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1 Fast attrition of springtail communities by experimental drought and
2 richness-decomposition relationships across Europe

3 *Running title: Decline of springtail richness by drought*

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31 **Abstract**

32 Soil fauna play a fundamental role on key ecosystem functions like organic matter
33 decomposition, although how local assemblages are responding to climate change and
34 whether these changes may have consequences to ecosystem functioning is less clear.
35 Previous studies have revealed that a continued environmental stress may result in poorer
36 communities by filtering out the most sensitive species. However, these experiments have
37 rarely been applied to climate change factors combining multi-year and multi-site
38 standardized field treatments across climatically contrasting regions, which has limited
39 drawing general conclusions. Moreover, other facets of biodiversity such as functional and
40 phylogenetic diversity, potentially more closely linked to ecosystem functioning, have been
41 largely neglected. Here, we report that the abundance, species richness, phylogenetic
42 diversity and functional richness of springtails (Subclass Collembola), a major group of
43 fungivores and detritivores, decreased within four years of experimental drought across six
44 European shrublands. The loss of phylogenetic and functional richness were higher than
45 expected by the loss of species richness, leading to communities of phylogenetically similar
46 species sharing evolutionary conserved traits. Additionally, despite the great climatic
47 differences among study sites, we found that taxonomic, phylogenetic and functional richness
48 of springtail communities alone were able to explain up to 30% of the variation in annual
49 decomposition rates. Altogether, our results suggest that the forecasted reductions in
50 precipitation associated with climate change may erode springtail communities and likely
51 other drought-sensitive soil invertebrates, thereby retarding litter decomposition and nutrient
52 cycling in ecosystems.

53

54 *Keywords:* Biodiversity-Ecosystem Functioning, Climate Change, Collembola, Drought,
55 Litter Decomposition, Shrublands, Soil Fauna

56 **Introduction**

57 Climate change is considered a major threat for biodiversity (Urban, 2015), potentially
58 eroding biological communities and altering their fundamental functions (Peñuelas et al.,
59 2013). Ecological theory predicts that a continued stress, such as increased drought and
60 warming, may result in poorer assemblages by filtering out the most sensitive species (Chase,
61 2007), either because the new abiotic regime precludes their population growth (strict
62 environmental filtering) or because it decreases their competitive performance (Cadotte &
63 Tucker, 2017; Kraft et al., 2015). By selectively removing species with traits poorly fitted to
64 the new environmental conditions, an enduring stress might also erode functional richness
65 and even cause a shift in the occupation of the functional space (Mouillot, Graham, Villéger,
66 Mason, & Bellwood, 2013). If the functional traits that provide sensitivity to the stress are
67 phylogenetically conserved, then these sustained environmental pressures might also result in
68 simplified communities populated by closely-related species (Helmus et al., 2010). Since
69 fundamental processes such as productivity and decomposition are functionally linked with
70 community properties like taxonomic, phylogenetic and functional richness (Hooper et al.,
71 2012; Kardol, Fanin, & Wardle, 2018; Tilman, Isbell, & Cowles, 2014), these climate change
72 impacts on biological diversity may have important consequences on ecosystem functioning
73 and thus on nutrient cycling.

74 Despite the growing concern over the effects of climate change on biological communities, it
75 is still uncertain how biodiversity will respond by the rise of temperatures and the increase in
76 the frequency and severity of droughts. Most previous research has examined shifts in species
77 abundance and richness, generally finding evidence for declines (Urban, 2015). However,
78 there has been a disproportionate focus on aboveground communities, particularly vertebrates
79 and plants, overlooking that belowground thrives an extremely rich diversity of soil

80 invertebrates that are key for ecosystem functioning and are at high risk (Bardgett & van der
81 Putten, 2014; Eisenhauer, Bonn, & A. Guerra, 2019). Moreover, it is increasingly appreciated
82 that changes in species abundance and richness provide an incomplete picture of the
83 connection between biodiversity and ecosystem functioning because they may be lost at
84 different rates than functional and phylogenetic diversity (Tilman et al., 2014). Because
85 anticipation of responses is the basis to build realistic biodiversity scenarios, these gaps in
86 knowledge limit our ability to develop conservation efforts and future planning to mitigate
87 the impact of climate change.

88 Here, we investigate changes in springtail communities (Subclass Collembola) in response to
89 climate manipulations in a standardized field experiment replicated at six natural shrubland
90 sites across Europe (Fig. 1; Table 1). Although logistically challenging, combining multi-year
91 and multi-site standardized field experimental approaches across climatically contrasting
92 regions is crucial to draw conclusions that are realistic and apply across large regions (Kröel-
93 Dulay et al., 2015). Springtails are a highly diverse and abundant group of soil fauna
94 involved in many key ecosystem functions such as leaf-litter decomposition and nutrient
95 cycling (Bardgett & van der Putten, 2014; Filser et al., 2016; Handa et al., 2014).

96 Notwithstanding, our current knowledge of whether and how their phylogenetic and
97 functional diversity will be altered by climate change is still poor despite recent advances
98 with some biodiversity metrics and in particular ecosystem types (Alatalo, Jägerbrand, &
99 Čuchta, 2015; Blankinship, Niklaus, & Hungate, 2011; Holmstrup et al., 2013, 2017, 2018;
100 Kardol, Reynolds, Norby, & Classen, 2011; Lindberg, Bengtsson, & Persson, 2002;
101 Makkonen et al., 2011; Petersen, 2011). To simulate climate change, we applied two types of
102 treatments on natural vegetation plots: 1) a drought treatment, using transparent plastic
103 coverings during rain events to decrease rainfall; and 2) a warming treatment, increasing heat
104 retention by means of reflective curtains extended between sunset and sunrise throughout the

105 year. At each study site, these treatments were replicated in three randomly selected plots,
106 and compared to three adjacent control plots with the same scaffolding but no treatment.
107 Between 1 to 4 years since the onset of the climate manipulations, springtail communities
108 were comprehensively sampled from topsoil as well as soil and vegetation surface. To
109 investigate how our warming and drought treatments affected taxonomic, phylogenetic and
110 functional richness, we identified all recorded specimens to the species level, reconstructed
111 their phylogenetic relationships with two molecular markers, and compiled published
112 information on 28 relevant functional traits. As diversity loss may alter ecosystem
113 functioning (Hooper et al., 2012; Kardol et al., 2018; Tilman et al., 2014), we also assessed
114 rates of decomposition by means of a simultaneous litterbag experiment with leaf-litter of the
115 dominant local plant species, and tested whether variation in this key ecosystem function
116 correlated with these newly gathered biodiversity measures. We hypothesized that warming
117 and drought treatments would reduce springtail abundance as well as taxonomic,
118 phylogenetic and functional richness of springtail assemblages. Additionally, if the traits
119 analyzed are phylogenetically conserved, and the phylogenetic structure of springtail
120 communities in warmed and dried plots is relatively clustered compared to those in control
121 plots, this could suggest a non-random loss of springtail species. Finally, springtails are
122 involved in leaf-litter decomposition through multiple direct and indirect mechanisms (Filser
123 et al., 2016). However, to the best of our knowledge, direct assessments of the relationship
124 between springtail richness and decomposition are lacking. Therefore, we hypothesized that
125 if there is a diversity-decomposition relationship and springtails are to some extent a good
126 proxy of soil biodiversity, then we should find significant correlations between local
127 springtail richness and the rates of leaf-litter decomposition.

128 **Materials and Methods**

129 **Study sites.** The six shrublands studied comprised most of the broad-scale European climatic
 130 regions (Fig. 1). Mean annual temperature (MAT) at the sites ranged from 7.4 to 16.1 °C, and
 131 mean annual precipitation (MAP) ranged from 544 to 1263 mm (Table 1). The major types of
 132 shrubland present in temperate Europe were included: Atlantic heathland (UK - United
 133 Kingdom, NL - The Netherlands, DK - Denmark), continental forest steppe (HU - Hungary),
 134 and Mediterranean garriga/machia (SP - Spain and IT - Italy). The sites were established in
 135 1998 (UK, NL, DK, and SP) and 2001 (HU and IT). Climatic data were recorded in the
 136 control plots to obtain the characteristics of each experimental site (Table 1).

137 Figure 1 Location of the climatic manipulation experiments in Europe. Arrows depict broad-
 138 scale gradients of temperature and precipitation. DK, Denmark; HU, Hungary; IT, Italy; NL,
 139 The Netherlands; SP, Spain; UK, United Kingdom.

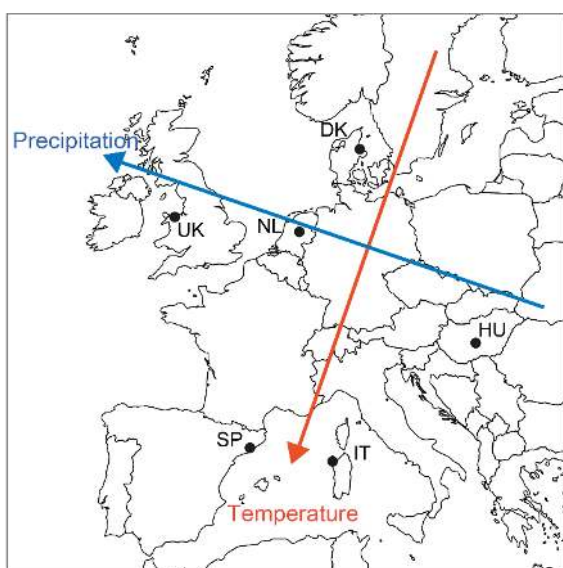


Table 1. Characteristics of the study sites.

Site code	UK	NL	DK	HU	SP	IT
Country	United Kingdom	The Netherlands	Denmark	Hungary	Spain	Italy
Site name	Clocaenog	Oldebroek	Mols	Kiskunság	Garraf	Capo Caccia
Coordinates	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

Soil type (FAO)	Peaty Podzol	Haplic Arenosol	Sandy Podzol	Calcaric Arenosol	Petrocalcic Calcixerept	Luvisol and Leptosol
MAT (°C)	7.4	8.9	8.7	10.5	15.2	16.1
MAP (mm)	1263	1005	669	558	559	544
Growing season	April-September	April-October	April-September	April-September	January-May October-December	January-May October-December
Dominant species	<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).

Growing season refers to the period of vegetation growth.

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

140

141 **Experimental climatic manipulations.** In each study site, we defined nine 20-m² plots
142 divided in three blocks and randomly assigned one plot at each block to 1) drought treatment,
143 2) warming treatment or 3) control. Drought plots were covered with a transparent plastic
144 roof during rain events in a pre-specified experimental drought period. The roof was
145 automatically withdrawn after the rain, thus avoiding any warming effect (Beier et al., 2004).
146 Warming plots were covered with reflective curtains between sunset and sunrise throughout
147 the year, inducing a passive night-time warming (Beier et al., 2004, see picture S1 at the
148 Supporting Information). All experimental methods to manipulate climate have specific
149 strengths and weaknesses due to their particular unrealistic and/or unintended effects (Beier
150 et al., 2004; Harte et al., 1995). Notwithstanding, a comparison of different passive and active
151 experimental warming methods concluded that passive night time warming is among the
152 most realistic and applicable (Aronson & McNulty, 2009), agreeing with evidence in the
153 ongoing global warming that there is a higher rate of heating during the night (Alward,
154 Detling, & Milchunas, 1999). Warming obtained with this method is greatest at night, but
155 there is also some carry-over effect during the day (Bruhn et al., 2013). Control plots were
156 equipped with the same metallic scaffolding but no treatment was applied (cf. Harte et al.,
157 1995). While the same technology was used for the climatic manipulations (warming,

158 drought, control) at each study site, timing and duration of the experimental drought were
 159 adjusted to the local conditions according to climatic predictions (Table 2).

160

Table 2. Experimental manipulations at the study sites.

Site code	UK	NL	DK	HU	SP	IT
Start of the experiment (pre-treatment year)	1998	1998	1998	2001	1998	2001
First treatment year	1999	1999	1999	2002	1999	2002
Drought*						
Timing	May- September	May-August	May-July	May-June	May-June October-Nov.	April-October
Precipitation excluded (% of Control, yearly total)	-25	-19	-18	-22	-49	-16
Reduction in soil moisture (% of Control, 0-20 cm)	-45	-43	-41	-23	-28	-27
Warming**						
Timing	Year-round	Year-round	Year-round	Year-round	Year-round	Year-round
Increase in MAT (C)	0.2	0.3	0.9	0.4	0.6	0.4
Increase air temperature (C) (month of fauna sampling)	+1.4	+1.0	+1.0	+0.9	+0.9	+0.5

DK, Denmark; HU, Hungary; IT, Italy; MAT, mean annual temperature; NL, Netherlands; SP, Spain; UK, United Kingdom.

*Drought treatment effects are average changes for the sampling year (2003).

**Increase in MAT are averages during the 1998-2012 period (Kröel-Dulay et al., 2015) and the increase of air temperature refer to the sampling year (2003).

161

162 **Taxon sampling.** Springtails (Subclass Collembola) were sampled from April to July 2003
 163 sequentially (i.e. IT, SP, HU, DK, NL and UK) to equalize mean temperatures across sites
 164 (Petersen, 2011). Five quadrats (1.25 m² each) representative of the most dominant plant
 165 species were selected within each experimental plot. Springtails from vegetation were
 166 suctioned with an adapted vacuum cleaner connected to a fauna trap. Specimens dropped
 167 were recovered through polythene boxes with aqueous benzoic acid placed beneath the
 168 plants. Ground-dwelling springtails were also suctioned with the same method for the same
 169 area and, subsequently, 10-cm deep soil cores with a surface of 25 cm² were taken to the lab
 170 to recover springtails from the soil through high-gradient extraction (10 days of gradually
 171 increasing temperature from 25 to 60°C, Gjelstrup & Petersen, 1987). The sampling methods
 172 were slightly adapted in the UK and IT due to an excess of soil moisture and stones,
 173 respectively (see Petersen, 2011). Once extracted and sorted, springtails were conserved in

174 glycerol and identified to the species level following references cited in (Petersen, 2011).
175 Some dubious specimens were kindly revised by Drs. L. Dányí, R. Jordana and E. Mateos.
176 This sampling resulted in 19641 springtail specimens that were classified into 102 species-
177 level entities (Table S7). An initial assessment of these data can be found in Petersen (2011)
178 and the specimens are deposited in his personal collection.

179 **Phylogenetic data.** The phylogeny of springtails was constructed with sequence data of two
180 genes (*cox1* and *28s*), obtained from public repositories (Table S7). The tree obtained was
181 consistent with previous systematic works integrating molecular and morphological
182 information (Yu et al., 2016). See figure S4 and supplementary methods for a detailed
183 description about the procedures.

184 **Trait data.** We obtained data of 28 traits for the 64 species that were present in our study
185 sites from the ColTrait database (Salmon & Ponge, 2012). This springtail database is the
186 most comprehensive to date and the traits collated encompass different dimensions of
187 ecological and functional niche (Table S8), including abiotic components of habitat (e.g.
188 preferred strata, temperature and precipitation range), dispersal ability (e.g. locomotory
189 appendages, furcula), features involved in biotic interactions (e.g. specific sensory organs and
190 defensive features) and life history strategies (e.g. parthenogenetic, sexual or mixed). These
191 traits have shown high potential to explain springtails distribution and community
192 composition (Salmon et al., 2014; Salmon & Ponge, 2012).

193 **Litterbag decomposition experiment.** Leaf litter from the dominant ericaceous plant species
194 at each site (i.e. *Calluna vulgaris* and *Erica vulgaris*, Table 1) was collected in DK, NL, UK
195 and SP between September-November 1999. After air drying and sorting to obtain
196 homogeneous samples, 3 g of dried leaves and shoots were placed in nylon bags with a mesh
197 size of 1 mm for *Calluna vulgaris* and 0.71 mm for *Erica vulgaris* due to the smaller size of

198 the leaves of this species. This protocol allows the entrance of medium-sized decomposers,
199 including all juveniles and the adults of almost all springtail species as well as other
200 invertebrate fauna (Handa et al., 2014). The bags were incubated over a period of 2 years
201 divided in 10-12 time-periods. Three replicates for each time-period were placed either
202 randomly (UK), beneath *Calluna* plants (DK), stratified beneath *Calluna* plants and open
203 areas (NL) or beneath *Erica* plants (SP) due to the specific characteristics of vegetation cover
204 at each site. Litterbags were then sequentially retrieved and sorted to remove non-target
205 material and then oven-dried. We calculated the annual decomposition rates as the annual
206 fractional weight loss (k) for each plot using the following equation: $M_t = M_o \cdot e^{-kt}$, where
207 M_t is leaf-litter mass loss at time t and M_o is the initial mass (Emmett et al., 2004). HU and IT
208 were not included in the litterbag experiment due to the delay in the onset of the climatic
209 manipulations in both sites (Table 2). A previous analysis of these decomposition experiment
210 can be found in Emmett *et al.* (2004).

211 **Data analysis.** All metric estimations and statistical analyses we describe here were carried
212 out with R v3.4.3 (R Core Team, 2016). To assess if taxonomic, phylogenetic and functional
213 trait-based dimensions of springtail richness responded in the same way to experimental
214 climate change treatments, we characterized springtail assemblages in terms of: (i) abundance
215 (total number of individuals of all species per plot); (ii) species richness (SR, number of
216 species per plot); (iii) Faith's phylogenetic diversity index (PD, sum of branch lengths
217 connecting all species in an assemblage (Faith, 1992)); (iv) mean neighbor taxon distance
218 (MNTD, mean phylogenetic shortest distance for each species from an assemblage (Kembel
219 et al., 2010)); (v) variance in nearest taxonomic distance (VNTD, variance of phylogenetic
220 shortest distance for each species from the distance matrix of an assemblage (Tucker et al.,
221 2016)); (vi) functional richness (FR, the multidimensional volume occupied by all species in
222 an assemblage within a functional space, where the axes are functional traits along which

223 species placed according to their trait values (Mouillot et al., 2013; Villéger, Mason, &
224 Mouillot, 2008)); (vii) functional divergence (FD, divergence in the distribution of abundance
225 within the volume or functional space occupied by a community (Villéger et al., 2008)); and
226 (viii) functional evenness (FE, regularity in the distribution of abundance within the volume
227 or functional space occupied by a community (Villéger et al., 2008)). These metrics were
228 selected following the framework proposed by Tucker et al. (Tucker et al., 2016; Tucker,
229 Davies, Cadotte, & Pearse, 2018), according to which PD *vs* FR, MNTD *vs* FD and VNTD *vs*
230 FE are phylogenetic and functional equivalent indices associated to richness (i.e. the sum of
231 accumulated phylogenetic and functional differences among taxa in an assemblage),
232 divergence (i.e. the mean phylogenetic and functional relatedness among taxa in an
233 assemblage), and regularity (i.e. the variance in differences among taxa, representing how
234 regular are the phylogenetic and functional differences between taxa in an assemblage)
235 dimensions of biological communities, respectively.

236 Metrics for the phylogenetic community structure were calculated with the package *picante*
237 (Kembel et al., 2010) using the reference ML-Bayesian consensus phylogeny. To account for
238 baseline differences in species richness among sites and treatments, we standardized
239 phylogenetic measures against 999 community randomizations using ‘richness’ and
240 ‘independent swap’ as null model specifications, i.e. constraining the randomized
241 communities only to observed species richness or also to the frequency of species occurrence.
242 This was done by means of the built-in functions ‘ses.pd’ and ‘ses.mntd’ and with a modified
243 version of the latter for VNTD. The standardized effect size was then calculated as the
244 difference between the value observed in the community and the mean value of the null
245 communities divided by the standard deviation of the distances in the null data. The same
246 approach was applied to FR, FD and FE, which were calculated with the package *FD*
247 (Laliberte & Legendre, 2010) and standardized with our own script applying the same

248 constraints as with PD, MNTD and VNTD. Additionally, we estimated the phylogenetic
249 signal of trait data, i.e. the correlation between trait similarity and species' evolutionary
250 distance. We used the D-statistic and Pagel's λ for discrete and continuous traits, respectively
251 (Fritz & Purvis, 2010; Pagel, 1999) through the packages *caper* and *phylosig* (Orme, 2013;
252 Revell, 2012). Values near or below 0 and close to 1 mean strong phylogenetic signal for the
253 D-statistic and for Pagel's λ , respectively. The existence of phylogenetic signal suggests that
254 ecological similarity is linked to phylogenetic relatedness (Losos, 2008).

255 We investigated how taxonomic, phylogenetic and functional metrics of springtail
256 assemblages changed due to climatic manipulation by means of linear mixed-effects models,
257 as implemented in the R-package *lme4* (Bates, Mächler, Bolker, & Walker, 2014). Our
258 response variables (i.e. each of the above diversity metrics estimated at a community level)
259 were modelled separately as a function of the experimental treatments (coded as a fixed
260 effect) and study site (coded as a random intercept factor to cope with the heterogeneity in
261 abiotic conditions across sites.). We estimated the *P*-values for fixed-effects by means of a
262 Satterthwaite approximation to the number of degrees of freedom with *lmerTest* (Kuznetsova,
263 Brockhoff, & Christensen, 2018). To assess for potential interactions between the effect of
264 climatic treatments and sites, we also built models where site, treatment and their interactions
265 were included as fixed-effects terms. We used variation in second-order Akaike's
266 Information Criterion ($\Delta AICc$), marginal and conditional coefficients of determination (R^2_m
267 and R^2_c) and residuals diagnostic plots to compare model performance and assess model
268 assumptions. For visualization, the observed changes in abundance, SR, PD and FR are
269 represented as proportions relative to control plots (Emmett et al., 2004). Additionally, to
270 validate the consistency of the community patterns detected, we carried out a series of
271 sensitivity analyses. First, to discard that SR differences were only due to variation in
272 abundance, we repeated the analyses with SR estimated after rarefying communities to

273 median, first and third quartile of the observed abundance. Second, since we did not have
274 molecular and trait information for all the species pool, we assessed the potential effect of
275 missing species repeating all the analyses restricting the community datasets to only those
276 species present in the phylogeny and to only those with trait data available. Third, the
277 reconstruction of the phylogenetic relationships of a given set of species necessarily implies a
278 degree of uncertainty around the topology, and thereby of the derived metrics extracted from
279 the trees. Hence, to assess the effect of phylogenetic uncertainty we iterated all the preceding
280 phylogenetic measures and the corresponding linear models with 1000 trees drawn from the
281 Bayesian posterior distribution.

282 Finally, we tested if our climate manipulations affected annual decomposition rates and
283 whether the richness of springtail communities correlated with this key ecosystem function
284 using linear mixed-effects models. Rather than trying to establish purely causal relationships,
285 which is not possible with the design of our litterbag experiment, we aimed to assess the
286 predictive power of springtail richness over litter decomposition, that is the amount of
287 variance in litter decomposition that each richness metric is able to explain. So, we built
288 different models with decomposition rate as response variable varying the inclusion of
289 climate manipulation treatments, SR, PD and FR and their interaction as fixed effect terms.
290 We additionally tested if these models differed when site was included as a random intercept
291 term (i.e. the variation in large-scale abiotic conditions across sites may determine different
292 baseline rates of decomposition), or additionally, by letting each covariate (SR, PD and FR)
293 have a random slope correlated with each site (group) intercept (i.e. the potential diversity-
294 function relationship may differ between sites due to the contrasting abiotic conditions). The
295 inclusion of site as a random intercept term allowed to cope with the heterogeneity in abiotic
296 conditions across sites. By letting each covariate (i.e. SR, PD and FR) to have a different
297 slope at each site, the model also accounted for the possibility that the same large-scale

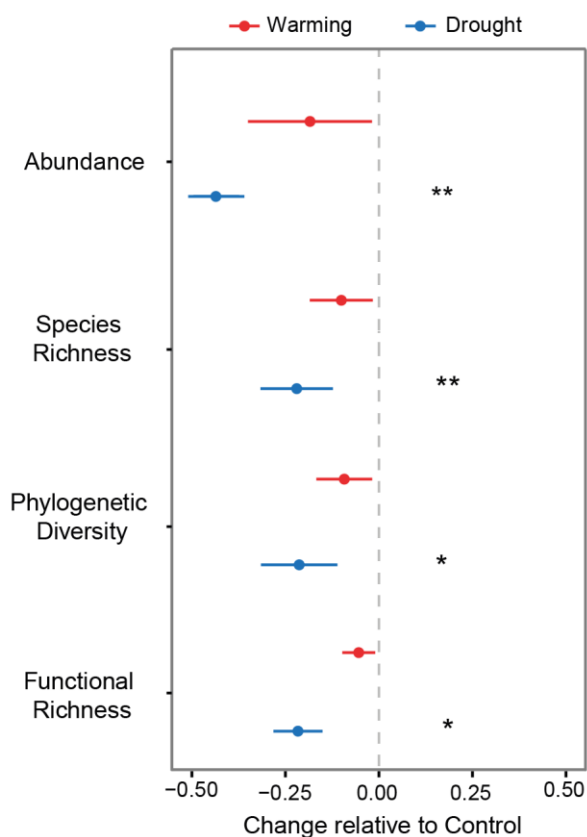
298 abiotic controls may modulate the potential relationship between local richness-related
299 metrics with decomposition. See Bradford et al. for a similar analytical approach (Bradford et
300 al., 2014). To assess these distinct model structures, we compared both types of models by
301 means of likelihood ratio tests and evaluated their predictive ability through R^2_m and R^2_c with
302 the package *MuMIn* (Barton, 2018), which capture the explanatory power of both fixed and
303 random terms. We estimated P -values for the fixed terms through a Satterthwaite
304 approximation to the number of degrees of freedom and used residuals diagnostic plots to
305 assess model performance and assumptions. For model visualization we used the *visreg*
306 package, which allows to plot best-fitted models focusing on the variables of interest and
307 holding the other factors constant (i.e. partial residuals regression plots) (Breheny &
308 Burchett, 2016).

309 **Results**

310 The experimentally warmed plots did not differ from the control plots in any of the diversity
311 metrics, despite an average increase of 0.43°C in mean annual temperature (MAT, Table 2 and
312 Table S1). In contrast, the drought treatment, which on average reduced annual precipitation
313 by 22% and soil moisture by 36%, considerably altered springtail communities. This resulted
314 in a decline on average of $22 \pm 10\%$ (mean ± 1 standard error, hereinafter) of the species
315 richness compared to control plots ($P < 0.01$; Fig. 2). The drought treatment also reduced on
316 average $44 \pm 7\%$ the number of springtails per plot ($P < 0.01$; Fig. 2), raising the possibility
317 that the observed species loss was a random consequence of a community downsizing.
318 However, the decline of species richness with the drought was consistent even when
319 communities were rarefied to equalize total abundances (always $P < 0.05$ when rarefied to
320 median, first and third quartile, see Table S2). The ‘drought effect’ on both abundance and

321 species richness was also robust to the exclusion of species for which no information was
322 available on functional traits and/or phylogenetic relationships (Table S2).

323 Figure 2 Change of springtail communities in response to climatic manipulation. We used
324 linear mixed-effects models to assess the change of springtail communities after 1 to 4 years
325 of drought and warming in an experiment replicated at six sites across Europe. Values are
326 treatment means \pm 1 standard error. Phylogenetic diversity and functional richness are based
327 on standardized measures using community randomizations (see text for further details).
328 Asterisks denote statistically significant differences of drought communities relative to control:
329 * $P < 0.05$; ** $P < 0.01$.



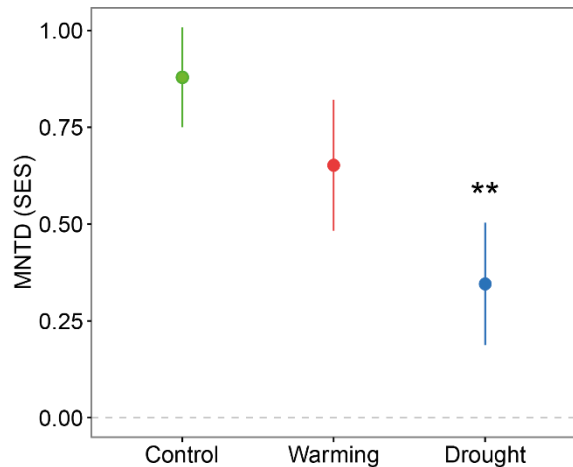
330
331 In parallel to the loss of species, the drought plots exhibited significant reductions in
332 phylogenetic diversity and functional richness compared to control plots ($P < 0.05$; Fig. 2).
333 Both metrics are known to decrease with species loss, a pattern also detected in our analyses.

334 However, the standardized effect sizes of phylogenetic diversity and functional richness were
335 still significantly lower in drought plots than in control plots ($P < 0.05$; Table S1), indicating
336 that the reduction did not only reflect a decline in species richness. Although the study sites
337 largely differed in species composition due to their large geographic spread and broad-scale
338 climatic gradients, the local drought-induced responses were remarkably consistent across
339 regions (Fig. S1).

340 The drought treatment eroded the phylogenetic and functional richness of springtail
341 assemblages apparently without important shifts in the distribution of species abundances or
342 in the regularity of these abundances within the functional trait space. Indeed, functional
343 evenness and divergence showed no sign of change in springtail communities exposed to
344 climatic manipulations (Table S1). However, the species persisting the drought were on
345 average more closely related to each other than expected by chance (Fig. 3 and Table S1).
346 This pattern was robust to phylogenetic uncertainty and the type of null model used for
347 community randomizations (Fig. S2 and Table S3), and it also exhibited a remarkable
348 consistency across study sites (Fig. S1). It is also important to note that almost all springtail
349 traits studied here were strongly phylogenetically conserved (Table S4), which imply that
350 phylogenetic distance is to some extent related with trait distance between springtail species.

351 Figure 3 Change in the phylogenetic structure of springtail communities in response to climatic
352 manipulations. We used linear mixed-effects models to evaluate the change on the
353 phylogenetic structure of springtail communities after 1 to 4 years of experimental drought and
354 warming. Values are treatment means \pm 1 standard error of the standardized effect size (SES)
355 of the mean neighbor taxon distance (MNTD). Lower MNTD values denote communities
356 populated by species more closely related. Asterisks denote significantly lower MNTD values
357 in drought communities relative to control: ** $P < 0.01$.

358

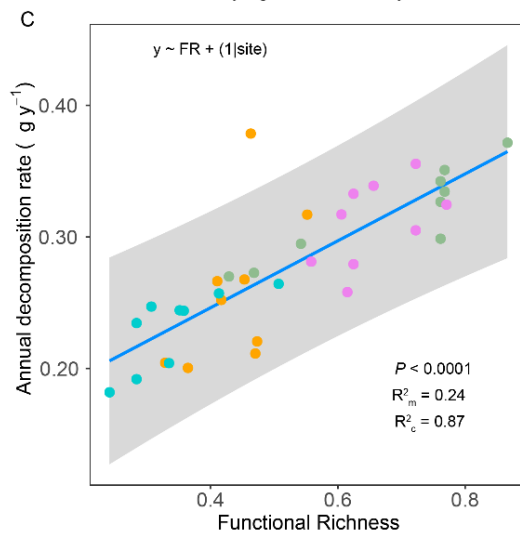
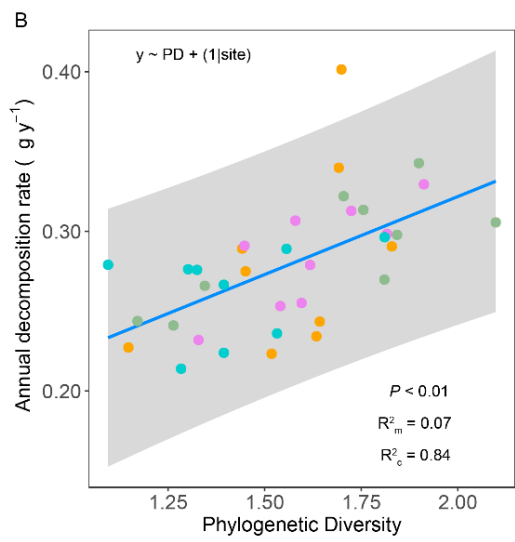
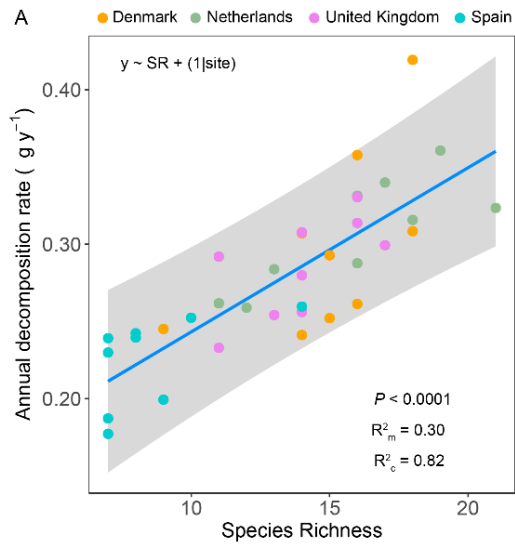


359

360 The loss of biodiversity due to drought might, if sustained, amplify the consequences of
361 climate change to leaf-litter decomposition, a process in which springtails are known to play
362 an important role (Bardgett & van der Putten, 2014; Handa et al., 2014). Consistent with this
363 possibility, taxonomic, phylogenetic and functional richness-related metrics all showed
364 highly significant correlations with annual decomposition rates (Fig. 4 and Table S5a and
365 5b): The greater the richness of the local springtail community, the higher the rate of leaf-
366 litter decomposition. The strength of this association was fundamentally regular across sites
367 irrespective of the random effects structure included in the models (Table S6), and it was
368 particularly high for taxonomic and functional richness (Fig. 4 and Table S5a and 5b).
369 When comparing the effect of climatic manipulations between treated and control plots the
370 changes in leaf-litter decomposition were rather modest (Fig. S3). Litterbags in drought plots
371 were decomposed at slightly lower rates on average whereas in warmed plots decomposition
372 was marginally accelerated (-3.5 in drought versus +2.6 g y⁻¹ in warming, with associated *P*-
373 values < 0.05 and < 0.1 compared to control plots, Fig. S3 and Table S5). Although
374 moderate, these effects were consistent despite the great among-site variation in annual
375 decomposition rates (the variance explained by the model increased from 0.07 up to 0.89
376 when including sites' random intercept effect, Fig. S3 and Table S5), mirroring the broad-
377 scale gradients in abiotic conditions across Europe (Fig. 1 and Table 1). When taxonomic,

378 phylogenetic or functional richness of the springtail community were accommodated as
379 covariates in their respective models (Fig. S3 and Table S5), the effects of the climatic
380 manipulations turned out non-significant masked by the effects of the local springtail richness
381 metrics.

382 Figure 4 Relationships between annual rates of leaf-litter decomposition and species richness
383 (A), phylogenetic diversity (B) and functional richness (C) of springtail communities across
384 Europe. We used linear mixed-effects models to assess the correlations allowing each site to
385 have its own random intercept to capture large-scale climatic differences among sites. We
386 used marginal and conditional coefficients of determination (R^2_m and R^2_c) to assess the
387 predictive ability of fixed alone and fixed + random terms, respectively. Partial residuals
388 regression plots of the best-fitted models show the relationships between response and
389 explanatory variables holding the random term constant.



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392

393 **Discussion**

394 Our experiment replicated on a large-scale showed that the number of species and the size of
395 the communities of springtails declined within four years of simulating the drought induced
396 by climate change. Similar declines in both abundance and species richness of soil fauna after
397 experimental droughts have also been documented in arctic and temperate ecosystems
398 (Kardol et al., 2011; Lindberg et al., 2002; Makkonen et al., 2011), although in some cases
399 the response was rather weak (Eisenhauer, Cesarz, Koller, Worm, & Reich, 2012; Holmstrup
400 et al., 2013). Our results, however, extend these previous findings in three important
401 directions. We first demonstrate that the richness contraction after drought was
402 fundamentally consistent across climatically contrasting sites, thereby generalizing at a
403 continental scale the effects of climate change upon a major soil animal group. The
404 robustness of the results is remarkable considering the notable differences in springtail
405 diversity found across the study sites.

406 Second, we provide evidence that drought not only reduced species richness (Petersen, 2011)
407 but also caused a disproportionate loss of phylogenetic diversity, resulting in increasingly
408 phylogenetically clustered springtail assemblages. A continued stress is expected to increase
409 the phylogenetic similarity of species in a community whenever their sensitivity to a
410 particular environmental factor is phylogenetically conserved (Helmus et al., 2010).

411 Accumulating evidence suggests that species filtering by stress disturbance, like sustained
412 drought, is partly driven by species' traits (Chase, 2007; Mouillot et al., 2013). However, it is
413 yet unclear whether the changes in phylogenetic structure arise from strict environmental
414 filtering, from a modification of species' competitive performance due to the new abiotic
415 regime, or from a combination of both processes (Cadotte & Tucker, 2017; Kraft et al.,
416 2015).

417 Finally, we report that the drought-induced impoverishment of springtail communities also
418 resulted in a fast reduction of the overall functional trait space. Again, according to
419 community randomizations the decline was higher than simply expected by the loss of
420 species. The drought eroded the phylogenetic and functional richness of springtail
421 assemblages apparently without important shifts in functional evenness and divergence. This
422 result may reflect that our trait dataset did not fully capture those features more associated to
423 drought sensitivity in Collembola. Further research, perhaps including phenological and
424 trophic characteristics, should allow to establish the linkages between particular traits, the
425 environment and the functions performed by springtails as well as other groups of soil
426 invertebrates (Pey et al., 2014).

427 In addition to providing evidence for a non-random drought-induced attrition of a major soil
428 fauna group, our results also warn over the possibility that diversity loss due to climate
429 change may have a negative amplifying consequence to ecosystem functioning (Peñuelas et
430 al., 2013). Our experiments yielded clear evidence that the annual rate of leaf-litter
431 decomposition, a key ecosystem process in which springtails are involved through multiple
432 direct and indirect mechanisms (Filser et al., 2016), increases with their taxonomic,
433 phylogenetic and functional richness, a relationship that deserves attention beyond a purely
434 phenomenological consideration. Certainly, most of the variation in decomposition was
435 associated with differences among our study sites likely caused by the great disparity in
436 temperature and soil moisture regime along the broad environmental gradient included
437 (Emmett et al., 2004; Reinsch et al., 2017). This highlights the importance of large-scale
438 abiotic controls on leaf-litter decomposition (García-Palacios, Maestre, Kattge, & Wall,
439 2013). However, the fact that up to 30% of the variation in annual decomposition rates was
440 explained by local variation in taxonomic phylogenetic and functional richness of springtails
441 underscores the role of soil fauna modulating the effect of these large-scale abiotic factors

442 (García-Palacios et al., 2013; Handa et al., 2014). In fact, recent estimations pinpoint that
443 invertebrates enhance leaf-litter decomposition by 37% at a global scale (García-Palacios et
444 al., 2013), which implies that reducing its functional diversity will necessarily lessen the
445 cycling of carbon and nitrogen in terrestrial and aquatic ecosystems (Handa et al., 2014). But
446 additionally, these results provide further evidence that local-scale biotic factors can reach a
447 great explanatory power, so that they must be explicitly incorporated in Earth-system models
448 if we are to adequately forecast how decomposition will respond to climate change at a global
449 scale (Bradford et al., 2014, 2017).

450 Although we cannot deduce a specific mechanistic explanation, the association between the
451 richness of local springtail communities and the rates of litter decomposition reported here
452 may have a causal origin. Generally, higher biodiversity levels enhance interspecific
453 complementarity and nutrient-cycling feedbacks that increase nutrient stores and supply rates
454 over the long term throughout food-webs (Tilman et al., 2014). So, springtails could be a
455 reliable proxy of soil biodiversity particularly sensitive to increasingly drying conditions
456 (Holmstrup et al., 2018; Kærsgaard, Holmstrup, Malte, & Bayley, 2004). Additionally, it is
457 possible that drought treatments have also affected other decomposers besides springtails.
458 Indeed, previous work has shown declines associated with droughts in a variety of
459 decomposers, including microbial communities (Sowerby et al., 2005; Yuste et al., 2011),
460 enchytraeid earthworms and oribatid mites (Holmstrup et al., 2012; Lindberg et al., 2002), as
461 well as in fungivorous springtails and other invertebrates known to top-down regulate
462 microbial communities (Crowther, Boddy, & Jones, 2011). Therefore, the observed
463 contraction of springtail richness may represent the effect of drought throughout the entire
464 detritus-based food web. Moreover, increasingly warmer and drier conditions may reduce
465 feeding of soil detritivores (Thakur et al., 2018), amplifying the effects of the treatments on
466 decomposition rates through a drop in soil fauna activity. Future experiments that

467 simultaneously manipulate species richness and environmental factors concurrently are
468 therefore warranted to disentangle the relative importance of biotic and abiotic factors in litter
469 decomposition (Boyero, Cardinale, Bastian, & Pearson, 2014).

470 The community shifts in springtail assemblages induced by drought contrast with the general
471 lack of effects of the warming treatment. The interaction between experimental warming and
472 soil moisture are long known (Harte et al., 1995). Likely, the intensity of the warming applied
473 was moderate not only for collembolans (although see Petersen, 2011, for a further discussion
474 on the modest warming effects found in some of the sites), but also for plant communities
475 and ecosystem functions like net primary productivity and respiration, which were also rather
476 insensitive to the warming treatment (Kröel-Dulay et al., 2015; Reinsch et al., 2017). The
477 night-time warming treatment resulted in a moderate increase of MAT (range 0.2-0.9 K,
478 Table 2), which matches past changes recorded at a multi-decadal (50 years) time scale
479 (Christensen et al., 2007). Recent findings have nonetheless revealed that springtails, and in
480 general soil fauna, may be quite resistant to increases in temperature (Alatalo et al., 2015;
481 Holmstrup et al., 2017, 2018). Moreover, a recent meta-analysis has identified reduced
482 precipitation as the most threatening global change driver to soil biodiversity (Blankinship et
483 al., 2011) because many soil invertebrates, like springtails, are essentially freshwater
484 organisms in physiological terms (Kærsgaard et al., 2004).

485 Most of our current understanding of the responses of soil fauna to climate change comes
486 from controlled microcosm experiments with unnatural low-diversity levels (Boyero et al.,
487 2014; Cragg & Bardgett, 2001; Heemsbergen et al., 2004). Studies like ours that manipulate
488 abiotic conditions in natural communities exposed to contrasting climatic regimes are rare,
489 although they are essential to build realistic scenarios of the impact of climate change on
490 biodiversity and its consequences for ecosystem functioning. Our analyses demonstrate that

491 under such realistic conditions, climate change has a great potential to alter the abundance,
492 species richness, phylogenetic diversity and functional richness of springtail communities.
493 The analyses also suggest that these springtail declines, if sustained, may be linked to
494 reductions on litter decomposition that could dwindle nutrient cycling and ultimately the
495 productivity of terrestrial ecosystems. We cannot completely discard that the fast responses to
496 drought reported here are in part a transient state within the resilience space of natural
497 ecosystems, as within the wealth of soil organisms contributing to decomposition processes
498 some groups like oribatid mites, millipedes and isopods may be more resistant in the long-
499 term (Holmstrup et al., 2012; Maraldo et al., 2010). Likewise, it cannot be dismissed that fast
500 evolutionary adaptations could counteract increasingly stressful conditions due to climate
501 change (Hoffmann & Sgro, 2011). However, a previous study with an enchytraeid species
502 showed a limited adaptive ability to drought (Maraldo, Schmidt, Beier, & Holmstrup, 2008)
503 and on-going research suggests that this would also be the case with springtails (Kutcherov et
504 al. *unpublished*). In any case, our finding that soil biodiversity loss embraces multiple
505 biodiversity facets and is non-random with respect to functional traits supports the view that a
506 reduction in precipitation may result in a lasting attrition of springtail communities. If similar
507 effects occur in other drought-sensitive soil organisms, this may carry critical consequences
508 for ecosystem functioning such as slow-downs on litter decomposition rates.

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