponge, 2020](#)). There  
385 are hopeful examples of soil fauna showing rapid evolutionary changes in response to  
386 climate change ([Bataillon et al., 2016](#)), and although the only example with a springtail  
387 species reported some degree of ontogenetic plasticity (i.e. steeper reaction norms of  
388 developmental rates of juveniles than those of adults), there was almost no sign of local  
389 adaptation to geothermal warming ([Kutcherov et al., 2020](#)). If so, this calls for urgent  
390 studies assessing the adaptive potential of springtails, and more generally tracking  
391 population dynamics and functional trait shifts at a community level ([Bardgett & Putten,](#)  
392 [2014](#); [Berg et al., 2010](#); [Guerra et al., 2021](#)), specially taking into account that for  
393 conservation purposes collembolan functional diversity indices may outperform  
394 phylogenetic metrics and better correlate with ecosystem functioning ([Peguero et al.,](#)  
395 [2019](#)).

396 Finally, our study also warns out that our interpretations of the trait-environment  
 397 relationships behind the current biodiversity reorganizations of soil fauna may change  
 398 or even be reversed as climate change continues. As pointed out by previous studies  
 399 (Alatalo et al., 2015; Holmstrup et al., 2013, 2018b), our work also suggests that the  
 400 observed shifts of springtail communities to climate manipulations may be transient in  
 401 time, with epigeic species showing faster responses probably due to their higher  
 402 vagility. Thus, the resultant relative edaphization we have observed in the springtail  
 403 communities of our experimentally drought plots could change and even be reversed  
 404 after some time, in light of the clear and strong selection towards more epigeic  
 405 assemblages that the aridity gradient has exerted at a larger spatiotemporal scale. To the  
 406 best of our knowledge there are no studies simultaneously assessing long-term  
 407 macroecological drivers with short-term climate manipulations at relevant spatial scales  
 408 and this study demonstrates how important this is if we are to adequately forecast soil  
 409 fauna responses to climate change.

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## 614 TABLES

<b>Table 1.</b> List of Collembolan traits analysed.				
Type	Trait	Type of variable	Values	Species <sup>1</sup>
Body aspect	Length	Continuous	0.18 – 6.5 mm	60
	Shape	Categorical	Spherical Cylindrical Wide-cylindrical	61
Reproductive strategy	Reproduction	Categorical	Parthenogenesis Sexual Mixed	47
Dispersal capacity	Furcula <sup>2</sup>	Discrete Binomial	0 – 1	61
	Furcula length <sup>2</sup>	Semi-quantitative	0 – 4	53
	Leg-body ratio	Continuous	0.11 – 0.69	52
Sensory organs	Antennal length	Semi-quantitative	1 – 3	55
	Antenna-head ratio	Continuous	0.40 – 3.50	51
	Ocelli	Discrete Binomial	0 – 1	62
	Ocelli number	Discrete	0 – 8	62
	Post Antennal Organ (PAO)	Discrete Binomial	0 – 1	58
	PAO number	Discrete	0 – 190	56
	Trichobothria	Discrete Binomial	0 – 1	60
Protective features	Scales	Discrete Binomial	0 – 1	61
	Pigmentation	Discrete Binomial	0 – 1	60
	Pseudocelli	Discrete Binomial	0 – 1	64
	Pseudocelli number	Discrete	0 – 56	64

<sup>1</sup> Number of species with trait data available.  
<sup>2</sup> Note that furcula as presence/absence and its length are also protective features related with defensive evasion.  
 Trait data collated from COLTRAIT database (Salmon et al., 2014). Some continuous or discrete numerical traits (e.g. Length, Ocelli, PAO number, Pseudocelli) have minimum and maximum values recorded separately. See Table S4 for further information on the traits included in this study.

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<b>Table 2.</b> Statistically significant interactions between springtail traits and environmental conditions.					
Trait	Drought	Warming	Aridity	P-value	Nº of species
Parthenogenesis	-0.63±0.67	-1.19±0.66 *	-2.44±1.20 *	0.0087	46
Sexual reproduction	0.05±0.43	0.53±0.43 *	0.87±0.81 *	0.0087	46
Furcula length (1)	0.44±1.53	-1.53±1.72	5.76±3.43 *	0.0000	53
Furcula length (2)	-0.75±1.47	-0.71±1.44	5.02±2.85 *	0.0000	53
Furcula length (4)	-0.05±0.69	0.44±0.66	7.78±1.77 *	0.0000	53
Antennal length (2)	-0.47±3.45	-0.26±3.79	7.21±6.10 *	0.0002	55
Antennal length (3)	-0.42±0.56	0.26±0.50	3.07±1.34 *	0.0002	55
Antenna-head ratio (min.)	0.01±0.38	0.24±0.34	2.05±0.76 *	0.0000	51
Antenna-head ratio (max.)	0.07±0.35	0.40±0.32	2.12±0.71 *	0.0000	51
Ocelli	-0.65±0.62 *	0.58±0.61	0.61±1.57	0.0199	61
Ocelli number (min.)	-0.16±0.23	0.36±0.27 *	3.18±0.86 *	0.0018	62
Ocelli number (max.)	-0.09±0.28	0.44±0.27 *	1.73±0.75 *	0.0001	62
Post Antennal Organ (PAO)	0.27±0.51	-0.31±0.52	-2.54±1.35 *	0.0024	58
PAO number (min.)	0.53±0.54	0.26±0.44	1.30±0.51 *	0.0000	56
PAO number (max.)	0.46±0.41 *	0.20±0.36	1.15±0.44 *	0.0002	56
Trichobothria	0.07±0.48	0.50±0.45 ·	1.46±1.19 ·	0.0828	60
Pigmentation	-0.60±0.59 *	0.53±0.58	-0.09±1.35	0.0055	60
Pseudocelli	1.28±0.67 *	-0.31±0.93	-0.82±3.67	0.0031	63
Pseudocelli number (min.)	0.53±0.28 *	-0.01±0.24	-0.04±0.58	0.0002	63
Pseudocelli number (max.)	0.53±0.28 *	-0.01±0.24	0.01±0.55	0.0002	63

Each line corresponds to a fourth corner model based on Generalized Linear Latent Variable Models. Effect estimates are followed by its 95% Confidence Interval. Significant and marginal interactions are represented by “\*\*” and “·”, respectively. P-values show the result of a LRT against an equivalent model without the corresponding trait-environment interaction. Last column indicates the number of species with data available for each trait and thus included in the models.

## 618 FIGURE CAPTIONS

619 **Figure 1.** Schematic representation of the morphological and functional adaptations to  
 620 living in different soil layers by the main phylogenetic lineages of Collembola (Order  
 621 Entomobryomorpha, Symphypleona and Poduromorpha) along with the corresponding  
 622 range for the Eco-Morphological Index (EMI). Based on Parisi et al. (2005), Potapov et  
 623 al. (2016) and Salmon et al. (2014).

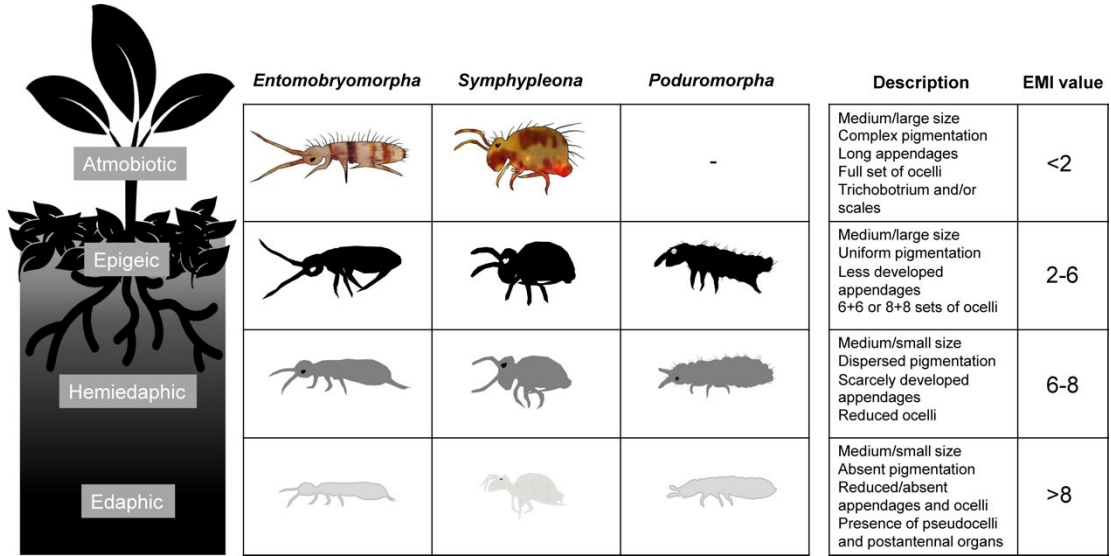
624 **Figure 2.** Phylogenetic reconstruction of the Eco-Morphological Index (EMI) across the  
 625 clade Collembola. Red to yellow indicate lower EMI values associated to atmobiotic  
 626 and epigeic species, while green to blue denote higher EMI values related to  
 627 hemiedaphic and edaphic species. Drawings are placed along with the corresponding  
 628 species or its closest relative to illustrate their morphological and functional adaptations.  
 629 See the Supplementary Methods and Table S3 in the Supporting Information for further  
 630 details about the phylogeny and for the species abbreviations.

631 **Figure 3.** Ordination based on a generalized linear latent variable model fitted to the  
 632 collembolan community data (102 species) without environmental predictors (a) and  
 633 after controlling for the effects of the aridity index (b). Symbol shape correspond to the  
 634 countries included in the study (DK, Denmark; HU, Hungary; IT, Italy; NL,  
 635 Netherlands; SP, Spain and UK, United Kingdom), and colour refer to the experimental  
 636 climate manipulation applied to each plot. Taxa with the largest factor loadings are  
 637 included as indicator species. See Table S3 in the Supporting Information for species  
 638 abbreviations. Inset in panel b shows the result of a likelihood-ratio test between the  
 639 unconstrained and the constrained model along with the increase in variance explained  
 640 by the aridity index.

641 **Figure 4.** Level plot for the empirical significant interactions between collembolan  
 642 traits and short-term experimental drought and the long-term large-scale aridity gradient  
 643 present in Europe according to generalized linear latent variable models (GLLVM).  
 644 Each trait-environment interaction was modelled with a separate GLLVM maximizing  
 645 the number of species with trait data available (47 to 64 species). See Table 2 in the  
 646 Supporting Information for a complete list of interactions and model outputs. Statistical  
 647 significance was assessed by means of likelihood-ratio tests between equivalent models  
 648 with or without the trait-environment interaction. Coloured squares show significant  
 649 interactions ( $P < 0.05$ ) with (·) denoting marginal significance ( $P < 0.1$ ). The colour  
 650 scale offers an indication of the sign and magnitude of the selection exerted over each  
 651 trait in the collembolan communities.

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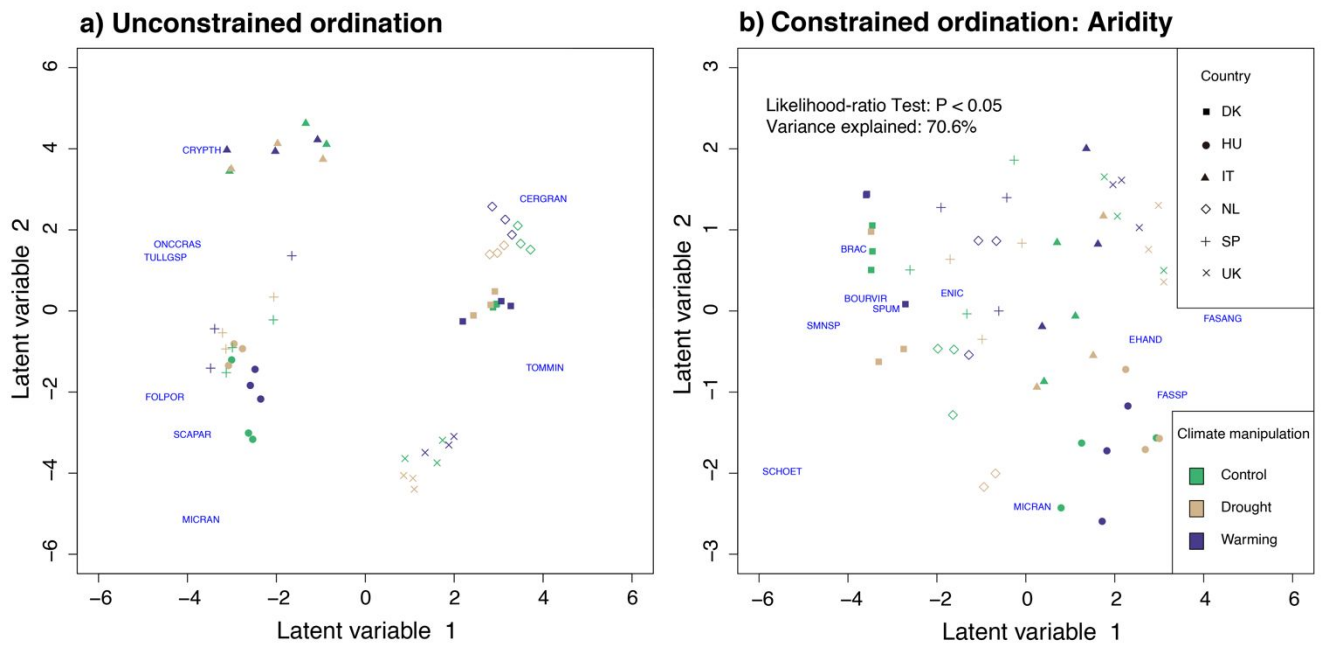
653 FIGURE 1



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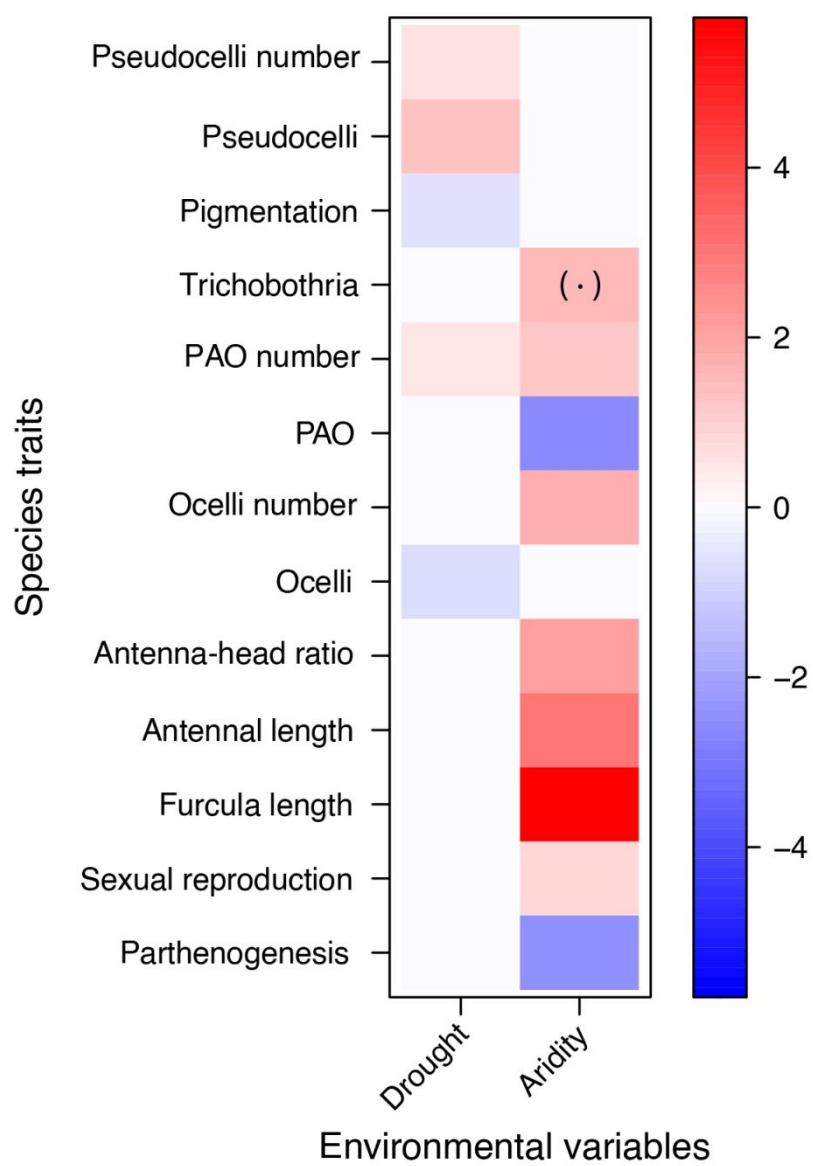


659 FIGURE 3



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662 FIGURE 4



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SUPPORTING INFORMATION

**Trait-mediated responses to aridity and experimental drought by springtail communities across Europe**

FIGURE S1

Location of the climatic manipulation experiments in Europe. Arrows depict broad-scale gradients of temperature and precipitation that result in an aridity gradient crossing Europe from North-West to South-East. DK, Denmark; HU, Hungary; IT, Italy; NL, the Netherlands; SP, Spain; UK, United Kingdom.

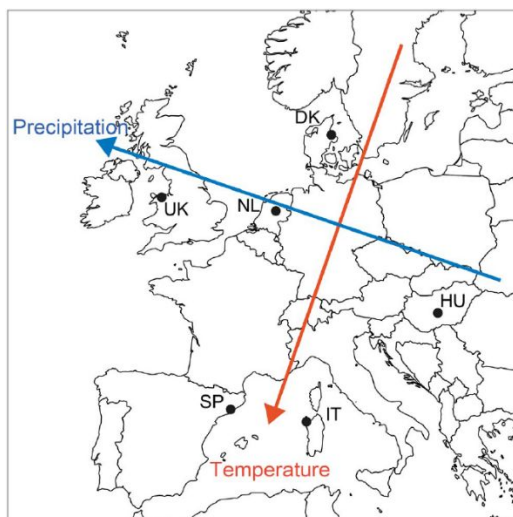


TABLE S1

<b>Table S1. Characteristics of the study sites.</b>						
<b>Site code</b>	<b>UK</b>	<b>NL</b>	<b>DK</b>	<b>HU</b>	<b>SP</b>	<b>IT</b>
<b>Country</b>	United Kingdom	The Netherlands	Denmark	Hungary	Spain	Italy
<b>Site name</b>	Clocaenog	Oldebroek	Mols	Kiskunság	Garraf	Capo Caccia
<b>Coordinates</b>	53°03'N 3°28'W	52°24'N 5°55'E	56°23'N 10°57'E	46°53'N 19°23'E	41°18'N 1°49'E	40°36'N 8°9'E
<b>Soil type (FAO)</b>	Peaty Podzol	Haplic Arenosol	Sandy Podzol	Calcaric Arenosol	Petrocalcic Calcixerepts	Luvisol and Leptosol
<b>MAT (°C)</b>	7.4	8.9	8.7	10.5	15.2	16.1
<b>MAP (mm)</b>	1263	1005	669	558	559	544
<b>Growing season</b>	April-September	April-October	April-September	April-September	January-May October-December	January-May October-December
<b>Dominant species</b>	<i>Calluna vulgaris</i>	<i>Calluna vulgaris</i>	<i>Calluna vulgaris</i> <i>Deschampsia flexuosa</i>	<i>Populus alba</i> <i>Festuca vaginata</i>	<i>Erica multiflora</i> <i>Globularia alypum</i>	<i>Cistus monspeliensis</i> <i>Helichrysum italicum</i> <i>Dorycnium pentaphyllum</i>

MAT, mean annual temperature; MAP, mean annual precipitation.

MATs and MAPs apply to the study period (see Table 2).

Species with relative cover above 10% in the control plots during the study period are listed as dominant species.

TABLE S2

<b>Table S2. Experimental manipulations at the study sites.</b>						
<b>Site code</b>	<b>UK</b>	<b>NL</b>	<b>DK</b>	<b>HU</b>	<b>SP</b>	<b>IT</b>
<b>Start of the experiment (pre-treatment year)</b>	1998	1998	1998	2001	1998	2001
<b>First treatment year</b>	1999	1999	1999	2002	1999	2002
<b>Drought</b>						
<b>Timing</b>	May-September	April-July	May-July	May-June	May-June October-November	April-October
<b>Precipitation excluded (% of yearly total)</b>	25	19	18	22	49	16
<b>Reduction in soil moisture (% of control, 0-20 cm)</b>	45	43	41	23	28	27
<b>Warming</b>						
<b>Timing</b>	Year-round	Year-round	Year-round	Year-round	Year-round	Year-round
<b>Increase in MAT (C)</b>	0.2	0.3	0.9	0.4	0.6	0.4
DK, Denmark; HU, Hungary; IT, Italy; MAT, mean annual temperature; NL, Netherlands; SP, Spain; UK, United Kingdom.						
Drought and warming effects are averages during the study period.						
Soil moisture reduction applies to the end of the experimental drought period.						

TABLE S3

List of the 102 springtail species identified. See Petersen (2011) for further information. Accession numbers for the molecular markers (28S rDNA and *cox1* mtDNA) used to infer their evolutionary relationships and the availability of trait data are also shown.

Abbreviation	Order	Family	Species	Authority	28S	<i>cox1</i>	Trait data
ARR	Symphyleona	Arrhopalitidae	<i>Arrhopalites_sericus</i>	Gisin, 1947	AF483417.1	MHCLB233-09	Yes
ARRPRI	Symphyleona	Arrhopalitidae	<i>Arrhopalites_principalis</i>	Stach, 1945	AY239037.1	MHCLB073-09	Yes
BOURHOR	Symphyleona	Bourletiellidae	<i>Bourletiella_hortensis</i>	Fitch, 1863			No
BOURPIG	Symphyleona	Bourletiellidae	<i>Bourletiellidae_g_sp</i>		FJ411426.1	BBCCS308-10	No
BOURVIR	Symphyleona	Bourletiellidae	<i>Bourletiella_viridescens</i>	Stach, 1920	FJ411426.1	KM617234	Yes
BRAC	Poduromorpha	Brachystomellidae	<i>Brachystomella_parvula</i>	Schäffer, 1896	AF483360.1	SMTTPP1428-15	Yes
CER	Poduromorpha	Hypogastruridae	<i>Ceratophysella_sp</i>				No
CERDEN	Poduromorpha	Hypogastruridae	<i>Ceratophysella_denticulata</i>	Bagnall, 1941	KF684424.1	KU374568.1	Yes
CERGRAN	Poduromorpha	Hypogastruridae	<i>Ceratophysella_granulata</i>	Stach, 1949	KF684413.1	HM399009.1	Yes
CRYP	Entomobryomorpha	Isotomidae	<i>Cryptopygus_sp</i>				No
CRYPALB	Entomobryomorpha	Isotomidae	<i>Cryptopygus_albaredai/delamarei</i>	Selga, 1962/ Poinso, 1970			No
CRYPSP	Entomobryomorpha	Isotomidae	<i>Cryptopygus_sp</i>				No
CRYPTH	Entomobryomorpha	Isotomidae	<i>Cryptopygus_thermophilus</i>	Axelsson, 1900	HQ592746.1	KJ419039.1	Yes
CYPALB	Entomobryomorpha	Cyphoderidae	<i>Cyphoderus_albinus</i>	Nicolet, 1842	KM978338.1	KM617184	Yes
DEUPAL	Symphyleona	Bourletiellidae	<i>Deuterosminthurus_pallipes_cf</i>	Bourlet, 1843	FJ411426.1	MHCLB277-09	Yes
DIC	Symphyleona	Dicyrtomidae	<i>Dicyrtoma_sp</i>		LK024302.1	KM621738	No
DICFUSC	Symphyleona	Dicyrtomidae	<i>Dicyrtoma_fusca</i>	Lubbock, 1893	LK024301.1	KT808355.1	Yes
DICORN	Symphyleona	Dicyrtomidae	<i>Dicyrtomina_ornata</i>	Nicolet, 1841	LK024305.1	KM623796.1	Yes
DICSAU	Symphyleona	Dicyrtomidae	<i>Dicyrtomina_saundersi</i>	Lubbock, 1862	EF199974.2	BBCCS138-10	Yes
DICSP	Symphyleona	Dicyrtomidae	<i>Dicyrtomina_sp</i>				No
EHAND	Entomobryomorpha	Entomobryidae	<i>Entomobrya_handschini</i>	Stach, 1922	KC236317.1	KR119034.1	Yes
ELAN	Entomobryomorpha	Entomobryidae	<i>Entomobrya_lanuginosa</i>	Nicolet, 1842	AF483423.1	JN970907.1	Yes
EMAR	Entomobryomorpha	Entomobryidae	<i>Entomobrya_marginata</i>	Tullberg, 1871	LK024312.1	GENHP1210-12	Yes
EMULT	Entomobryomorpha	Entomobryidae	<i>Entomobrya_multifasciata</i>	Tullberg, 1871	KC236316.1	KM978392.1	Yes

ENIC	Entomobryomorpha	Entomobryidae	<i>Entomobrya nicoleti</i>	Lubbock, 1868	KC236319.1	KM617653	Yes
ENIV	Entomobryomorpha	Entomobryidae	<i>Entomobrya nivalis</i>	Linné, 1758	LK024318.1	KT707112.1	Yes
ENT	Entomobryomorpha	Entomobryidae	<i>Entomobrya</i> sp				No
ENTQUI	Entomobryomorpha	Entomobryidae	<i>Entomobrya quinquelineata</i> cf	Börner, 1901	LK024308.1	KM618447	Yes
ENTSL	Entomobryomorpha	Entomobryidae	<i>Entomobryoides myrmecophilus</i> cf	Reuter, 1886	KC236315.1	KR114833	Yes
FASANG	Symphyleona	Bourletiellidae	<i>Fasciosminthurus angulipunctatus</i>	Loksa & Bogojevic, 1970			No
FASBED	Symphyleona	Bourletiellidae	<i>Fasciosminthurus bedosae</i> cf	Nayrolles, 1994			No
FASSP	Symphyleona	Bourletiellidae	<i>Fasciosminthurus cassagnai/ cugnyi</i> cf	Nayrolles, 1994			No
FBREV	Entomobryomorpha	Isotomidae	<i>Folsomia brevicauda</i>	Agrell, 1939	LK024329.1	COLNO068-09	Yes
FLAW	Entomobryomorpha	Isotomidae	<i>Folsomia litsteri</i>	Bagnall, 1939	LK024328.1	COLNO067-09	Yes
FMAN	Entomobryomorpha	Isotomidae	<i>Folsomia manolachei</i>	Bagnall, 1939	LK024327.1	COLNO069-09	Yes
FOLPAR	Entomobryomorpha	Isotomidae	<i>Folsomides parvulus</i>	Stach, 1922	JN981041.1	JN981069	Yes
FOLPOR	Entomobryomorpha	Isotomidae	<i>Folsomides portulacensis</i> cf	Gama, 1961			No
FPEN	Entomobryomorpha	Isotomidae	<i>Folsomia penicula</i>	Bagnall, 1939	JN981049.1	GBCO2496-14	Yes
FQOC	Entomobryomorpha	Isotomidae	<i>Folsomia quadrioculata</i>	Tullberg, 1871	JN981050.1	KU373191.1	Yes
FRIMIR	Poduromorpha	Neanuridae	<i>Friesea mirabilis</i>	Tullberg, 1871	AF483426.1	GENHP1269-12	Yes
FRITRU	Poduromorpha	Neanuridae	<i>Friesea truncata</i>	Cassagnau, 1958	AF483427.1	GENHP1270-12	Yes
HETBIL	Symphyleona	Bourletiellidae	<i>Heterosminthurus bilineatus</i>	Bourlet, 1842	FJ411426.1	JF884240	Yes
HETCLA	Symphyleona	Bourletiellidae	<i>Heterosminthurus claviger</i>	Gisin, 1958			No
HETMAJ	Entomobryomorpha	Entomobryidae	<i>Heteromurus major</i>	Moniez, 1889	JX261654.1	HM397736.1	Yes
IANGVIR	Entomobryomorpha	Isotomidae	<i>Isotoma viridis</i> sl	Bourlet, 1839	JN981061.1	KT808360.1	Yes
ICAER	Entomobryomorpha	Isotomidae	<i>Isotoma caerulea</i>	Bourlet, 1839			No
IMIN	Entomobryomorpha	Isotomidae	<i>Isotomiella minor</i>	Schäffer, 1896	JN981062.1	KJ186386	Yes
IMOD	Entomobryomorpha	Isotomidae	<i>Isotomodes</i> sp		JN981042.1	JN981070	No
INOT	Entomobryomorpha	Isotomidae	<i>Parisotoma notabilis</i>	Schäffer, 1896	KJ792158.1	KT808351.1	Yes
ISMUR	Entomobryomorpha	Isotomidae	<i>Isotomurus graminis</i> cf	Fjellberg, 2007	JN981063.1	JN981085	No
LCYAN	Entomobryomorpha	Entomobryidae	<i>Lepidocyrtus cyaneus</i>	Tullberg, 1871	KC236291.1	KM623832.1	Yes
LEPAP	Entomobryomorpha	Entomobryidae	<i>Lepidocyrtus apicalis</i>	Mateos & Petersen 2012			No
LEPLAN	Entomobryomorpha	Entomobryidae	<i>Lepidocyrtus lanuginosus</i>	Gmelin, 1790	KC236289	JQ801596.1	Yes

LEPLYS	Entomobryomorpha	Entomobryidae	Lepidocyrtus lignorum_cf	Fabricius, 1793	LK024362.1	KM623980.1	Yes
LEPSEL	Entomobryomorpha	Entomobryidae	Lepidocyrtus selvaticus_cf	Arbea & Ariza, 2007	KC236329	KT707770.1	No
MEG	Neelipleona	Neelidae	Megalothorax minimus	Willem, 1900	KC900207.1	KC900195.1	Yes
MES	Poduromorpha	Tullbergiidae	Mesaphorura_sp				No
MIC	Poduromorpha	Neanuridae	Micranurida pygmaea	Börner, 1901	AF483435.1	GENHP1168-12	Yes
MICRAN	Entomobryomorpha	Isotomidae	Micranurophorus musci	Bernard, 1977	LK024298.1	HM893776	Yes
MMAC	Poduromorpha	Tullbergiidae	Mesaphorura macrochaeta	Rusek, 1976	AF483375.1	COLNO048-09	Yes
NEAN	Poduromorpha	Neanuridae	Neanura muscorum	Templeton, 1835	AJ251733.2	KT808329.1	Yes
NEANSP	Poduromorpha	Neanuridae	Neanura_sp				No
NEOTUL	Poduromorpha	Tullbergiidae	Neotullbergia ramicuspis	Gisin, 1953	AF483434.1	COLNO042-09	Yes
ONCCRAS	Entomobryomorpha	Oncopoduridae	Oncopodura crassicornis	Shoebbotham, 1911	DQ016581.1	KR117530	Yes
ONYGSP	Poduromorpha	Onychiuridae	Onychiurus_sp2	without anal spines			No
ONYSP	Poduromorpha	Onychiuridae	Onychiurus_sp1	with anal spines	AF483442.1	HQ732075.1	No
ORCC	Entomobryomorpha	Entomobryidae	Orchesella cincta	Linné, 1758	LK024377.1	KM623648.1	Yes
ORCHSP	Entomobryomorpha	Entomobryidae	Orchesella_sp1				No
PFLAV	Entomobryomorpha	Tomoceridae	Pogonognathellus flavescens	Tullberg, 1871	EU376053.2	KT808376.1	Yes
PLON	Entomobryomorpha	Tomoceridae	Pogonognathellus longicornis	Müller, 1776	KF592009.1	KT808381.1	Yes
PROQUER	Poduromorpha	Onychiuridae	Protaphorura quercetana_cf	Mateos & Arbea, 1986	LK024409.1	GENHP1278-12	No
PROTAPH	Poduromorpha	Onychiuridae	Protaphorura armata_s.l.	Tullberg, 1869	HQ731965.1	HQ732078	Yes
PSAC	Poduromorpha	Neanuridae	Pseudachorudina subcrassus_cf	Tullberg, 1871	LK024411.1	LK024514	No
PSALB	Entomobryomorpha	Entomobryidae	Pseudosinella alba_sp_group	Packard, 1873	KC236295.1	COLNO062-09	No
PSEUDAC	Poduromorpha	Neanuridae	Pseudachorudina meridionalis_cf	Bonet, 1929	X90680.1	HG422637.2	Yes
PSISOT	Entomobryomorpha	Isotomidae	Pseudisotoma sensibilis	Tullberg, 1876	JN981065.1	JN981086.1	Yes
PSPAR	Poduromorpha	Neanuridae	Pseudachorutes parvulus	Börner, 1901	HQ731966.1	KR117034	Yes
SCAPAR	Poduromorpha	Tullbergiidae	Scaphaphorura arenaria	Petersen, 1965	AF483434.1	HQ732072	Yes
SCHOET	Poduromorpha	Hypogastruridae	Schoettella ununguiculata	Tullberg, 1869	HQ731967.1	HQ732079.1	Yes
SEIDOM	Entomobryomorpha	Entomobryidae	Seira domestica	Nicolet, 1841	KC236298.1	KM978395.1	Yes
SMAC	Symphypleona	Sminthuridae	Sminthurus maculatus	Tömösvary, 1883			No
SMEL	Symphypleona	Katiannidae	Sminthurinus elegans	Fitch, 1863	LK024418.1	JQ909220	Yes

SMIDPAR	Symphyleona	Sminthuridae	Sminthurides parvulus	Krausbauer, 1898	DQ016590.1	GENHP1309-12	Yes
SMIGSPS	Symphyleona	Sminthuridae	Sminthuridae_g.sp				No
SMINBOUR	Symphyleona	Sminthuridae	Sminthurus bourgeoisi_cf	Nayrolles, 1995			No
SMNAU	Symphyleona	Katiannidae	Sminthurinus aureus	Lubbock, 1862	LK024419.1	KU374396.1	Yes
SMNSP	Symphyleona	Katiannidae	Sminthurinus alpinus_cf	Gisin, 1953	LK024422.1	KR117243	No
SNIG	Symphyleona	Katiannidae	Sminthurinus niger	Lubbock, 1867	LK024423.1	KT808361.1	Yes
SNIGMAC	Symphyleona	Sminthuridae	Sminthurus nigromaculatus	Tullberg, 1872	EF199973.2	JN970939	Yes
SPAFLA	Symphyleona	Sminthuridae	Spatulosminthurus flaviceps	Tullberg, 1871			No
SPUM	Symphyleona	Sminthuridae	Sphaeridia pumilis	Krausbauer, 1898	EF192443.1	HM424143	Yes
STEVIOL	Symphyleona	Sminthuridae	Stenacidia violacea_cf	Reuter, 1878	AF483455.1	GENHP1309-12	Yes
TETRAC	Entomobryomorpha	Isotomidae	Tetracanthella sp				No
TETRHYG	Entomobryomorpha	Isotomidae	Tetracanthella hygropetrica_cf	Cassagnau, 1954	JN981043.1	HM366594	Yes
TOMMIN	Entomobryomorpha	Tomoceridae	Tomocerus minor	Lubbock, 1862	KF592037.1	KT808378.1	Yes
TULGSP	Poduromorpha	Tullbergiidae	Tullbergiinae_gspit				No
TULLGSP	Poduromorpha	Tullbergiidae	Tullbergiinae_gspsp				No
WIL	Poduromorpha	Hypogastruridae	Willemia sp				No
WILAN	Poduromorpha	Hypogastruridae	Willemia anophthalma	Börner, 1901	HQ731973.1	KF642103.1	Yes
XEN	Poduromorpha	Hypogastruridae	Xenylla maritima	Tullberg, 1869	LK024444.1	KT808347.1	Yes
XENLOD	Poduromorpha	Odontellidae	Xenyllodes sp		AF483469.1	HQ732089	No
XENMED	Poduromorpha	Hypogastruridae	Xenylla mediterranea_cf	Gama, 1964	LK024443.1	SMTPF8667-14	No

TABLE S4

List of the springtail functional traits included in the study. Completeness is the proportion of species with data for a given trait relative to the entire species pool.

Trait	Definitions and related functions	No. species with data
reproduction	sexual vs. parthenogenetic or mixed (reproductive strategy)	47
body shape	spherical vs. cylindrical or wide_cylindrical (body aspect)	61
length.min	minimum body length (morphology)	60
length.max	maximum body length (morphology)	60
furcula	presence or absence of furcula (evasive organ)	61
furc.length	furcula length, semi-quantitative scale (escaping ability)	53
legbody	leg/body length ratio (locomotive skills)	52
scales	presence or absence (defensive feature)	62
pigmentation	presence or absence (protection)	60
pseudocelli	presence or absence of pseudocelli (defensive structure)	64
pseudo.min	minimum number of vesicles in pseudocelli	64
pseudo.max	maximum number of vesicles in pseudocelli	64
ocelli	presence or absence of ocelli (sensory organ, photoreception)	61
ocelli.min	minimum number of ocelli	61
ocelli.max	maximum number of ocelli	61
ant	antennal length, semi-quantitative scale (sensory organ. chemoreception)	54
anratio.min	antenna/head minimum length	51
anratio.max	antenna/head maximum length	51
post-antennal organ	presence or absence of PAO (sensory organ, unknown function)	58
pao.min	minimum number of PAO vesicles	56
pao.max	maximum number of PAO vesicles	56
trichobotria	presence or absence (sensory organ, mechanoreception)	60

### Supplementary Methods

**Phylogenetic data.** The phylogeny of springtails was constructed with sequence data of two genes (*cox1* and *28s*), obtained from public repositories (GenBank and BOLD). We found information for 77 species (75.5% of all species recorded), although in some cases we had to use sequences for the closest taxa within genus or family level (Table S3). The two genes were aligned separately with CLUSTAL W (Larkin et al., 2007) and then concatenated with GENEIOUS v10.1 (Kearse et al., 2012). The best partition scheme and evolutionary model was selected with PartitionFinder v1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) using the BIC criterion. The optimal partition scheme assigned different models to the three codon positions of the *cox1* and to the *28s* genes (SYM+I+G, GTR+I+G, TM+G+I, GTR+G models, respectively). The best Maximum Likelihood (ML) tree was inferred with the RAxML v.7.2.8 (Stamatakis, 2006) with the help of the RAxMLGUI v1.1 (Silvestro & Michalak, 2012) interface. Each partition was assigned a GTR+CAT model to speed up computation and the best tree and bootstrap support obtained using the ML+ rapid bootstrap option and the ‘autoMRE’ approach to select the optimal number of bootstrap replicates (Pattengale, Alipour, Bininda-Emonds, Moret, & Stamatakis, 2010). Bayesian best trees were inferred with MrBayes v.3.2 (Ronquist et al., 2012), implementing the preferred partition scheme and evolutionary models and running two independent chains for 10 million generations. The correct mixing and the burn-in were evaluated with the help of the program TRACER v1.6 (Rambaut, 2009). Finally, we inferred an ultrametric tree with the program BEAST v1.8.1 (Drummond, Suchard, Xie, & Rambaut, 2012). The bristletail *Dilta littoralis* and the dipluran *Lepidocampa weberi* were used as outgroups, i.e. a group of organisms that allow determining the phylogenetic root of a clade or ingroup with which they are closely related but of which they are not members. Outgroups were removed from the matrix before the analyses and the root of the ingroup was assigned based on the results of the previous phylogenetic analyses. A single relaxed lognormal clock to all partitions was preferred due to the large number of incomplete sequences. The Birth Death model was selected as tree prior. Because the goal of the analyses was to obtain an ultrametric tree, we assigned an arbitrary rate of 1 to the ‘ucl.d.mean’ parameter of the relaxed clock. The accompanying programs LOGCOMBINER and TREEANNOTATOR were used to remove the burn-in generations, to combine the results of three independent chains, and to select the optimal distribution of posterior parameters and tree values. Despite the inherent topological uncertainty of any phylogenetic reconstruction, the tree

