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1 Title

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

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

68 **Abstract**

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

76 2. We analyzed this issue with springtails (Class Collembola), one of the dominant soil
77 fauna groups, in a standardized climate manipulation experiment conducted across six
78 European countries encompassing broad climate gradients. We combined community
79 data (near 20K specimens classified into 102 species) with 22 eco-morphological traits
80 and reconstructed their phylogenetic relationships to track the evolution of adaptations
81 to live at different soil depths, which is key to cope with desiccation. We then applied
82 joint species distribution models to investigate the combined effect of the regional
83 aridity gradient with the local experimental treatment (drought and warming) over the

84 assembly of springtail communities and tested for significant trait-environment
85 relationships mediating their community-level responses.

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

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

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

100 **Abstract / Resumen**

101 1. La capacidad de predecir los efectos negativos del cambio climático sobre la
102 biodiversidad depende en gran medida de identificar aquellos atributos que capturan
103 relaciones mecánicas con el ambiente mediante experimentos manipulativos de campo
104 distribuidos a escalas espaciales relevantes. No obstante, los efectos de las
105 manipulaciones experimentales a corto plazo sobre las comunidades locales pueden
106 solaparse con los gradientes climáticos regionales que han operado durante periodos de
107 tiempo más prolongados. No obstante, de acuerdo a nuestro conocimiento, no hay
108 estudios que hayan evaluado simultáneamente factores macroecológicos a largo plazo
109 junto con manipulaciones climáticas a corto plazo a escalas espaciales relevantes.

110 2. Analizamos este asunto usando como ejemplo a los colémbolos (subclase
111 Collembola), un importante grupo de la fauna del suelo, mediante un experimento de
112 campo de manipulación climática estandarizado y llevado a cabo en 6 países europeos
113 abarcando así amplios gradientes de temperatura y precipitación. Combinamos datos de
114 comunidades de colémbolos (cerca de 20 mil especímenes clasificados en 102 especies)

115 con 22 atributos eco-morfológicos y reconstruimos sus relaciones filogenéticas para
116 rastrear la evolución de las adaptaciones para vivir a distintas profundidades del suelo,
117 lo cual es clave para lidiar con la sequedad. Aplicamos entonces modelos de
118 distribución conjunta de especies para investigar el efecto combinado del gradiente
119 regional de aridez con el tratamiento experimental local (sequía y calentamiento) sobre
120 el ensamblado de las comunidades de colémbolos, y además, testamos la existencia de
121 relaciones atributo-ambiente significativas mediando las respuestas de las comunidades
122 de colémbolos a las manipulaciones climáticas.

123 3. Nuestros resultados muestran: (1) una evolución convergente en los tres linajes
124 principales de colémbolos de especies adaptadas a habitar en distintos estratos del suelo.
125 (2) una clara signatura de la aridez seleccionando atributos de especies más epigeas a
126 escala biogeográfica, y (3) la asociación de la sequía experimental a corto plazo con
127 atributos relacionados con formas de vida más eu-edáficas.

128 4. La condición hemiedáfica sería el estado plesiomórfico de Collembola mientras que
129 las adaptaciones a una vida completamente epigea habrían sido desarrolladas
130 secundariamente y de manera repetida en distintos linajes. Los colémbolos epigeos son
131 más resistentes a la sequía pero también presentan una capacidad de dispersión mayor lo
132 cual les permite buscar activamente micro-hábitats más favorables tras experimentar
133 condiciones ambientales adversas. La relativa edafización de las comunidades de
134 colémbolos observada tras la sequía experimental a corto plazo sería por lo tanto una
135 respuesta transitoria de la comunidad.

136 5. La disparidad entre las tendencias macroecológicas y las rápidas respuestas a nivel de
137 comunidad tras las manipulaciones climáticas ponen de manifiesto la necesidad de
138 evaluar simultáneamente factores de cambio ambiental operando a corto y a largo plazo,
139 y a escalas espaciales amplias, para poder interpretar adecuadamente las relaciones entre
140 atributos y ambiente y así poder predecir mejor las respuestas de la biodiversidad al
141 cambio climático.

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

144 **1. Introduction**

145 Global biodiversity patterns are undergoing rapid shifts driven by on-going climate
146 change (Blowes et al., 2019). Our capacity to forecast such biodiversity responses rely,
147 however, on detailed knowledge of the processes behind species' population rates and
148 the corresponding community reorganizations. Ecological theory predicts that a
149 continued stress will filter out the species with the most vulnerable combinations of
150 traits leading to changes on the functional structure of communities (Mouillot et al.,
151 2013). This selection process may be either the result of the new abiotic conditions
152 impairing the population growth of some species (strict environmental filtering) or the
153 outcome of a reduced competitive performance under the new environmental conditions
154 (Cadotte & Tucker, 2017). Traits, defined as any morphological, physiological,
155 behavioural or phenological feature measurable at an individual level with impacts on
156 species fitness via their effect on growth, reproduction and survival, are thus posited as
157 the common currency for functional biogeography (McGill et al., 2006; Violle et al.,
158 2014). Because trait selection generally precedes diversity loss, it is therefore
159 fundamental to detect those traits capturing mechanistic relationships with stress factors
160 such as climate change if we are to anticipate shifts on species composition and
161 ultimately on ecosystem functioning (Berg et al., 2010; Haddad et al., 2008).

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

176 Despite the growing concern over the impact of climate change on biodiversity, there
177 has been a disproportionate focus on aboveground communities disregarding the key
178 role of soil fauna on ecosystem functioning (Bardgett & van der Putten, 2014; Filser et
179 al., 2016; Guerra et al., 2021). Among this neglected soil biodiversity there are the
180 springtails (Class Collembola), an abundant and diverse group of small arthropods
181 whose communities show fast reductions in taxonomic, phylogenetic and functional
182 richness due to drought, and additionally, are also a good proxy of ecosystem functions
183 like litter decomposition (Peguero et al., 2019). Springtails present a diverse array of
184 adaptations related to dwelling in specific soil layers (Figure 1). Smaller collembolan
185 species with unpigmented bodies, shorter appendages, reduced sensory organs and
186 mostly parthenogenetic reproduction are associated with more euedaphic habitats
187 (Christiansen, 1964; Gisin, 1943; Rusek, 1989), while larger species with pigmented
188 bodies, longer appendages, sexual reproduction and conspicuous mechanic and light
189 receptors such as trichobothria and ocelli respectively, are typical from epigeic
190 environments (Salmon et al., 2014). The species inhabiting the upper soil horizons have
191 a greater drought resistance due to a lower cuticular permeability that allow them to
192 resist desiccation (Kærsgaard et al., 2004). On the other hand, living deeper in the soil
193 profile implies a lower exposure to variability in temperature and soil moisture, and
194 additionally, soil-dwelling species also present biochemical, physiological and
195 behavioural mechanisms to cope with drought (Holmstrup et al., 2001). Accordingly, a
196 multi-site replicated experiment suggested that increasingly drier conditions may
197 eventually favour euedaphic over epigeic springtail species after short-term climate
198 manipulations (Petersen, 2011). Even though, this relative edaphization may show
199 idiosyncratic responses to short-term climate manipulations since in single-site studies
200 at sub-arctic latitudes epigeic species seem to be favoured by experimental warming
201 (Bokhorst et al., 2012; Makkonen et al., 2011). Hence, potentially divergent community
202 responses across large spatial scales may hamper our ability to detect general trends,
203 and in particular to identify those traits behind the current climate-induced community
204 reorganizations. This may be even more difficult if broad climate constraints have had
205 time to differentially shape springtail assemblages across such environmental gradients,
206 although this macroecological dimension, to the best of our knowledge, has never been
207 included in studies assessing soil fauna responses to climate change.

208 The present study unfolds from a standardized climate manipulation experiment
209 replicated across six natural shrublands encompassing the broad gradients of
210 temperature and precipitation present in Europe (Beier et al., 2004). Here, we
211 investigated the simultaneous effect of short-term experimental climate treatments (i.e.
212 drought and warming) and the regional long-term climate gradient synthesized in the
213 aridity index, an indicator based on mean annual temperature and precipitation, over the
214 composition and trait distribution of springtail communities. First, we extracted data
215 from a comprehensive sampling of nearly 20 thousand springtail specimens consisting
216 of 102 species (Petersen, 2011). We then combined it with 22 eco-morphological traits
217 (Salmon et al., 2014) to track across the springtail phylogeny the evolution of the suite
218 of adaptations to inhabit specific soil layers (Table 1). Finally, we leveraged this
219 community data to build joint species distribution models (JSDM) to test for significant
220 associations between traits with climate manipulation treatments and aridity that could
221 be mediating the assembly of collembolan communities. We specifically addressed the
222 following hypotheses and predictions: (i) the adaptations that allow springtails to thrive
223 at different layers of the soil matrix will show a pattern of repeated convergent
224 evolution across the main lineages of Collembola; (ii) the long-term environmental
225 impact of the large-scale climatic gradient present across Europe has driven a selection
226 of drought-tolerant springtail species with increasing aridity; (iii) the experimental
227 short-term increase in local dryness and warming will be a major disturbance driving
228 fast responses that eventually favour more euedaphic springtail assemblages.

229 **2. Materials and Methods**

230 **2.1 Study sites and climatic manipulations**

231 The six shrublands studied comprised most of the European climatic regions (Figure S1
232 and Table S1). Mean annual precipitation (MAP) at the sites ranged from 544 to 1,263
233 mm, and mean annual temperature (MAT) ranged from 7.4 to 16.1 °C. The major types
234 of shrublands present in the study area were: Atlantic heathland (UK, United Kingdom;
235 NL, The Netherlands; DK, Denmark), continental forest steppe (HU, Hungary), and
236 Mediterranean garrigue (SP, Spain; IT, Italy). In each study site, nine 20 m² plots were
237 divided into three blocks and randomly assigned one plot at each block to a warming
238 treatment, a drought treatment, or as a control. Warming plots were covered with
239 reflective covers during the night throughout the year inducing a passive night-time
240 warming, while drought plots were automatically covered by transparent polythene

241 curtains during precipitation events that retracted as soon as rain stopped thus avoiding
242 any warming effect (Beier et al., 2004). Manipulations of temperature and precipitation
243 were carried out in the same way in all sites, but the timing and duration of the
244 experimental drought were adjusted to the local climate regime (Table S2). The sites
245 were established in 1998 (UK, NL, DK, and SP) and 2001 (HU and IT), and on average
246 the warming treatment produced an increase of 0.5 °C of MAT and the drought
247 treatment a 35% reduction of soil moisture (Table S2). This field experiments did not
248 require of any specific permission.

249 **2.2 Springtail sampling, phylogeny and trait information**

250 Springtails were sampled sequentially, to equalize mean temperatures across sites, from
251 April to July 2003 as it follows: Italy (Apr. 29–May 4), Spain (May 13–17), Hungary
252 (May 27–June 1), Denmark (June 23–27), Netherlands (July 9–13) and U.K. (July 19–
253 23). Five quadrats of 1.25 m² representative of the most dominant plant species were
254 chosen in each plot. Springtails were sampled from all plants in the quadrat by
255 suctioning with an adapted vacuum cleaner connected to a fauna trap. Springtails from
256 the soil surface were sampled using the same suction method, from the same five 1.25
257 m² quadrats in Italy and from smaller 78.6 cm² quadrats in the other 5 sites. Specimens
258 dropped were also recovered by placing small polythene boxes with aqueous benzoic
259 acid beneath the plants. Soil springtails were sampled in 10 cm deep soil cores with a
260 surface of 25 cm² taken to the lab. After 2 to 6 days stored in refrigerated boxes,
261 samples were put through high-gradient extraction funnels during 10 days (Gjelstrup &
262 Petersen, 1987). These procedures were slightly adapted in UK and IT due to an excess
263 of soil moisture and stones, respectively (Petersen, 2011). Springtails were identified to
264 species level based on general and group-specific keys (Baquero & Jordana, 2008;
265 Bretfeld, 1999; Carapelli et al., 2001; Fjellberg, 1998, 2007; Gisin, 1960; Jordana et al.,
266 1997; Mateos, 2008; Potapov, 2001; Rusek, 2002). Additionally, some dubious
267 specimens were revised by Drs. L. Dányi, R. Jordana, and E. Mateos. A total of 19,641
268 springtail specimens were collected and classified into 102 species-level entities (Tables
269 S3) and are conserved in glycerol in H. Petersen's personal collection. This sampling
270 did not required any specific approval from an animal ethics committee.

271 We reconstructed the phylogenetic relationships of springtails by means of sequence
272 data gathered from public repositories (GenBank and BOLD). The DNA barcodes best
273 represented in our species pool belonged to cox1 and 28s genes, covering 75% of the

274 species found (see accession numbers in Table S3). We applied Maximum Likelihood
275 and Bayesian procedures to obtain a highly-supported consensus tree that agrees with
276 previous systematic works integrating molecular and morphological information (Yu et
277 al., 2016). See supplementary methods and figure S2 for further details.

278 Additionally, we collated 22 eco-morphological traits from the ColTrait database
279 (Salmon et al., 2014) for 47 up to 64 out of the 102 species present in our study sites
280 (Table 1, Table S4 and S5). These traits encompass different dimensions of their
281 ecological niche such as life history (e.g., reproduction strategy), dispersal ability (e.g.,
282 leg length) and biotic interactions (e.g., sensory organs and defensive structures). In
283 addition, for each species with available traits data, we calculated its Eco-
284 Morphological Index (EMI, Parisi et al., 2005). This trait-based index provides a simple
285 continuous metric ranging from 1 to 20 and indicates the level of adaptation of a given
286 springtail species to a specific soil layer. Accordingly, they may be classified as
287 atmobiotic ($EMI < 2$), epigeic ($EMI < 6$), hemiedaphic ($EMI = [6-8]$) or euedaphic
288 ($EMI > 8$, Figure 1).

289 **2.3 Data analysis**

290 All data handling, visualization and statistical analyses were carried out using R v4.0.0
291 (R Core Team, 2020). First, we investigated the evolution of the adaptations that allow
292 springtail species to live in specific soil layers by means of the reconstruction of the
293 ancestral EMI score across the phylogenetic tree. This was done with the function
294 *fastAnc* of the R package *phylosig* (Revell, 2012) and assuming a Brownian-Motion
295 model of evolution of the suite of traits associated to the EMI. We also estimated the
296 correlation between the similarity in EMI and species' evolutionary distance (i.e. the
297 phylogenetic signal) through Pagel's λ . Then, we assessed how the evolution across
298 Collembola of the suite of traits associated with the EMI may lead to specific patterns in
299 the phylogenetic structure of springtail assemblages in response to the drought and
300 warming treatments separately. Thus, we obtained the mean neighbour taxon distance
301 (MNTD) and the mean pairwise distance (MPD) of each springtail assemblage
302 standardized against 999 community randomizations with the R package *picante*
303 (Kembel et al., 2010). By accounting for both indexes we explored possible non-random
304 patterns occurring at different phylogenetic depths since MNTD can capture changes at
305 the tips of the phylogeny (e.g. selection of sister species sharing specific adaptations)
306 while MPD can detect shifts in the in-depth phylogenetic structure (e.g. selection of

307 species belonging to specific lineages with highly conserved adaptations) (Cadotte &
308 Davies, 2016).

309 Second, we assessed the role of aridity and the experimental climate manipulations on
310 the trait-based assembly of springtail communities across Europe. To do so, we carried
311 out a series of generalized linear latent variable models (GLLVM), as implemented in
312 the R package *gllvm* (Niku et al., 2019). GLLVMs are a type of Joint Species Distribution
313 model (JSDM) that extend the basic generalized linear mixed-effects model to
314 multivariate abundance data incorporating a small number of latent variables
315 accompanied by species-specific factor loadings to model correlations between response
316 variables (i.e. all species in the community matrix). These latent variables have a natural
317 interpretation as ordination axes, but have also the capacity to predict new values
318 controlling for known environmental factors using standard model selection tools (Niku
319 et al., 2019). Additionally, GLLVMs allow us to test for trait-environment associations
320 and the potential effects of biotic interactions. Although the effects of the environment
321 and biotic interactions cannot be teased apart, the inclusion of the latter are a major
322 advance of JSDM compared with previous species distribution tools and ‘fourth corner’
323 models that do not include the co-variation of the abundances between all species within
324 a series of sites or communities (Poggiato et al., 2021; Warton et al., 2015). Hence, we
325 first built an unconstrained model (without environmental predictors) with two latent
326 variables and a negative binomial distribution and a log link function. The selection of
327 the best number of latent variables and distribution family followed the
328 recommendations of Niku et al. (2019), which are based on goodness-of-fit and residual
329 diagnostics. Afterwards, we added sequentially the aridity index and the local climate
330 manipulation treatments as environmental constraints and performed likelihood-ratio
331 tests (LRT) to assess the predictive improvement of these increasingly complex models,
332 and if so, we computed the percentage of deviance explained by the best model. The
333 aridity index of each site was calculated by means of a modified version of the inverse
334 of the Gausson Index (iGI) as: $iGI = 1/(MAP/(2 * MAT)) * 100$ (Reinsch et al., 2017).
335 This index captures the large-scale gradient of aridity currently present across Europe
336 and that can be traced back to the beginning of the Holocene about 10,000 years ago
337 after the last Younger Dryas cold spell came to an end (Hewitt, 1999). Finally, to see
338 whether specific traits were selected by aridity and by the climate manipulation
339 treatments favouring more euedaphic or epigeic springtail species, we built a series of

340 GLLVMs including or not the interaction between a given trait and these two
341 environmental variables and tested their significance via LRT (Niku et al., 2019).

342 **3. Results**

343 Comparative analyses of the EMI revealed multiple independent evolutions of the
344 collembolan traits associated to live in specific soil layers (Figure 2). In all the major
345 lineages of Class Collembola there are groups of species showing either an epigeic
346 habitus (orders Symphypleona and Entomobryomorpha) or, to a lesser extent, a more
347 euedaphic habitus (order Poduromorpha), apparently as a result of a convergent
348 adaptive evolution of a distinctive suite of eco-morphological traits as depicted in
349 Figure 1. The high and significant phylogenetic signal of the EMI (Pagel's $\lambda = 0.757$)
350 pointed out, however, that once fixed phenotypic reversions in these set of traits within
351 a clade are rare and only in a few cases sister species show contrasting soil layer
352 preferences (e.g. *Tomocerus minor* and *Oncopodura crassicornis*; TOMMIN and
353 ONCCRAS respectively in Figure 2). The analysis of the phylogenetic structure of
354 springtail assemblages showed that under the experimental drought there was a relative
355 increase in phylogenetic clustering according to the MNTD, i.e. the mean distance of
356 the more closely related species in the assemblage was smaller under drought relative to
357 control conditions ($P < 0.01$). However, the MPD showed no differences across
358 climatic treatments ($P = 0.37$), suggesting that under all experimental conditions there
359 were rather similar phylogenetic community structure.

360 The unconstrained ordination of springtail communities displayed a clear grouping of
361 all springtail assemblages according to the country of origin (Figure 3a). This clustered
362 pattern captured the species turnover among our experimental sites, but additionally, the
363 two latent variables implicitly highlighted the steep aridity gradient that pervades the
364 European geography by grouping together the Spanish assemblages close to those from
365 the Italian and the Hungarian sites. Accordingly, this pattern disappeared when the
366 aridity index was included as a constraining predictor (Figure 3b), thus confirming
367 water availability and mean annual temperature as major drivers of springtail
368 communities across Europe. Indeed, the aridity index alone captured 70.6 % of the
369 whole compositional variability (LRT $P < 0.05$). Regarding the interaction between
370 traits and the environment, the structuring power of aridity was stronger than that of the
371 short-term effect of the experimental climate manipulations (Figure 4). Among the 22
372 traits tested for trait-environment associations, 8 showed significant ($P < 0.05$)

373 relationships with aridity, 6 with the experimental drought and only 3 with the warming
374 treatment based on LRTs between equivalent models with and without the
375 corresponding trait-environment interaction (see Table 2 for a complete list of all
376 significant trait-environment relationships).

377 At a biogeographic scale, all traits showing significant interactions with aridity
378 indicated a clear trend towards more epigeic springtail assemblages as mean annual
379 temperatures increased and precipitation decreased. Indeed, species with predominance
380 for sexual reproduction over parthenogenesis, higher numbers of ocelli and longer
381 furcula and antennae were positively selected by increasing aridity (Figure 4). On the
382 other hand, the lower presence and abundance of pigmented species and with
383 photoreceptors (ocelli) in the plots under the experimental drought, along with the
384 increase of species with pseudocelli as typically euedaphic defensive organ and with a
385 greater minimum and maximum number of vesicles in postantennal organ pointed out to
386 a relative edaphization of the springtail assemblages after this short-term experimental
387 treatment. Warming only reduced the presence of species with parthenogenesis and
388 slightly increased the number of ocelli in the springtail assemblages.

389 **4. Discussion**

390 The capacity to forecast the effects of climate change on biodiversity largely rely on
391 identifying those traits capturing mechanistic relationships with the environment
392 through standardized field experiments distributed across macro-ecologically relevant
393 spatial scales (Halbritter et al., 2020; Mouquet et al., 2015). Our results demonstrate,
394 however, that the effects of local climate manipulations on communities of springtails
395 overlap with the regional gradients that have been operating during longer time periods.
396 The broad aridity gradient present across Europe promoted assemblages of species with
397 more epigeic traits as water availability decreases and temperature increases. Despite
398 this long-term and strong aridity driver, the effect of the drought treatment led to a
399 relative edaphization of springtail communities. We discuss below how this disparity of
400 community responses against short versus long-term climate restrictions result from the
401 trait differences between epigeic and more euedaphic springtails and why this also
402 cautions that our interpretations of the trait-environment relationships behind the current
403 biodiversity reorganizations of soil fauna may change or even be reversed as climate
404 change continues.

405 **4.1 Evolutionary convergence of euedaphic traits in Collembola**

406 Springtail species adapted to inhabit a specific soil strata typically share a suite of eco-
407 morphological traits and, to some extent, they even share a similar trophic niche
408 irrespective of their phylogenetic affiliation (Ponge, 2000; Potapov et al., 2016; Salmon
409 et al., 2014). Our results complement these earlier findings demonstrating that this is the
410 result of an adaptive convergence that has repeatedly happened in the lineages of the
411 three major Collembolan orders. The ancestral ecology of springtails has been of
412 particular interest in light of the still unknown terrestrialization path followed by the
413 subphylum Hexapoda (Ghilarov, 1958; van Straalen, 2021). According to our dataset,
414 the hemiedaphic condition would be the plesiomorphic state for Collembola while the
415 adaptation to a truly epigeic life would have been secondarily gained, particularly by
416 Entomobryomorpha and Symphypleona. This conclusion agrees with previous
417 morphological assessments (D'Haese, 2003), thus bridging together the cladistics
418 approach with our phylogenetic analysis.

419 The development of an epigeic habitus is associated with larger and pigmented bodies
420 with longer appendages, sexual reproduction and more developed sensory organs, while
421 the specialized euedaphic life-form typically imply a smaller unpigmented body, shorter
422 appendages, reduced or absent sensory organs along with the development of the ability
423 to reproduce through parthenogenesis (Chahartaghi et al., 2006; Salmon et al., 2014).
424 Despite the repeated convergent evolution of these traits at a broad phylogenetic scale,
425 the transitions between epigeic and euedaphic life-forms, however, are rarely reversed
426 within a clade so that sister species usually share a similar habitus and hence soil layer
427 preferences. A previous study at a smaller spatial scale has shown that evolutionary
428 close species tend to co-occur due to their akin ecological preferences and competitive
429 exclusion of sister species may be rare notwithstanding (Ponge & Salmon, 2013). This
430 suggests that the relative phylogenetic clustering observed under the experimental
431 drought according to the MNTD metric may mirror springtail assemblages where sister
432 species are coexisting. The apparent discrepancy with the MPD, which points out to a
433 lack of phylogenetic clustering due to the climate manipulations, may actually arise by
434 the fact that in all major springtail lineages there are species relatively specialized to
435 either an epigeic or euedaphic lifestyle. Thus, the presence of species from all
436 evolutionary lineages under all experimental treatments results in similar in-depth
437 phylogenetic community structure and may preclude any phylogenetic imbalance in the

438 resulting assemblages. Therefore, this adaptive convergence may explain why
439 Collembola phylogenetic diversity measures are less sensitive to species losses or
440 community shifts due to warming and drought than functional richness or other trait-
441 based diversity metrics (Peguero et al., 2019).

442 **4.2 Long-term climate gradients versus short-term climate manipulations**

443 The current climate gradients present in Europe date back to around 10000 years BP and
444 by 6000 year BP the vegetation patterns already resembled that of today (Hewitt, 1999).
445 Atmobiote and epigeic species have a higher resistance to drought and thermal stress
446 than specialized soil-dwelling springtails due to biochemical and physiological
447 mechanisms that include a lower cuticular permeability, the production of sugars and
448 polyols to regulate internal osmolality and a greater plasticity in the fatty acid
449 composition of their cellular membranes (Dooremalen et al., 2013; Kærsgaard et al.,
450 2004). But additionally, their larger body size, longer appendages and fully functional
451 visual organs provide these epigeic species with a greater dispersal capacity (Ojala &
452 Huhta, 2001), which allows them to migrate to avoid adverse conditions and choose
453 more favourable micro-habitats within their home range (Chauvat et al., 2014; Ponge et
454 al., 2006), ultimately making them more resilient against local disturbances (Lindberg
455 & Bengtsson, 2006; Malmström, 2012).

456 In contrast to epigeic springtails, the species adapted to live deeper in the soil profile
457 typically migrate downwards to escape from desiccation (Detsis, 2000; Hopkin, 1997).
458 This behavioural difference may be behind the observed relative edaphization of
459 springtail assemblages under the experimental drought. Atmobiote and epigeic species
460 may have dispersed seeking for better patches nearby (Chauvat et al., 2014; Ojala &
461 Huhta, 2001; Ponge et al., 2006) after experiencing between 2 up to 4 years of drought,
462 while euedaphic species were still there likely retreated below and perhaps migrating
463 across the soil profile tracking the daily variation in moisture (Detsis, 2000; Hopkin,
464 1997). Indeed, the soil matrix provides a remarkable buffering capacity against
465 environmental variation (Geiger et al., 2009). However, the euedaphic species are
466 generally more vulnerable to desiccation and thermal stress than epigeic collembolans
467 (Dooremalen et al., 2013; Kærsgaard et al., 2004; Liu et al., 2020, 2021) in spite of their
468 biochemical and physiological adaptations (Holmstrup et al., 2001). The effectiveness
469 of this vertical migration strategy may therefore be limited if the drought episode lasts
470 too long. The response to the warming treatments did not lead to major changes in the

471 functional structure of the communities. Our warming treatment was rather mild,
472 increasing the MAT of the experimental plots from 0.2 to just 0.9 °C over 4 months
473 (Table S2). Additionally, previous research suggests that the diversity and composition
474 of springtail communities may be fairly resistant and resilient to moderate warming
475 (Alatalo et al., 2015; Holmstrup et al., 2013, 2018; Peguero et al., 2019; Petersen,
476 2011).

477 **5. Conclusions**

478 There is a solid consensus around the fact that the responses of species to withstand
479 climate change can be grouped around two major strategies: to disperse or to adapt
480 (Berg et al., 2010; Jump & Penuelas, 2005). Springtails, and most likely all soil fauna,
481 are no exception and when experiencing increasingly adverse environmental conditions
482 may either ‘move or change’ (Ponge, 2020). To move implies from local dispersion up
483 to distribution range shifts. The effectiveness of this strategy relies, however, first on
484 the buffering capacity of the local microhabitats, and secondly on the mismatch (or not)
485 between compositional changes of communities tracking environmental suitability and
486 the velocity of climate change itself (Devictor et al., 2012). Dispersal estimates for
487 collembolan species are scarce but lie in the range of few (~5) centimetres per week
488 during the favourable season. Thus springtail assemblages, at a community level, are
489 expected to select habitats by active movement within a diameters of up to 200 meters
490 (Chauvat et al., 2014; Ojala & Huhta, 2001; J. F. Ponge & Salmon, 2013; J.-F. Ponge,
491 2020; Treasure & Chown, 2013). Taking into account that birds and butterflies, which
492 both have notably high dispersal capacities, are already experiencing climatic debts of
493 212 and 135 km respectively (Devictor et al., 2012), we may have serious doubts about
494 the ability of Collembola to keep up with climate change through their active dispersal.
495 Like other organisms such as plants that are unlikely to migrate fast enough to track the
496 rapidly changing climate, adaptation must play an increasingly important role (Jump &
497 Penuelas, 2005; Ponge, 2020). There are hopeful examples of soil fauna showing rapid
498 evolutionary changes in response to climate change (Bataillon et al., 2016). Even
499 though the only example with a springtail species reported some degree of ontogenetic
500 plasticity (i.e. steeper reaction norms of developmental rates of juveniles than those of
501 adults), there was almost no sign of local adaptation to geothermal warming (Kutcherov
502 et al., 2020). If so, this calls for urgent studies assessing the adaptive potential of
503 springtails, and more generally tracking population dynamics and functional trait shifts

504 at a community level (Bardgett & van der Putten, 2014; Berg et al., 2010; Guerra et al.,
505 2021). This is especially relevant considering that for conservation purposes
506 collembolan functional diversity indices may outperform phylogenetic metrics and
507 better correlate with ecosystem functioning (Peguero et al., 2019).

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

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Table 1. List of Collembolan traits analysed.				
Type	Trait	Type of variable	Values	Species ¹
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 ²	Discrete Binomial	0 – 1	61
	Furcula length ²	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 of vesicles	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

¹ Number of species with trait data available.

² Note that furcula as presence/absence and *i* as its length is 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 and S5 for further information on the traits included in this study.

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Table 2. Statistically significant interactions between springtail traits and environmental conditions.

Trait	Drought	Warming	Aridity	<i>P</i> -value	N° 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 Likelihood-ratio test (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.

756 FIGURE CAPTIONS

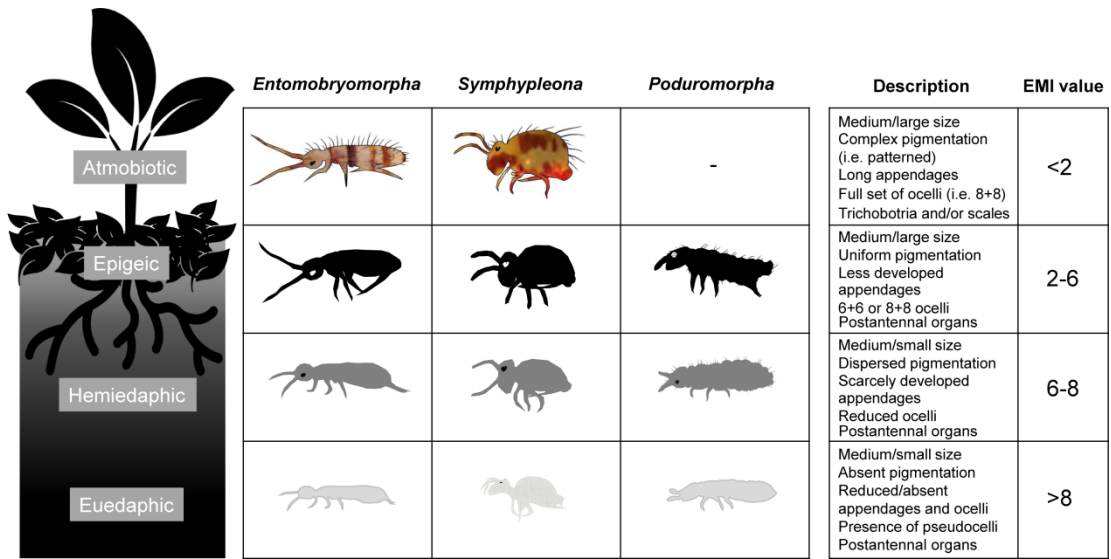
757 **Figure 1.** Schematic representation of the morphological and functional adaptations to
758 living in different soil layers by the main phylogenetic lineages of Collembola (Order
759 Entomobryomorpha, Symphypleona and Poduromorpha) along with the corresponding
760 range for the Eco-Morphological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

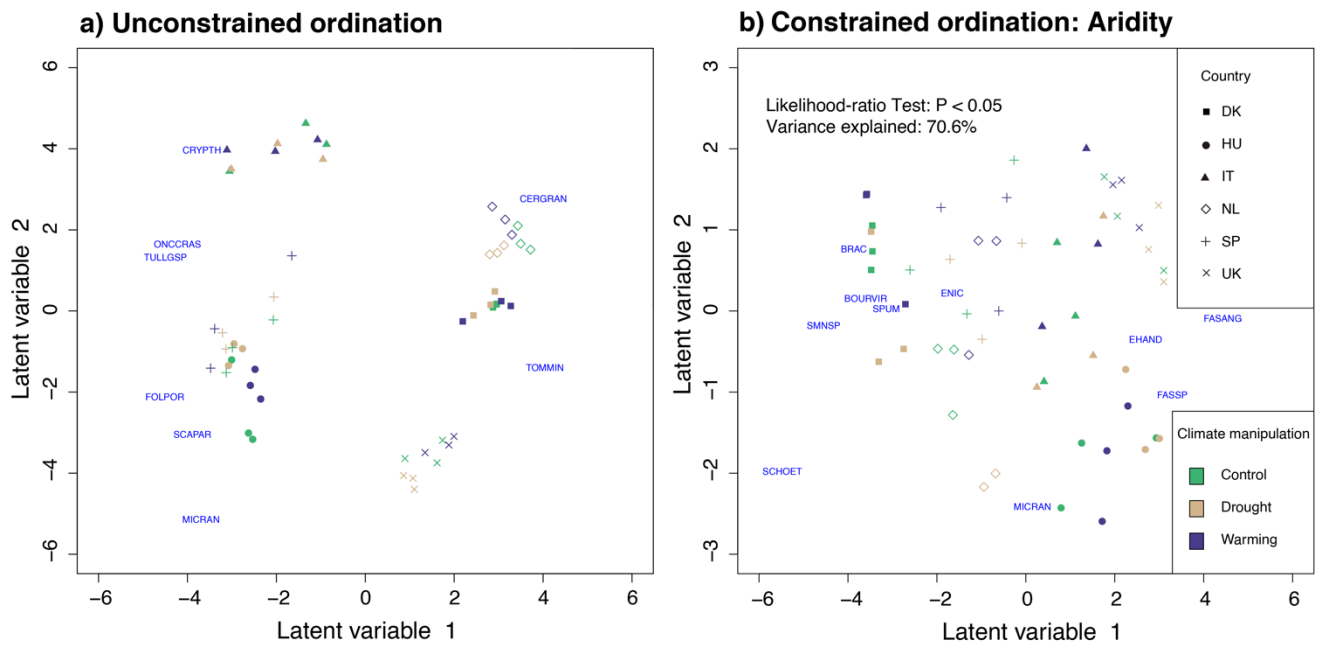
762 **Figure 2.** Phylogenetic reconstruction of the Eco-Morphological Index (EMI) across the
763 clade Collembola. Red to yellow indicate lower EMI values associated to atmobiotic
764 and epigeic species, while green to blue denote higher EMI values related to
765 hemiedaphic and euedaphic species. Numbers at the nodes are branch-support values
766 according to the posterior probabilities drawn from on an ultrametric Bayesian
767 consensus tree. Drawings are placed along with the corresponding species or its closest
768 relative to illustrate their morphological and functional adaptations. See the
769 Supplementary Methods and Table S3 in the Supporting Information for further details
770 about the phylogeny and for the species abbreviations.

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

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

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