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

Running title: Decline of springtail richness by drought

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Abstract

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

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

Introduction

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

Despite the growing concern over the effects of climate change on biological communities, it is still uncertain how biodiversity will respond by the rise of temperatures and the increase in the frequency and severity of droughts. Most previous research has examined shifts in species abundance and richness, generally finding evidence for declines (Urban, 2015). However, there has been a disproportionate focus on aboveground communities, particularly vertebrates and plants, overlooking that belowground thrives an extremely rich diversity of soil invertebrates that are key for ecosystem functioning and are at high risk (Bardgett & van der Putten, 2014; Eisenhauer, Bonn, & A. Guerra, 2019). Moreover, it is increasingly appreciated that changes in species abundance and richness provide an incomplete picture of the connection between biodiversity and ecosystem functioning because they may be lost at different rates than functional and phylogenetic diversity (Tilman et al., 2014). Because anticipation of responses is the basis to build realistic biodiversity scenarios, these gaps in knowledge limit our ability to develop conservation efforts and future planning to mitigate the impact of climate change.

Here, we investigate changes in springtail communities (Subclass Collembola) in response to climate manipulations in a standardized field experiment replicated at six natural shrubland sites across Europe (Fig. 1; Table 1). Although logistically challenging, combining multi-year and multi-site standardized field experimental approaches across climatically contrasting regions is crucial to draw conclusions that are realistic and apply across large regions (Kröel-Dulay et al., 2015). Springtails are a highly diverse and abundant group of soil fauna involved in many key ecosystem functions such as leaf-litter decomposition and nutrient cycling (Bardgett & van der Putten, 2014; Filser et al., 2016; Handa et al., 2014). Notwithstanding, our current knowledge of whether and how their phylogenetic and functional diversity will be altered by climate change is still poor despite recent advances with some biodiversity metrics and in particular ecosystem types (Alatalo, Jägerbrand, & Čuchta, 2015; Blankinship, Niklaus, & Hungate, 2011; Holmstrup et al., 2013, 2017, 2018; Kardol, Reynolds, Norby, & Classen, 2011; Lindberg, Bengtsson, & Persson, 2002; Makkonen et al., 2011; Petersen, 2011). To simulate climate change, we applied two types of treatments on natural vegetation plots: 1) a drought treatment, using transparent plastic coverings during rain events to decrease rainfall; and 2) a warming treatment, increasing heat retention by means of reflective curtains extended between sunset and sunrise throughout the year. At each study site, these treatments were replicated in three randomly selected plots, and compared to three adjacent control plots with the same scaffolding but no treatment. Between 1 to 4 years since the onset of the climate manipulations, springtail communities were comprehensively sampled from topsoil as well as soil and vegetation surface. To investigate how our warming and drought treatments affected taxonomic, phylogenetic and functional richness, we identified all recorded specimens to the species level, reconstructed their phylogenetic relationships with two molecular markers, and compiled published information on 28 relevant functional traits. As diversity loss may alter ecosystem functioning (Hooper et al., 2012; Kardol et al., 2018; Tilman et al., 2014), we also assessed rates of decomposition by means of a simultaneous litterbag experiment with leaf-litter of the dominant local plant species, and tested whether variation in this key ecosystem function correlated with these newly gathered biodiversity measures. We hypothesized that warming and drought treatments would reduce springtail abundance as well as taxonomic, phylogenetic and functional richness of springtail assemblages. Additionally, if the traits analyzed are phylogenetically conserved, and the phylogenetic structure of springtail communities in warmed and dried plots is relatively clustered compared to those in control plots, this could suggest a non-random loss of springtail species. Finally, springtails are involved in leaf-litter decomposition through multiple direct and indirect mechanisms (Filser et al., 2016). However, to the best of our knowledge, direct assessments of the relationship between springtail richness and decomposition are lacking. Therefore, we hypothesized that if there is a diversity-decomposition relationship and springtails are to some extent a good proxy of soil biodiversity, then we should find significant correlations between local springtail richness and the rates of leaf-litter decomposition.

Materials and Methods

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

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

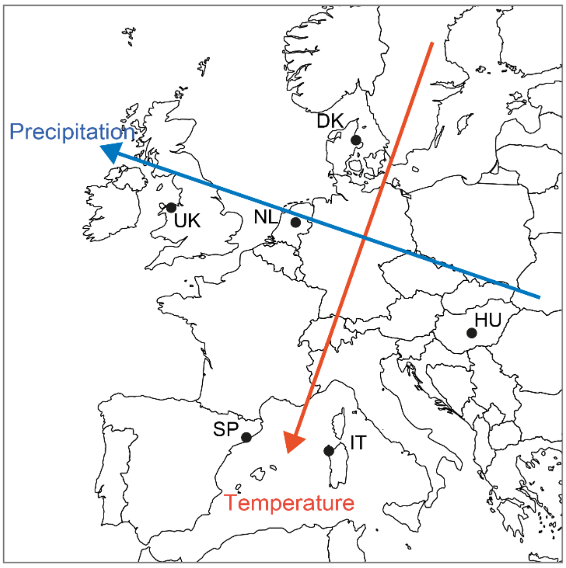


Table 1. Characteristics of the study sites.

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	*Calluna vulgaris*	*Calluna vulgaris*	*Calluna vulgaris* *Deschampsia flexuosa*	*Populus alba* *Festuca vaginata*	*Erica multiflora* *Globularia alypum*	*Cistus monspeliensis* *Helichrysum italicum* *Dorycnium pentaphyllum*

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.

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

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).

Taxon sampling. Springtails (Subclass Collembola) were sampled from April to July 2003 sequentially (i.e. IT, SP, HU, DK, NL and UK) to equalize mean temperatures across sites (Petersen, 2011). Five quadrats (1.25 m^2 each) representative of the most dominant plant species were selected within each experimental plot. Springtails from vegetation were suctioned with an adapted vacuum cleaner connected to a fauna trap. Specimens dropped were recovered through polythene boxes with aqueous benzoic acid placed beneath the plants. Ground-dwelling springtails were also suctioned with the same method for the same area and, subsequently, 10-cm deep soil cores with a surface of 25 cm^2 were taken to the lab to recover springtails from the soil through high-gradient extraction (10 days of gradually increasing temperature from 25 to 60ºC, Gjelstrup & Petersen, 1987). The sampling methods were slightly adapted in the UK and IT due to an excess of soil moisture and stones, respectively (see Petersen, 2011). Once extracted and sorted, springtails were conserved in glycerol and identified to the species level following references cited in (Petersen, 2011). Some dubious specimens were kindly revised by Drs. L. Dányí, R. Jordana and E. Mateos. This sampling resulted in 19641 springtail specimens that were classified into 102 species-level entities (Table S7). An initial assessment of these data can be found in Petersen (2011) and the specimens are deposited in his personal collection.

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

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

Litterbag decomposition experiment. Leaf litter from the dominant ericaceous plant species at each site (i.e. *Calluna vulgaris* and *Erica vulgaris*, Table 1) was collected in DK, NL, UK and SP between September-November 1999. After air drying and sorting to obtain homogeneous samples, 3 g of dried leaves and shoots were placed in nylon bags with a mesh size of 1 mm for *Calluna vulgaris* and 0.71 mm for *Erica vulgaris* due to the smaller size of the leaves of this species. This protocol allows the entrance of medium-sized decomposers, including all juveniles and the adults of almost all springtail species as well as other invertebrate fauna (Handa et al., 2014). The bags were incubated over a period of 2 years divided in 10-12 time-periods. Three replicates for each time-period were placed either randomly (UK), beneath *Calluna* plants (DK), stratified beneath *Calluna* plants and open areas (NL) or beneath *Erica* plants (SP) due to the specific characteristics of vegetation cover at each site. Litterbags were then sequentially retrieved and sorted to remove non-target material and then oven-dried. We calculated the annual decomposition rates as the annual fractional weight loss (k) for each plot using the following equation: $M_t = M_o \cdot e^{-kt}$, where M_t is leaf-litter mass loss at time t and M_o is the initial mass (Emmett et al., 2004). HU and IT were not included in the litterbag experiment due to the delay in the onset of the climatic manipulations in both sites (Table 2). A previous analysis of these decomposition experiment can be found in Emmett *et al.* (2004).

Data analysis. All metric estimations and statistical analyses we describe here were carried out with R v3.4.3 (R Core Team, 2016). To assess if taxonomic, phylogenetic and functional trait-based dimensions of springtail richness responded in the same way to experimental climate change treatments, we characterized springtail assemblages in terms of: (i) abundance (total number of individuals of all species per plot); (ii) species richness (SR, number of species per plot); (iii) Faith's phylogenetic diversity index (PD, sum of branch lengths connecting all species in an assemblage (Faith, 1992)); (iv) mean neighbor taxon distance (MNTD, mean phylogenetic shortest distance for each species from an assemblage (Kembel et al., 2010)); (v) variance in nearest taxonomic distance (VNTD, variance of phylogenetic shortest distance for each species from the distance matrix of an assemblage (Tucker et al., 2016)); (vi) functional richness (FR, the multidimensional volume occupied by all species in an assemblage within a functional space, where the axes are functional traits along which species placed according to their trait values (Mouillot et al., 2013; Villéger, Mason, & Mouillot, 2008)); (vii) functional divergence (FD, divergence in the distribution of abundance within the volume or functional space occupied by a community (Villéger et al., 2008)); and (viii) functional evenness (FE, regularity in the distribution of abundance within the volume or functional space occupied by a community (Villéger et al., 2008)). These metrics were selected following the framework proposed by Tucker et al. (Tucker et al., 2016; Tucker, Davies, Cadotte, & Pearse, 2018), according to which PD *vs* FR, MNTD *vs* FD and VNTD *vs* FE are phylogenetic and functional equivalent indices associated to richness (i.e. the sum of accumulated phylogenetic and functional differences among taxa in an assemblage), divergence (i.e. the mean phylogenetic and functional relatedness among taxa in an assemblage), and regularity (i.e. the variance in differences among taxa, representing how regular are the phylogenetic and functional differences between taxa in an assemblage) dimensions of biological communities, respectively.

Metrics for the phylogenetic community structure were calculated with the package *picante* (Kembel et al., 2010) using the reference ML-Bayesian consensus phylogeny. To account for baseline differences in species richness among sites and treatments, we standardized phylogenetic measures against 999 community randomizations using ‘richness’ and ‘independent swap’ as null model specifications, i.e. constraining the randomized communities only to observed species richness or also to the frequency of species occurrence. This was done by means of the built-in functions ‘ses.pd’ and ‘ses.mntd’ and with a modified version of the latter for VNTD. The standardized effect size was then calculated as the difference between the value observed in the community and the mean value of the null communities divided by the standard deviation of the distances in the null data. The same approach was applied to FR, FD and FE, which were calculated with the package *FD* (Laliberte & Legendre, 2010) and standardized with our own script applying the same constraints as with PD, MNTD and VNTD. Additionally, we estimated the phylogenetic signal of trait data, i.e. the correlation between trait similarity and species' evolutionary distance. We used the D-statistic and Pagel's λ for discrete and continuous traits, respectively (Fritz & Purvis, 2010; Pagel, 1999) through the packages *caper* and *phylosig* (Orme, 2013; Revell, 2012). Values near or below 0 and close to 1 mean strong phylogenetic signal for the D-statistic and for Pagel's λ, respectively. The existence of phylogenetic signal suggests that ecological similarity is linked to phylogenetic relatedness (Losos, 2008).

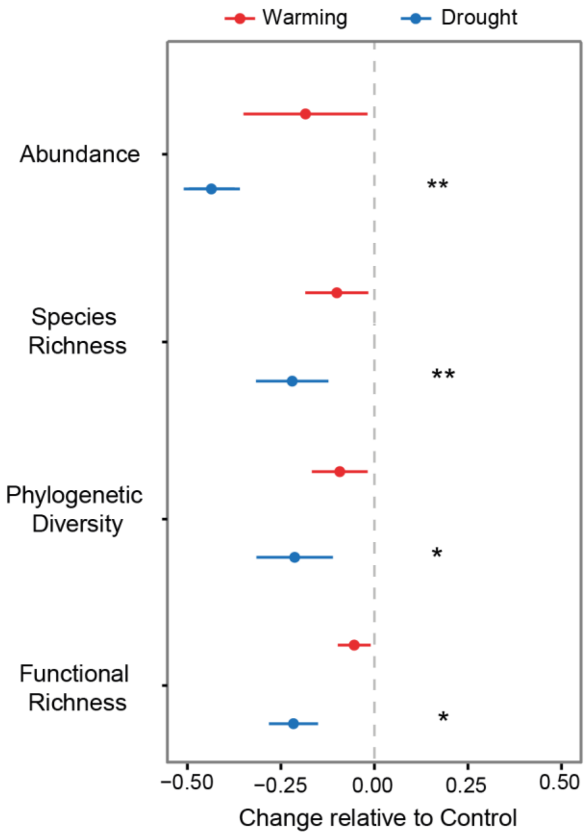
We investigated how taxonomic, phylogenetic and functional metrics of springtail assemblages changed due to climatic manipulation by means of linear mixed-effects models, as implemented in the R-package *lme4* (Bates, Mächler, Bolker, & Walker, 2014). Our response variables (i.e. each of the above diversity metrics estimated at a community level) were modelled separately as a function of the experimental treatments (coded as a fixed effect) and study site (coded as a random intercept factor to cope with the heterogeneity in abiotic conditions across sites.). We estimated the *P*-values for fixed-effects by means of a Satterthwaite approximation to the number of degrees of freedom with *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2018). To assess for potential interactions between the effect of climatic treatments and sites, we also built models where site, treatment and their interactions were included as fixed-effects terms. We used variation in second-order Akaike's Information Criterion (ΔAICc), marginal and conditional coefficients of determination (R^2_m and R^2_c) and residuals diagnostic plots to compare model performance and assess model assumptions. For visualization, the observed changes in abundance, SR, PD and FR are represented as proportions relative to control plots (Emmett et al., 2004). Additionally, to validate the consistency of the community patterns detected, we carried out a series of sensitivity analyses. First, to discard that SR differences were only due to variation in abundance, we repeated the analyses with SR estimated after rarefying communities to median, first and third quartile of the observed abundance. Second, since we did not have molecular and trait information for all the species pool, we assessed the potential effect of missing species repeating all the analyses restricting the community datasets to only those species present in the phylogeny and to only those with trait data available. Third, the reconstruction of the phylogenetic relationships of a given set of species necessarily implies a degree of uncertainty around the topology, and thereby of the derived metrics extracted from the trees. Hence, to assess the effect of phylogenetic uncertainty we iterated all the preceding phylogenetic measures and the corresponding linear models with 1000 trees drawn from the Bayesian posterior distribution.

Finally, we tested if our climate manipulations affected annual decomposition rates and whether the richness of springtail communities correlated with this key ecosystem function using linear mixed-effects models. Rather than trying to establish purely causal relationships, which is not possible with the design of our litterbag experiment, we aimed to assess the predictive power of springtail richness over litter decomposition, that is the amount of variance in litter decomposition that each richness metric is able to explain. So, we built different models with decomposition rate as response variable varying the inclusion of climate manipulation treatments, SR, PD and FR and their interaction as fixed effect terms. We additionally tested if these models differed when site was included as a random intercept term (i.e. the variation in large-scale abiotic conditions across sites may determine different baseline rates of decomposition), or additionally, by letting each covariate (SR, PD and FR) have a random slope correlated with each site (group) intercept (i.e. the potential diversity-function relationship may differ between sites due to the contrasting abiotic conditions). The inclusion of site as a random intercept term allowed to cope with the heterogeneity in abiotic conditions across sites. By letting each covariate (i.e. SR, PD and FR) to have a different slope at each site, the model also accounted for the possibility that the same large-scale abiotic controls may modulate the potential relationship between local richness-related metrics with decomposition. See Bradford et al. for a similar analytical approach (Bradford et al., 2014). To assess these distinct model structures, we compared both types of models by means of likelihood ratio tests and evaluated their predictive ability through R^2_m and R^2_c with the package *MuMIn* (Barton, 2018), which capture the explanatory power of both fixed and random terms. We estimated P-values for the fixed terms through a Satterthwaite approximation to the number of degrees of freedom and used residuals diagnostic plots to assess model performance and assumptions. For model visualization we used the *visreg* package, which allows to plot best-fitted models focusing on the variables of interest and holding the other factors constant (i.e. partial residuals regression plots) (Breheny & Burchett, 2016).

Results

The experimentally warmed plots did not differ from the control plots in any of the diversity metrics, despite an average increase of 0.43° C in mean annual temperature (MAT, Table 2 and Table S1). In contrast, the drought treatment, which on average reduced annual precipitation by 22% and soil moisture by 36%, considerably altered springtail communities. This resulted in a decline on average of 22 ± 10% (mean ± 1 standard error, hereinafter) of the species richness compared to control plots ($P < 0.01$; Fig. 2). The drought treatment also reduced on average 44 ± 7% the number of springtails per plot ($P < 0.01$; Fig. 2), raising the possibility that the observed species loss was a random consequence of a community downsizing. However, the decline of species richness with the drought was consistent even when communities were rarefied to equalize total abundances (always $P < 0.05$ when rarefied to median, first and third quartile, see Table S2). The ‘drought effect’ on both abundance and species richness was also robust to the exclusion of species for which no information was available on functional traits and/or phylogenetic relationships (Table S2).

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

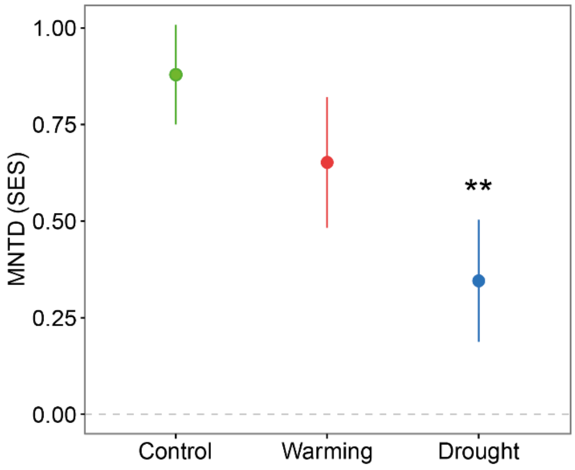


In parallel to the loss of species, the drought plots exhibited significant reductions in phylogenetic diversity and functional richness compared to control plots (*P* < 0.05; Fig. 2). Both metrics are known to decrease with species loss, a pattern also detected in our analyses.

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

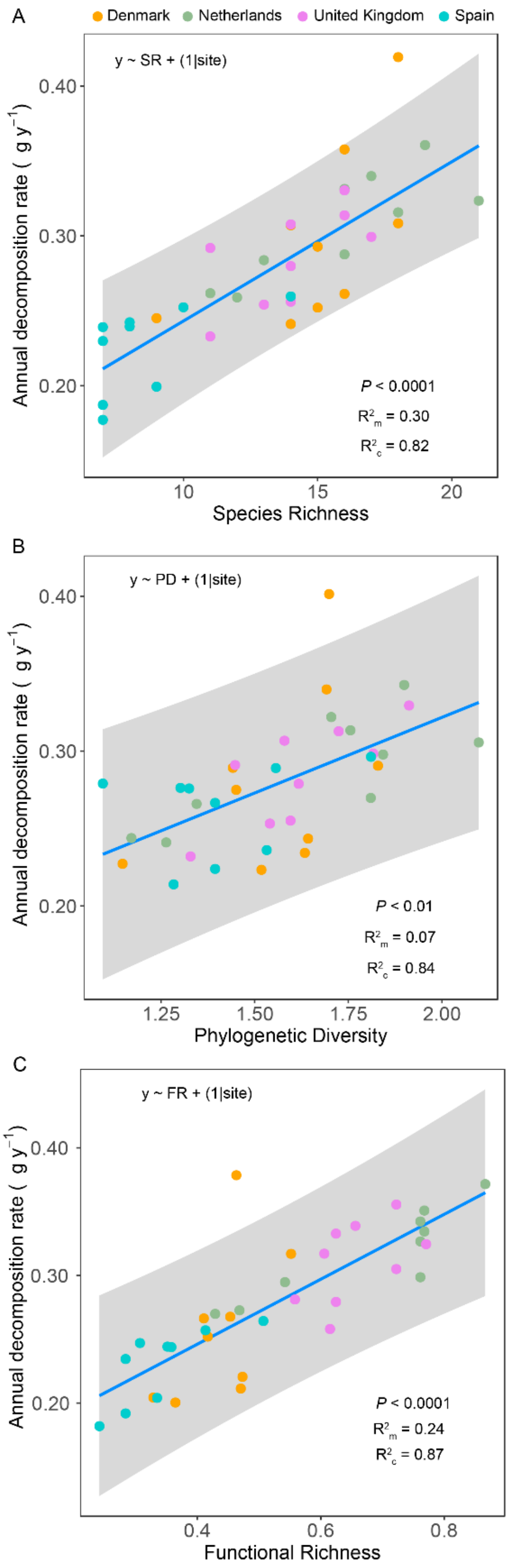
The drought treatment eroded the phylogenetic and functional richness of springtail assemblages apparently without important shifts in the distribution of species abundances or in the regularity of these abundances within the functional trait space. Indeed, functional evenness and divergence showed no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

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



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

Figure 4 Relationships between annual rates of leaf-litter decomposition and species richness (A), phylogenetic diversity (B) and functional richness (C) of springtail communities across Europe. We used linear mixed-effects models to assess the correlations allowing each site to have its own random intercept to capture large-scale climatic differences among sites. We used marginal and conditional coefficients of determination (R2m and R2c) to assess the predictive ability of fixed alone and fixed + random terms, respectively. Partial residuals regression plots of the best-fitted models show the relationships between response and explanatory variables holding the random term constant.


A
Denmark
Netherlands
United Kingdom
Spain
y ~ SR + (1|site)
Annual decomposition rate (g y^{-1})
0.40
0.30
0.20
P < 0.0001
R^2_m = 0.30
R^2_c = 0.82
10
15
20
Species Richness
B
y ~ PD + (1|site)
Annual decomposition rate (g y^{-1})
0.40
0.30
0.20
P < 0.01
R^2_m = 0.07
R^2_c = 0.84
1.25
1.50
1.75
2.00
Phylogenetic Diversity
C
y ~ FR + (1|site)
Annual decomposition rate (g y^{-1})
0.40
0.30
0.20
P < 0.0001
R^2_m = 0.24
R^2_c = 0.87
0.4
0.6
0.8
Functional Richness

Discussion

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

Second, we provide evidence that drought not only reduced species richness (Petersen, 2011) but also caused a disproportionate loss of phylogenetic diversity, resulting in increasingly phylogenetically clustered springtail assemblages. A continued stress is expected to increase the phylogenetic similarity of species in a community whenever their sensitivity to a particular environmental factor is phylogenetically conserved (Helmus et al., 2010). Accumulating evidence suggests that species filtering by stress disturbance, like sustained drought, is partly driven by species’ traits (Chase, 2007; Mouillot et al., 2013). However, it is yet unclear whether the changes in phylogenetic structure arise from strict environmental filtering, from a modification of species’ competitive performance due to the new abiotic regime, or from a combination of both processes (Cadotte & Tucker, 2017; Kraft et al., 2015).

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

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

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

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

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

Most of our current understanding of the responses of soil fauna to climate change comes from controlled microcosm experiments with unnatural low-diversity levels (Boyero et al., 2014; Cragg & Bardgett, 2001; Heemsbergen et al., 2004). Studies like ours that manipulate abiotic conditions in natural communities exposed to contrasting climatic regimes are rare, although they are essential to build realistic scenarios of the impact of climate change on biodiversity and its consequences for ecosystem functioning. Our analyses demonstrate that under such realistic conditions, climate change has a great potential to alter the abundance, species richness, phylogenetic diversity and functional richness of springtail communities. The analyses also suggest that these springtail declines, if sustained, may be linked to reductions on litter decomposition that could dwindle nutrient cycling and ultimately the productivity of terrestrial ecosystems. We cannot completely discard that the fast responses to drought reported here are in part a transient state within the resilience space of natural ecosystems, as within the wealth of soil organisms contributing to decomposition processes some groups like oribatid mites, millipedes and isopods may be more resistant in the long-term (Holmstrup et al., 2012; Maraldo et al., 2010). Likewise, it cannot be dismissed that fast evolutionary adaptations could counteract increasingly stressful conditions due to climate change (Hoffmann & Sgro, 2011). However, a previous study with an enchytraeid species showed a limited adaptive ability to drought (Maraldo, Schmidt, Beier, & Holmstrup, 2008) and on-going research suggests that this would also be the case with springtails (Kutcherov et al. *unpublished*). In any case, our finding that soil biodiversity loss embraces multiple biodiversity facets and is non-random with respect to functional traits supports the view that a reduction in precipitation may result in a lasting attrition of springtail communities. If similar effects occur in other drought-sensitive soil organisms, this may carry critical consequences for ecosystem functioning such as slow-downs on litter decomposition rates.

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