

## Article (refereed) - postprint

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Peguero, Guille; Sol, Daniel; Arnedo, Miquel; Petersen, Henning; Salmon, Sandrine; Ponge, Jean-François; Maspons, Joan; Emmett, Bridget; Beier, Claus; Schmidt, Inger K.; Tietema, Albert; De Angelis, Paolo; Kovács-Láng, Edit; Kröel-Dulay, György; Estiarte, Marc; Bartrons, Mireia; Holmstrup, Martin; Janssens, Ivan A.; Peñuelas, Josep. 2019. **Fast attrition of springtail communities by experimental drought and richness-decomposition relationships across Europe.** *Global Change Biology*, 25 (8). 2727-2738.  
<https://doi.org/10.1111/gcb.14685>

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Contact CEH NORA team at  
[noraceh@ceh.ac.uk](mailto:noraceh@ceh.ac.uk)

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*

4 Guille Peguero<sup>1,2</sup>, Daniel Sol<sup>3,4</sup>, Miquel Arnedo<sup>5</sup>, Henning Petersen<sup>6</sup>, Sandrine Salmon<sup>7</sup>,  
5 Jean-François Ponge<sup>7</sup>, Joan Maspons<sup>3</sup>, Bridget Emmett<sup>8</sup>, Claus Beier<sup>9</sup>, Inger K. Schmidt<sup>9</sup>,  
6 Albert Tietema<sup>10</sup>, Paolo De Angelis<sup>11</sup>, Edit Kovács-Láng<sup>12</sup>, György Kröel-Dulay<sup>12</sup>, Marc  
7 Estiarte<sup>2,3</sup>, Mireia Bartrons<sup>2,13</sup>, Martin Holmstrup<sup>14,15</sup>, Ivan A. Janssens<sup>1</sup>, Josep Peñuelas<sup>2,3</sup>

8 <sup>1</sup> Research Group of Plant and Vegetation Ecology, Department of Biology, University of Antwerp, 2610  
9 Wilrijk, Belgium.

10 <sup>2</sup> CSIC, Global Ecology Unit CREAM-CSIC-UAB, 08913 Bellaterra, Catalonia, Spain.

11 <sup>3</sup> CREAM, 08913 Cerdanyola del Vallès, Catalonia, Spain.

12 <sup>4</sup> CSIC, 08193 Cerdanyola del Vallès, Catalonia, Spain.

13 <sup>5</sup> Department of Evolutionary Biology, Ecology and Environmental Sciences, and Biodiversity Research  
14 Institute (IRBio), Universitat de Barcelona, Avinguda Diagonal 643, 08028 Barcelona, Spain.

15 <sup>6</sup> Natural History Museum, Mols Laboratory, Strandkaervej 6-8, Femmøller, DK8400 Ebeltoft, Denmark.

16 <sup>7</sup> Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 Avenue du Petit-Château, 91800 Brunoy, France.

17 <sup>8</sup> Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor LL57 2UW, UK.

18 <sup>9</sup> Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvvej 23,  
19 1958 Frederiksberg C, Denmark.

20 <sup>10</sup> Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 94240, 1090 GE Amsterdam,  
21 The Netherlands.

22 <sup>11</sup> Department for Innovation in Biological, Agro-food and Forest systems, University of Tuscia, Via San  
23 Camillo de Lellis snc, 01100 Viterbo, Italy.

24 <sup>12</sup> Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmany u. 2-4, 2163 Vacratot,  
25 Hungary.

26 <sup>13</sup> BETA Technological Centre (Tecnio), Aquatic Ecology Group, University of Vic-Central University of  
27 Catalonia, Vic 08500, Barcelona, Spain.

28 <sup>14</sup> Department of Bioscience, Aarhus University, Silkeborg, Denmark;

29 <sup>15</sup> Aarhus Institute of Advanced Studies, Aarhus University, Aarhus C, Denmark;

30 \*Correspondence author e-mail and telephone number: [guille.peguero@gmail.com](mailto:guille.peguero@gmail.com) (+34 93 5814667)

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).

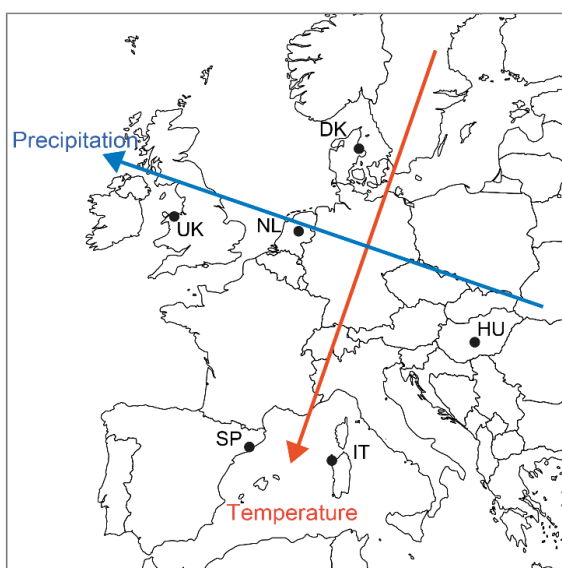
96 Notwithstanding, our current knowledge of whether and how their phylogenetic and  
97 functional diversity will be altered by climate change is still poor despite recent advances  
98 with some biodiversity metrics and in particular ecosystem types (Alatalo, Jägerbrand, &  
99 Čuchta, 2015; Blankinship, 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-m<sup>2</sup> 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 m<sup>2</sup> 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 cm<sup>2</sup> 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  $\lambda$  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  $\lambda$ , 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

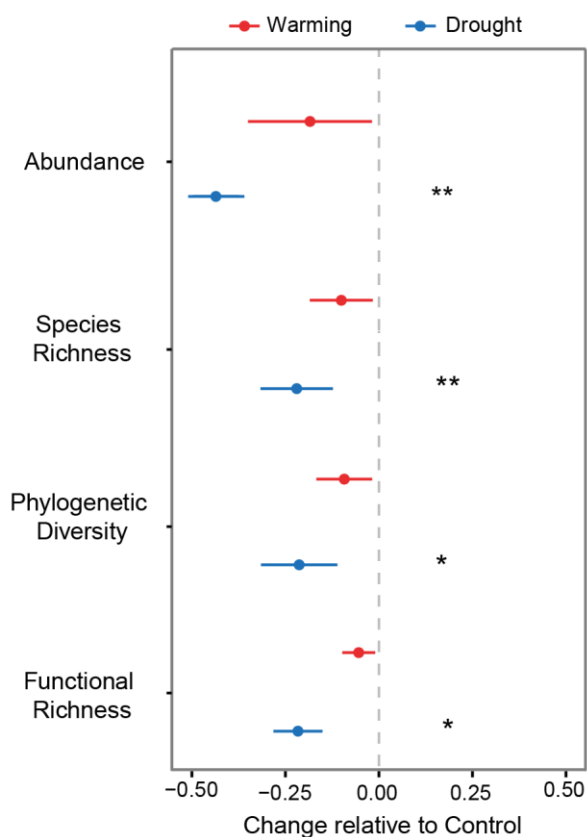
298 abiotic controls may modulate the potential relationship between local richness-related  
299 metrics with decomposition. See Bradford et al. for a similar analytical approach (Bradford et  
300 al., 2014). To assess these distinct model structures, we compared both types of models by  
301 means 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  $0.43^\circ\text{C}$  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  $\pm 1$  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.

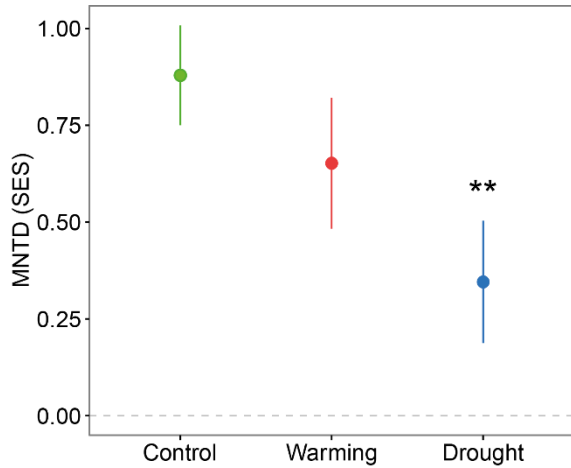


334 However, the standardized effect sizes of phylogenetic diversity and functional richness were  
335 still significantly lower in drought plots than in control plots ( $P < 0.05$ ; Table S1), indicating  
336 that the reduction did not only reflect a decline in species richness. Although the study 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



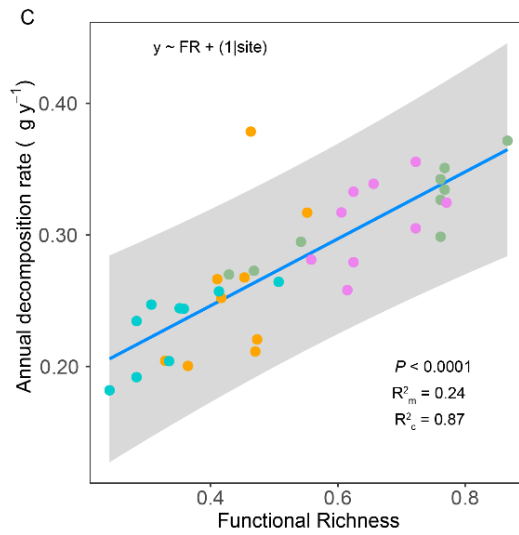
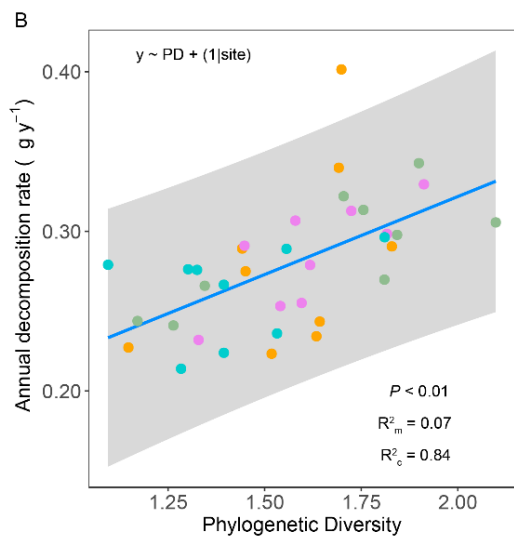
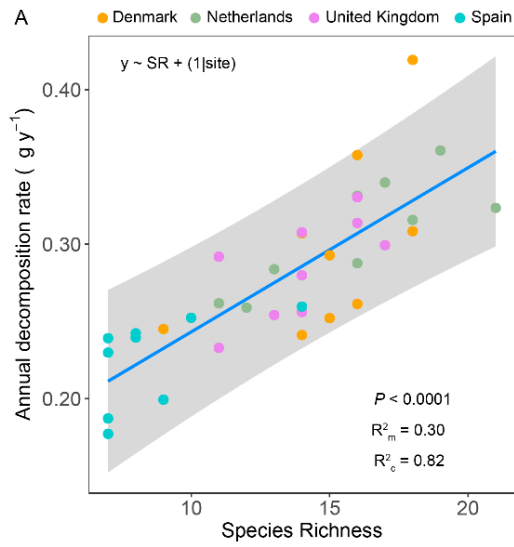
359

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<sup>-1</sup> 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.



390

391

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.

## 509 **Acknowledgements**

510 All authors thank the efforts of the many people that helped with the field-work during the  
511 VULCAN-INCREASE projects, the statistical advice of Roberto Molowny-Horas and the  
512 comments of the editor and three anonymous that greatly improved the manuscript. The  
513 authors acknowledge the financial support from the European Research Council Synergy  
514 grant ERC-SyG-2013-610028 IMBALANCE-P, the Spanish Government grant CGL2016-

515 79835-P and the Catalan Government grant SGR 2017-1005. G.P was supported by a Ramon  
516 Areces' Foundation postdoctoral fellowship.

## 517 **References**

518 Alatalo, J. M., Jägerbrand, A. K., & Čuchta, P. (2015). Collembola at three alpine subarctic  
519 sites resistant to twenty years of experimental warming. *Scientific Reports*, *5*, 18161.  
520 <http://doi.org/10.1038/srep18161>

521 Alward, R. D., Detling, J. K., & Milchunas, D. G. (1999). Grassland Vegetation Changes and  
522 Nocturnal Global Warming. *Science*, *283*(5399), 229–231.

523 Aronson, E. L., & McNulty, S. G. (2009). Appropriate experimental ecosystem warming  
524 methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*,  
525 *149*(11), 1791–1799. <http://doi.org/10.1016/j.agrformet.2009.06.007>

526 Bardgett, R. D., & van der Putten, W. H. (2014). Belowground biodiversity and ecosystem  
527 functioning. *Nature*, *515*(7528), 505–511. <http://doi.org/10.1038/nature13855>

528 Barton, K. (2018). MuMIn: multi-model inference. R package v.1.40.4. Retrieved from  
529 <https://cran.r-project.org/web/packages/MuMIn/index.html>

530 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects  
531 Models using lme4. *ArXiv Pre-Print*. Computation. Retrieved from  
532 <http://arxiv.org/abs/1406.5823>

533 Beier, C., Emmett, B., Gundersen, P., Tietema, A., Peñuelas, J., Estiarte, M., ... Williams, D.  
534 (2004). Novel approaches to study climate change effects on terrestrial ecosystems in  
535 the field: Drought and passive nighttime warming. *Ecosystems*, *7*(6), 583–597.  
536 <http://doi.org/10.1007/s10021-004-0178-8>

537 Blankinship, J. C., Niklaus, P. A., & Hungate, B. A. (2011). A meta-analysis of responses of  
538 soil biota to global change. *Oecologia*, *165*(3), 553–565. [http://doi.org/10.1007/s00442-](http://doi.org/10.1007/s00442-011-1909-0)  
539 [011-1909-0](http://doi.org/10.1007/s00442-011-1909-0)

540 Boyero, L., Cardinale, B. J., Bastian, M., & Pearson, R. G. (2014). Biotic vs. abiotic control  
541 of decomposition: A comparison of the effects of simulated extinctions and changes in  
542 temperature. *PLoS ONE*, *9*(1), 1–6. <http://doi.org/10.1371/journal.pone.0087426>

543 Bradford, M. A., Ciska, G. F., Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H.  
544 C., ... Van Der Putten, W. H. (2017). A test of the hierarchical model of litter  
545 decomposition. *Nature Ecology and Evolution*, *1*(12), 1836–1845.  
546 <http://doi.org/10.1038/s41559-017-0367-4>

547 Bradford, M. A., Warren, R. J., Baldrian, P., Crowther, T. W., Maynard, D. S., Oldfield, E.  
548 E., ... King, J. R. (2014). Climate fails to predict wood decomposition at regional scales.  
549 *Nature Climate Change*, *4*(7), 625–630. <http://doi.org/10.1038/nclimate2251>

550 Breheny, P., & Burchett, W. (2016). visreg: Visualization of Regression Models. Retrieved  
551 from <https://cran.r-project.org/package=visreg>

552 Bruhn, D., Larsen, K. S., de Dato, G. D., Duce, P., Zara, P., Beier, C., ... Mikkelsen, T. N.  
553 (2013). Improving the performance of infrared reflective night curtains for warming  
554 field plots. *Agricultural and Forest Meteorology*, *173*, 53–62.  
555 <http://doi.org/10.1016/j.agrformet.2013.01.004>

556 Cadotte, M. W., & Tucker, C. M. (2017). Should Environmental Filtering be Abandoned?  
557 *Trends in Ecology & Evolution*, *32*(6), 429–437.  
558 <http://doi.org/10.1016/j.tree.2017.03.004>

559 Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly.  
560 *Proceedings of the National Academy of Sciences*, 104(44), 17430–17434.  
561 <http://doi.org/10.1073/pnas.0704350104>

562 Christensen, J. H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., ... Whetton, P.  
563 (2007). Regional climate projections. In S. Solomon, D. Qin, M. Manning, Z. Chen, M.  
564 Marquis, K. B. Averyt, ... Miller, H.L. (Eds.), *Climate change 2007: The physical*  
565 *science basis. Contribution of Working Group I to the Fourth Assessment Report of the*  
566 *Intergovernmental Panel on Climate Change* (pp. 847–940). New York: Cambridge  
567 University Press. <http://doi.org/10.1080/07341510601092191>

568 Cragg, R. G., & Bardgett, R. D. (2001). How changes in soil faunal diversity and  
569 composition within a trophic group influence decomposition processes. *Soil Biology and*  
570 *Biochemistry*, 33(15), 2073–2081. [http://doi.org/10.1016/S0038-0717\(01\)00138-9](http://doi.org/10.1016/S0038-0717(01)00138-9)

571 Crowther, T. W., Boddy, L., & Jones, T. H. (2011). Outcomes of fungal interactions are  
572 determined by soil invertebrate grazers. *Ecology Letters*, 14(11), 1134–1142.  
573 <http://doi.org/10.1111/j.1461-0248.2011.01682.x>

574 Eisenhauer, N., Bonn, A., & A. Guerra, C. (2019). Recognizing the quiet extinction of  
575 invertebrates. *Nature Communications*, 10(1), 50. [http://doi.org/10.1038/s41467-018-](http://doi.org/10.1038/s41467-018-07916-1)  
576 [07916-1](http://doi.org/10.1038/s41467-018-07916-1)

577 Eisenhauer, N., Cesarz, S., Koller, R., Worm, K., & Reich, P. B. (2012). Global change  
578 belowground: Impacts of elevated CO<sub>2</sub>, nitrogen, and summer drought on soil food  
579 webs and biodiversity. *Global Change Biology*, 18(2), 435–447.  
580 <http://doi.org/10.1111/j.1365-2486.2011.02555.x>

581 Emmett, B. A., Beier, C., Estiarte, M., Tietema, A., Kristensen, H. L., Williams, D., ...

582 Sowerby, A. (2004). The response of soil processes to climate change: Results from  
583 manipulation studies of shrublands across an environmental gradient. *Ecosystems*, 7(6),  
584 625–637. <http://doi.org/10.1007/s10021-004-0220-x>

585 Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological*  
586 *Conservation*, 61(1), 1–10. [http://doi.org/10.1016/0006-3207\(92\)91201-3](http://doi.org/10.1016/0006-3207(92)91201-3)

587 Filser, J., Faber, J. H., Tiunov, A. V., Brussaard, L., Frouz, J., De Deyn, G., ... Jiménez, J. J.  
588 (2016). Soil fauna: Key to new carbon models. *Soil*, 2(4), 565–582.  
589 <http://doi.org/10.5194/soil-2-565-2016>

590 Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A  
591 new measure of phylogenetic signal strength in binary traits. *Conservation Biology*,  
592 24(4), 1042–1051. <http://doi.org/10.1111/j.1523-1739.2010.01455.x>

593 García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter  
594 quality differently modulate the effects of soil fauna on litter decomposition across  
595 biomes. *Ecology Letters*, 16(8), 1045–1053. <http://doi.org/10.1111/ele.12137>

596 Gjelstrup, P., & Petersen, H. (1987). Jordbundens mider og springhaler. *Natur Og Museum*,  
597 26(4), 1–32.

598 Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., ...  
599 Hättenschwiler, S. (2014). Consequences of biodiversity loss for litter decomposition  
600 across biomes. *Nature*, 509(7499), 218–21. <http://doi.org/10.1038/nature13247>

601 Harte, J., Torn, M. S., Chang, F., Feifarek, B., Kinzig, A. P., Chang, F., ... Shen, K. (1995).  
602 Global Warming and Soil Microclimate : Results from a Meadow-Warming Experiment  
603 Rebecca Shaw and Karin Shen Published by : Wiley on behalf of the Ecological Society

604 of America Stable URL : <http://www.jstor.org/stable/1942058> REFERENCES Linked  
605 references a. *Ecological Applications*, 5(1), 132–150.

606 Heemsbergen, D. A., Berg, M. P., Loreau, M., van Hal, J. R., Faber, J. H., & Verhoef, H. A.  
607 (2004). Biodiversity Effects on Soil Processes Explained by Interspecific Functional  
608 Dissimilarity. *Science*, 306(5698), 1019–1020. <http://doi.org/10.1126/science.1101865>

609 Helmus, M. R., Keller, W., Paterson, M. J., Yan, N. D., Cannon, C. H., & Rusak, J. A.  
610 (2010). Communities contain closely related species during ecosystem disturbance.  
611 *Ecology Letters*, 13(2), 162–174. <http://doi.org/10.1111/j.1461-0248.2009.01411.x>

612 Hoffmann, A. A., & Sgro, C. M. (2011). Climate change and evolutionary adaptation.  
613 *Nature*, 470(7335), 479–485. <http://doi.org/10.1038/nature09670>

614 Holmstrup, M., Damgaard, C., Schmidt, I. K., Arndal, M. F., Beier, C., Mikkelsen, T. N., ...  
615 Christensen, S. (2017). Long-term and realistic global change manipulations had low  
616 impact on diversity of soil biota in temperate heathland. *Scientific Reports*, 7(January),  
617 41388. <http://doi.org/10.1038/srep41388>

618 Holmstrup, M., Ehlers, B. K., Slotsbo, S., Ilieva-Makulec, K., Sigurdsson, B. D., Leblans, N.  
619 I. W., ... Berg, M. P. (2018). Functional diversity of Collembola is reduced in soils  
620 subjected to short-term, but not long-term, geothermal warming. *Functional Ecology*,  
621 (January), 1–13. <http://doi.org/10.1111/1365-2435.13058>

622 Holmstrup, M., Sørensen, J. G., Maraldo, K., Schmidt, I. K., Mason, S., Tietema, A., ...  
623 Ehlers, B. K. (2012). Increased frequency of drought reduces species richness of  
624 enchytraeid communities in both wet and dry heathland soils. *Soil Biology and*  
625 *Biochemistry*, 53, 43–49. <http://doi.org/10.1016/j.soilbio.2012.05.001>

626 Holmstrup, M., Sørensen, J. G., Schmidt, I. K., Nielsen, P. L., Mason, S., Tietema, A., ...  
627 Ehlers, B. K. (2013). Soil microarthropods are only weakly impacted after 13 years of  
628 repeated drought treatment in wet and dry heathland soils. *Soil Biology and*  
629 *Biochemistry*, 66, 110–118. <http://doi.org/10.1016/j.soilbio.2013.06.023>

630 Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. a., Matulich, K.  
631 L., ... O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major  
632 driver of ecosystem change. *Nature*, 486(7401), 105–108.  
633 <http://doi.org/10.1038/nature11118>

634 Kærsgaard, C. W., Holmstrup, M., Malte, H., & Bayley, M. (2004). The importance of  
635 cuticular permeability, osmolyte production and body size for the desiccation resistance  
636 of nine species of Collembola. *Journal of Insect Physiology*, 50(1), 5–15.

637 Kardol, P., Fanin, N., & Wardle, D. A. (2018). Long-term effects of species loss on  
638 community properties across contrasting ecosystems. *Nature*, 557(7707), 710–713.  
639 <http://doi.org/10.1038/s41586-018-0138-7>

640 Kardol, P., Reynolds, W. N., Norby, R. J., & Classen, A. T. (2011). Climate change effects  
641 on soil microarthropod abundance and community structure. *Applied Soil Ecology*,  
642 47(1), 37–44. <http://doi.org/10.1016/j.apsoil.2010.11.001>

643 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D.,  
644 ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology.  
645 *Bioinformatics*, 26(11), 1463–1464. <http://doi.org/10.1093/bioinformatics/btq166>

646 Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015).  
647 Community assembly, coexistence and the environmental filtering metaphor. *Functional*  
648 *Ecology*, 29(5), 592–599. <http://doi.org/10.1111/1365-2435.12345>

649 Kröel-Dulay, G., Ransijn, J., Schmidt, I. K., Beier, C., De Angelis, P., de Dato, G., ...  
650 Penuelas, J. (2015). Increased sensitivity to climate change in disturbed ecosystems.  
651 *Nature Communications*, 6, 6682. <http://doi.org/10.1038/ncomms7682>

652 Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2018). lmerTest: Tests in Linear  
653 Mixed Effects Models. R package v.3.0-1. Retrieved from [https://cran.r-](https://cran.r-project.org/web/packages/lmerTest/)  
654 [project.org/web/packages/lmerTest/](https://cran.r-project.org/web/packages/lmerTest/)

655 Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional  
656 diversity from multiple traits A distance-based framework for measuring from multiple  
657 traits functional diversity. *Ecology*, 91(1), 299–305. <http://doi.org/10.1890/08-2244.1>

658 Lindberg, N., Bengtsson, J., & Persson, T. (2002). Effects of experimental irrigation and  
659 drought on the composition and diversity of soil fauna in a coniferous stand. *Journal of*  
660 *Applied Ecology*, 39, 924–936.

661 Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the  
662 relationship between phylogenetic relatedness and ecological similarity among species.  
663 *Ecology Letters*, 11(10), 995–1003. <http://doi.org/10.1111/j.1461-0248.2008.01229.x>

664 Makkonen, M., Berg, M. P., van Hal, J. R., Callaghan, T. V., Press, M. C., & Aerts, R.  
665 (2011). Traits explain the responses of a sub-arctic Collembola community to climate  
666 manipulation. *Soil Biology and Biochemistry*, 43(2), 377–384.  
667 <http://doi.org/10.1016/j.soilbio.2010.11.004>

668 Maraldo, K., Krogh, P. H., van der Linden, L., Christensen, B., Mikkelsen, T. N., Beier, C.,  
669 & Holmstrup, M. (2010). The counteracting effects of elevated atmospheric CO<sub>2</sub>  
670 concentrations and drought episodes: studies of enchytraeid communities in a dry  
671 heathland. *Soil Biology and Biochemistry*, 42(11), 1958–1966.



672 Maraldo, K., Schmidt, I. K., Beier, C., & Holmstrup, M. (2008). Can field populations of the  
673 enchytraeid, *Cognettia sphagnetorum*, adapt to increased drought stress? *Soil Biology  
674 and Biochemistry*, 40(7), 1765–1771. <http://doi.org/10.1016/j.soilbio.2008.02.016>

675 Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A  
676 functional approach reveals community responses to disturbances. *Trends in Ecology  
677 and Evolution*, 28(3), 167–177. <http://doi.org/10.1016/j.tree.2012.10.004>

678 Orme, D. (2013). The caper package: comparative analysis of phylogenetics and evolution in  
679 *R. R Package Version*, 5(2).

680 Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401(6756),  
681 877–884. <http://doi.org/10.1038/44766>

682 Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., ... Jump, A. S.  
683 (2013). Evidence of current impact of climate change on life: A walk from genes to the  
684 biosphere. *Global Change Biology*, 19(8), 2303–2338. <http://doi.org/10.1111/gcb.12143>

685 Petersen, H. (2011). Collembolan communities in shrublands along climatic gradients in  
686 Europe and the effect of experimental warming and drought on population density,  
687 biomass and diversity. *Soil Organisms*, 83(3), 463–488.

688 Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., ... Hedde, M.  
689 (2014). Current use of and future needs for soil invertebrate functional traits in  
690 community ecology. *Basic and Applied Ecology*, 15(3), 194–206.  
691 <http://doi.org/10.1016/j.baae.2014.03.007>

692 R Core Team. (2016). R: A Language and Environment for Statistical Computing. Vienna,  
693 Austria. Retrieved from <https://www.r-project.org/>

694 Reinsch, S., Koller, E., Sowerby, A., de Dato, G., Estiarte, M., Guidolotti, G., ... Emmett, B.  
695 A. (2017). Shrubland primary production and soil respiration diverge along European  
696 climate gradient. *Scientific Reports*, 7(February), 43952.  
697 <http://doi.org/10.1038/srep43952>

698 Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other  
699 things). *Methods in Ecology and Evolution*, 3(2), 217–223.  
700 <http://doi.org/10.1111/j.2041-210X.2011.00169.x>

701 Salmon, S., & Ponge, J. F. (2012). Species traits and habitats in springtail communities: A  
702 regional scale study. *Pedobiologia*, 55(6), 295–301.  
703 <http://doi.org/10.1016/j.pedobi.2012.05.003>

704 Salmon, S., Ponge, J. F., Gachet, S., Deharveng, L., Lefebvre, N., & Delabrosse, F. (2014).  
705 Linking species, traits and habitat characteristics of Collembola at European scale. *Soil*  
706 *Biology and Biochemistry*, 75, 73–85. <http://doi.org/10.1016/j.soilbio.2014.04.002>

707 Sowerby, A., Emmett, B., Beier, C., Tietema, A., Peñuelas, J., Estiarte, M., ... Freeman, C.  
708 (2005). Microbial community changes in heathland soil communities along a  
709 geographical gradient: Interaction with climate change manipulations. *Soil Biology and*  
710 *Biochemistry*, 37(10), 1805–1813. <http://doi.org/10.1016/j.soilbio.2005.02.023>

711 Thakur, M. P., Reich, P. B., Hobbie, S. E., Stefanski, A., Rich, R., Rice, K. E., ...  
712 Eisenhauer, N. (2018). Reduced feeding activity of soil detritivores under warmer and  
713 drier conditions. *Nature Climate Change*, 8(1), 75–78. [http://doi.org/10.1038/s41558-](http://doi.org/10.1038/s41558-017-0032-6)  
714 [017-0032-6](http://doi.org/10.1038/s41558-017-0032-6)

715 Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning.  
716 *Annual Review of Ecology, Evolution, and Systematics*, 45, 471–493.

717 <http://doi.org/10.1126/science.1064088>

718 Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., ...  
719 Mazel, F. (2016). A guide to phylogenetic metrics for conservation, community ecology  
720 and macroecology. *Biological Reviews*, *92*, 698–715. <http://doi.org/10.1111/brv.12252>

721 Tucker, C. M., Davies, T. J., Cadotte, M. W., & Pearse, W. D. (2018). On the relationship  
722 between phylogenetic diversity and trait diversity. *Ecology*, *99*(6), 1473–1479.  
723 <http://doi.org/10.13748/j.cnki.issn1007-7693.2014.04.012>

724 Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234),  
725 571–573. Retrieved from  
726 [www.wpro.who.int/mediacentre/factsheets/fs\\_201001\\_climate\\_change/en/](http://www.wpro.who.int/mediacentre/factsheets/fs_201001_climate_change/en/)

727 Villéger, Mason, & Mouillot. (2008). New multidimensional functional diversity indices for a  
728 multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301.  
729 <http://doi.org/10.1890/07-1206.1>

730 Yu, D., Zhang, F., Stevens, M. I., Yan, Q., Liu, M., & Hu, F. (2016). New insight into the  
731 systematics of Tomoceridae (Hexapoda, Collembola) by integrating molecular and  
732 morphological evidence. *Zoologica Scripta*, *45*(3), 286–299.  
733 <http://doi.org/10.1111/zsc.12149>

734 Yuste, J. C., Peñuelas, J., Estiarte, M., Garcia-Mas, J., Mattana, S., Ogaya, R., ... Sardans, J.  
735 (2011). Drought-resistant fungi control soil organic matter decomposition and its  
736 response to temperature. *Global Change Biology*, *17*(3), 1475–1486.  
737 <http://doi.org/10.1111/j.1365-2486.2010.02300.x>

738