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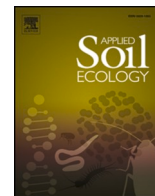
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Resilience of Collembola communities to extreme drought is moderated by land use at a regional scale

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ABSTRACT

In a world undergoing climate and usage change, soil biodiversity, which accounts to 25 % of the terrestrial biodiversity, is under severe threats. However, scenarios of climate change are based on known sensitivity of aboveground communities while there are differences on the responses to these changes with soil biodiversity. Here, we investigate the effects of an extreme climatic – due to an exceptionally drought year in 2011 - in various land use types (grassland, arable land, forest) through a study conducted at a regional scale (146 sites in Meuse, France) during 5 years. We characterized the responses of Collembola communities to climate change using (i) taxonomic indices and species dynamics, and (ii) species' functional traits and trait-based indices to reveal community assembly mechanisms. Our results demonstrated a total of 98 Collembola species collected during the five year project over the three land uses. Density and species richness were modulated by year, by land use and by their interaction. Three different distribution patterns in response to extreme drought events were demonstrated according to land use. Our findings thus reveal various effects according to land use, with a fast recovery of communities in arable lands, a long term effect for grasslands, and almost no effects observed in forests. These results show that the diversity of Collembola communities may be used as indicators of the resilience of ecosystems facing extreme climatic events.

1. Introduction

In terrestrial ecosystems, land use and climate change will probably have the greatest effect on biodiversity according to scenarios about changes in biodiversity for the year 2100 (FAO, 2020; Sala, 2000). While land uses and associated pressures are responsible for a large decrease in terrestrial biodiversity at local scales (Newbold et al., 2015), climate change is increasing these losses. It is likely, according to the models, that many plants and animals will disappear over the next century (Willis and Bhagwat, 2009). However, the interpretation of these models need to be careful for soil biodiversity, in particular for soil fauna communities, particularly diverse and abundant (Yin et al., 2020). Indeed, scenarios are based on known sensitivity of aboveground communities while there are differences both in patterns and knowledge of the responses to these changes between aboveground communities and soil biodiversity (Bokhorst et al., 2012; Cameron et al., 2019). Climate

change is expected to affect directly soil biodiversity by changing soil moisture and temperature, but also, indirectly, by altering plant communities and biomass and thus organic matter recycling processes, as it is the main (Jones et al., 2009).

However, until now, most of the studies concerning the effect of global change on soil biodiversity have focused on (i) controlled system experiments (Bonfanti et al., 2022; e.g. Holmstrup et al., 2017; Makkonen et al., 2011; Petersen, 2011), (ii) which often manipulate a single climate change factor, e.g. heat or drought, whereas, the future climate will probably have an alteration in both precipitations and temperatures (Yin et al., 2020) and with (iii) little temporal data (mostly synchronic). Also, knowledge of the effects of climate change on soil are still poorly understood (Jones et al., 2009). Moreover, the effects of weak long-term trends on climatic modification are difficult to analyse (Bonfanti et al., 2022). To better understand the future of soil ecosystems, we need to conduct more realistic observations on climate change including several

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disturbances (Korell et al., 2020; Rillig et al., 2019). We particularly need to better understand the interactions between climate change and land use dynamics.

In various national soil monitoring programmes across Europe, soil biodiversity, in particular Collembola, has been used for bioindication (George et al., 2017). Soil fauna provides a useful tool for assessing the effects of land use (Joimel et al., 2017; Vandewalle et al., 2010) and climate change (Krab, 2013), including the interaction between them (Yin et al., 2020). Several soil functions are provided by soil fauna such as litter decomposition (Cortet et al., 2003), or carbon and nitrogen cycles (Filsler, 2002). Reviewing functional traits related to adaptation and dispersal abilities in several taxa, Berg and Ellers (2010) brought a fruitful discussion on the 'adapt' and 'disperse' strategies facing environmental hazards. Through this prism, Ponge (2020) analysed the eco-evolutionary history of Collembola and suggested that these animals could follow two strategies to cope with global changes: "move" or "change". Move is used by species to emigrate and immigrate without adapting to environmental conditions, and is mostly observed in species living in open environment, having a high dispersal capacity and are often sexual. In contrast, some species are forced to "change", to adapt to global change by increasing their phenotypic plasticity due to their poor dispersal capacity, they are often parthenogenetic and live mainly in confined environments. Also, the Collembola responses to environmental changes have been shown to be related to their functional traits, which are, to a certain degree, species-specific (Krab et al., 2013). Given that both climate and land use conversions, especially from grasslands or forests to croplands, can lead to a decrease in the diversity and density of Collembola, the effects of climate change might be modulated by the type of considered land use and functional traits of species (Yin et al., 2020, 2019). Furthermore, it is highly plausible that global climate change will lead to longer and more frequent extreme weather periods (Hansen et al., 2012). These extreme temperatures, drought or conversely high rainfall events, may cause changes in communities which will closely depend on the organisms' traits (Easterling et al., 2000; Smith, 2011).

The functioning of ecosystems and their components (biocenosis, habitats) may be more or less altered, depending on their ability to face global changes. The ability for an ecosystem to absorb disturbances, without consistent structural and/or functional modifications is called resistance, the resilience is defined as being able to come back to the pre-condition state of the ecosystem following a disturbance, which means keeping both the structure and composition of the biodiversity within it (Holling, 1973). Here, we investigate the effects of an extreme drought – due to an exceptionally dry and warm year - in various land use types through a study conducted at a regional scale (Meuse, France) during 5 years. We characterized the responses of Collembola communities to climate change using (i) taxonomic indices and species dynamics, and (ii) species' functional traits and trait-based indices to reveal community assembly mechanisms. We hypothesized that (i) the extreme drought would cause a negative effect on Collembola communities with a decrease on diversity and density, (ii) and with a response pattern, which would differ according to the land use. Indeed, Collembola communities are known to differ taxonomically and functionally along different land uses from forests to grasslands and arable lands (Joimel et al., 2021, 2017). We suspect that the effects of climate change will be stronger on communities in agricultural soils than on those in forests or grasslands due to the lack of surface protection such as permanent vegetation cover or litter.

2. Material and methods

2.1. Study sites

The network of sampling sites was located in the study area of the long-term environmental observatory (OPE) of the French national agency for nuclear waste management (ANDRA) in the Grand-Est region

in the north-eastern part of France (Fig. 1, longitudes comprise between from 5.26 to 5.50 E and latitudes from 48.46 to 48.59 N) and consisted of 146 sampling sites. The area is under oceanic influences with a temperate continental climate and a mean annual air temperature ranging from 9.3 to 10.4 °C and a mean annual rainfall of 680 mm to 1000 mm between 2009 and 2013.

The climate events of the year 2011 in France could be considered as extreme, notably due to remarkably high temperatures and low precipitations periods. Firstly, it has been the warmest year in France since 1900. With an average annual temperature 1.5 °C above normal, 2011 was even warmer than 2003, a year which was notorious for the dramatic consequences of the heat wave on human mortality in France. The remarkably warm spring and autumn largely contributed to making 2011 an exceptionally warm year (the average month temperature was 4 °C and 2.4 °C above normal in April and May respectively). Due to an exceptionally dry spring (the driest since at least 1959), but also to a very dry autumn, 2011 is also one of the driest years France has seen in the last fifty years. Cumulated over the whole country, the amount of water collected in 2011 was significantly below the normal annual with a cumulative rainfall deficit of around 17 %. These national patterns of temperature and precipitation also applied to the Meuse department as shown in Fig. 2.

Calcosols, Calcisols, Rendosols and Brunisols (i.e. Calcaric Cambisol, Hypereutric Cambisol and Rendzic Leptosol according to the World Reference Base for Soil Resources classification) are the main soil types found on the sampling area. The studied area was based on a 1.5 × 1.5 km systematic grid covering approx. 250 km² with 146 sampling sites. In addition to biodiversity analyses, physical and chemical soil parameters and monitoring of agricultural practices were carried out (Swiderski et al., 2016). 146 survey plots reflected the land use structure of the region. The landscape was dominated by arable fields (N = 78, 54 % of the sampled sites), one-third was forest (N = 47, 32 %) and pastures covered only a 13 % of the area (N = 21, 14 %). These sites present a diversity of situations in terms of soil types and management due to the great variability of geological and pedological features (Table 1).

2.2. Collembola sampling methods and identification

Collembola were sampled 2 years before 2011 (2009 and 2010), 2011 (extreme drought event year) and 2 years after (2012, 2013). Samples were collected in the autumn of 2009 and in the Spring 2010, 2011, 2012 and 2013, when seasonal conditions (i.e. soil moisture and air temperatures) are considered optimal for soil fauna. Each year, several sites have been randomly selected among the 146 sites (Table 2).

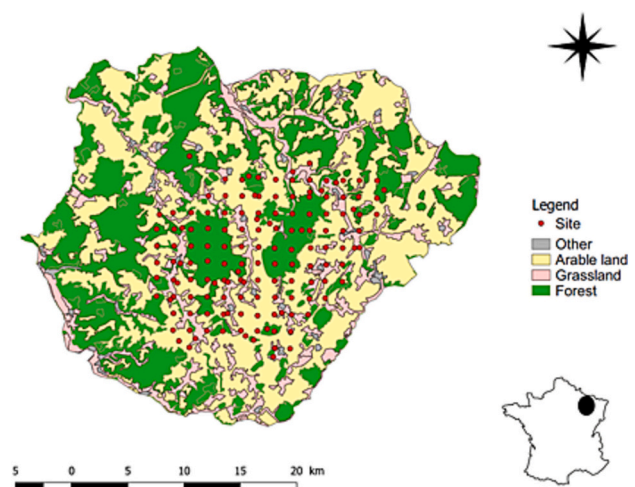


Fig. 1. Map of 146 sites sampled in Meuse (France) in three different land uses (adapted from CORINE Land Cover, 2012).

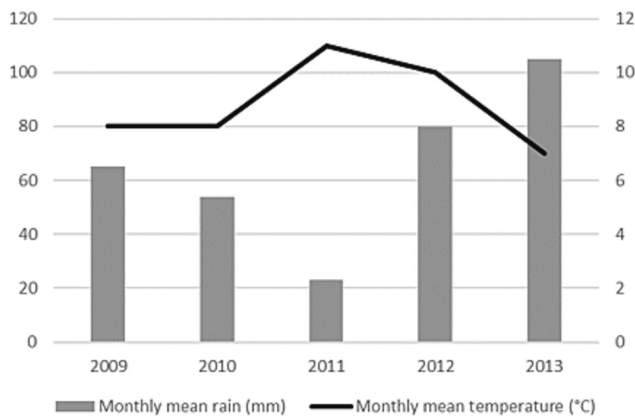


Fig. 2. Monthly mean rainfall and temperature during Spring (calculated from March to June) in Meuse from 2009 to 2013. Spring 2011 was an extreme climatic event (data from climatic portal, MétéoFrance/INRAE).

Table 1
Main characteristics of plant cover and soil type by land use in the area.

Land use	Main plant cover	Main soil type
Arable land	Conventional agriculture (wheat, rape, maize, black wheat)	Calciosols, Calciosols, Rendosols, Brunisols
Grassland	Grazed natural grassland	Calciosols, Rendosols,
Forest	Deciduous trees (beech, hornbeam)	Calciosols, Rendosols, Brunisols

Table 2
Number of sites sampled according to the year and the land use (3 replicates on each site were sampled and then averaged).

	2009	2010	2011	2012	2013
Arable land	54	30	48	63	39
Grassland	–	9	12	24	18
Forest	18	45	30	18	30

In each selected sites, three intact soil cores (sub-replicates) were extracted (5 cm depth, 6 cm diameter). The soil cores were positioned in each habitat, several metres away from the edges of the plots/habitats to limit any edge effect. Collembola were extracted from each soil core, through dry extraction for a week using a high-gradient Macfadyen extractor f (ISO 23611-2 2006). They were then counted and gathered under a binocular stereo-microscope at morpho-species level and then identified to species using dichotomous identification keys (Fjellberg, 1998; Hopkin, 2007; Potapov, 2001; Thibaud et al., 2004). Communities of each three replicates (soil cores) were then averaged in order to obtain values for each site. We thus obtained a dataset gathering 146 communities sampled during the 5-year study.

2.3. Collembola functional traits

In order to study the response to the extreme drought, we conducted a trait-based approach using ten functional traits. Ponge (2020) divided Collembola species into two categories facing global change, such as climate change: “move” species, with functional traits associated with a higher dispersal capacity, in opposition to “change” species, with lower dispersal ability involving the development of other strategies in order to survive. From this point of view, we selected 10 functional traits related to their dispersal capacity. We considered that a large body size (body-length trait), fully developed visual organs (8 ocelli), a long furcula, related to a sexual reproduction characterized “move” species. Moreover, they lived at the surface (mostly spherical body) and involved the presence of pigmentation and scales to protect them against UV and

predators. On the contrary, a small body, the absence of ocelli or even of a post antennal organ (PAO) or of Trichobothria characterized “change” species. We added the strategy of ecomorphosis, which informs about the ability of a Collembola species to display a reversible alternative form specifically responding to unsuitable elevated temperature conditions. Following Bonfanti (2021) and Bonfanti et al. (2022), we here use the ecomorphosis ability as a trait.

Trait values were provided from the BETSI database (Biological and Ecological functional Traits of Soil Invertebrates, portail.betsi.cnrs.fr) (Pey et al., 2014b). In order to compute values from various sources, mostly from identification keys, traits were split into two to seven attributes by a fuzzy coding approach. Body shape, pigmentation, scales, Post antennal organ (PAO), trichobothria, ecomorphosis and reproduction types were split into two attributes, furcula length and visual organs (ocelli) into three and body length into seven (Table 3) (Pey et al., 2014a).

2.4. Statistical analysis

For the taxonomic approach, collembolan communities were characterized by their species richness (mean number of species per site) and by species composition. In addition, density (abundance per m²) was used to calculate the Shannon diversity index and the evenness index for each site (Table 4). A mean β -diversity was also calculated for each land use, using the Jaccard dissimilarity between each site. The beta diversity ranges from 0 (100% similarity) to 1 (no similarity).

In the trait-based approach, we calculated the community-weighted mean (CWM) index for each site which is the mean of trait attribute values weighted by the relative abundances of species (Garnier et al., 2004). Because of the fuzzy coding approach, the attribute values are a percentage of the affinity of each species for a given attribute (the sum of

Table 3
Description and indication of the ten Collembola functional traits studied.

Trait	Attribute	Abbreviation	Indication of traits
Body shape	Spherical	Spherical.body	Move-change traits (Ponge, 2020)
	Cylindrical	Cylindrical.body	
Body length	<1 mm	X.0.1	
	1–1.5 mm	X.1.1.5	
	1.5–2 mm	X.1.5.2	
	2–2.5 mm	X.2.2.5	
	2.5–3 mm	X.2.5.3	
	3–4 mm	X.3.4	
Furca length	> 4 mm	X.4.7	Life habitat preference (da Silva et al., 2016)
	Absent or vestigial furcula	Furcula.absent	
	Reduced or short furcula	Short.furcula	
Pigmentation	Long furcula	Long.furcula	
	Pigmented	PIG_With	
Visual organ	Unpigmented	PIG_Without	Move-change traits (Ponge, 2020)
	Without ocelli	Oce.absent	
	1 + 1 to 3 + 3 ocelli	Oce1.3	
Reproduction type	>3 + 3 ocelli	Oce8.8	
	Parthenogenetic	Parth_reproduction	
Scales	Bisexual	Sexual_reproduction	Life habitat preference (da Silva et al., 2016)
	Presence	SCA_with	
Trichobothria	Absence	SCA_without	Move-change traits (Ponge, 2020)
	Presence	Tricho_with	
Post antennal organ (PAO)	Absence	Tricho_without	
	Presence	PAO_with	
Ecomorphosis	Absence	PAO_without	Resistance strategy to elevated temperature (Bonfanti et al., 2022)
	Presence	Ecomorphosis_with	
	Absence	Ecomorphosis_without	

Table 4
Taxonomic and functional diversity indices, CWM and betadiversity.

Indices	Formula
Number of species	Taxa number (N)
Density	Number of individuals by m ²
Beta diversity	$a / a + b + c$ where (a) number of species shared by two samples (b) number of species in sample 1 (c) number of species in sample 2
Shannon	$H = -\sum p_i \log_2 p_i$, where p_i is the proportional abundance of species i in each sample
Evenness	$H / (\log_2(N))$
CWM	$CMW = \sum [i = 1 \text{ à } N] p_i \text{ tik}$ Where tik : attribute of trait t for the i taxa
Functional richness	Quickhull algorithm
Functional Evenness	$[\sum_{i=1 \text{ à } N-1} \min(PEW_i; 1 / (N - 1)) - (1 / (N - 1))] / [1 - (1 / (N - 1))]$
Functional divergence	$\sum a_j z_j / \sum a_j$ Where a_j is the abundance of species, j and z_j is the distance of species j from the weighted centroid

(Adapted from Koleff et al., 2003; Lavorel et al., 2008; Mouchet et al., 2010.)

the attributes for a given trait is therefore 100 %). The quantitative data (size) and qualitative data (presence of PAO) therefore have a similar format. The CWM then gives a percentage presence of this attribute per community. Three functional diversity indices were calculated (Villéger, 2008) and represent different facets of the functional space occupied by the Collembola community. (i) Functional richness computes the functional volume of the community; (ii) Functional evenness is calculated to represent the regularity of the distribution of species abundance; (iii) Functional divergence allows to observe the distribution of abundance in the functional volume (Laliberte and Legendre, 2010; Mason et al., 2005).

In a second part of the analysis, Generalized Linear Models (GLM) with Poisson or Binomial distribution was used to compare the study year and land use effects and their interaction on taxonomic and functional index at regional scale. In order to study their influence on functional and taxonomic composition, a NMDS (non-metric multidimensional scaling) was performed using the Bray-Curtis dissimilarity index for each land use for a taxonomic approach. In order to investigate the functional composition, we used a matrix built with CWM values including ten functional traits (98 taxa \times 27 CWM calculated on each attributes of functional traits) and performed a Principal Components Analysis (PCA). In order to avoid auto-correlation and maintain the relative weight of each trait, we kept only one attribute for binary attributes in the PCA and weighted attributes by the total number of attributes for each functional trait.

All statistics were performed using R software version 3.5.0 (R Core Team, 2018), and the following packages: “FD” (Laliberté and Shipley, 2011), “FactomineR” (Lé et al., 2008), “factoextra” (Kassambara and Mundt, 2020), “ade4” (Dray and Dufour, 2007), “vegan” (Oksanen et al., 2014), “lsmmeans” and “lme4” (Bates et al., 2015). Data will be deposited on the repository of INRAE: doi:10.15454/UCYSLH.

3. Results

3.1. Community structure: taxonomic approach and trait-based approach

A total of 98 Collembola species were collected during the five years of the project in the three land uses (S1). Density and species richness were modulated by year, land use and their interaction (Table 5). No effect of these variables was observed for Shannon or Evenness index.

In forests, the mean number of species, the density, and the diversity were greater in 2011 compared to other years. In particular, the mean number of species significantly increased in 2011 compared to 2009 and 2010 (among 15 species versus 8 species) and then decreased in 2012 and in 2013 (with respectively 11 and 8 species), with a significant difference between 2011 and 2013. This pattern was similar for density

Table 5
Results of generalized linear mixed models testing the effects of years, land-use, and their interaction on taxonomic indices. Significant models were indicated by * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Y = Year, L = Land use.

	df	F	Pvalue
Collembola Density			
Year	4	29.192	<2.2e-16 ***
Land use	2	39.775	<2.2e-16 ***
Y * L	7	25.965	<2.2e-16 ***
Collembola taxonomic richness			
Year	4	3.16	0.01 *
Land use	2	4.43	0.01 *
Y * L	7	6.83	3.9e-08 ***
Shannon index			
Year	4	0.39	0.82
Land use	2	0.02	0.98
Y * L	7	0.41	0.89
Evenness index			
Year	4	1.30	0.27
Land use	2	0.38	0.68
Y * L	7	1.18	0.31

(8 10^3 individuals·m⁻² in 2009 and 2010 versus 20 10^3 individuals·m⁻² in 2011) (Table 6).

In grasslands, the patterns were different between density and diversity. The mean number of species was significantly greater in 2011 compared to other years, whereas Collembola density was lower in 2011 and following years compared to 2010 (around 3300 and 1700 individuals·m⁻² in 2012 and 2013 compared to 15,300 and 8400 individuals·m⁻² in respectively in 2010 and 2011).

Table 6
Taxonomic diversity indices (mean \pm standard deviation) of Collembola in the 3 land uses according to the year. Lower case letters indicate significant differences among years (alpha = 0.05).

		Forest	Grassland	Arable land
2009	Beta div	0.36b		0.58bc
	Mean number of species	8.0 \pm 1.3b		7.9 \pm 2.9ab
	Density (10 ³ individuals·m ⁻²)	8.4 \pm 4.7b		7.8 \pm 10a
	Shannon diversity index	1.4 \pm 0.1		1.5 \pm 0.5
2010	Evenness index	0.7 \pm 0.1		0.7 \pm 0.2b
	Beta div	0.62a	0.48ab	0.49c
	Mean number of species	8.1 \pm 3.6b	8.3 \pm 1.5	9.6 \pm 2.6a
	Density (10 ³ individuals·m ⁻²)	6.4 \pm 4.1b	15.3 \pm 17.0a	7.6 \pm 2.3a
2011	Shannon diversity index	1.4 \pm 0.6b	1.6 \pm 0.2ab	1.7 \pm 0.4
	Evenness index	0.6 \pm 0.2	0.7 \pm 0.1	0.7 \pm 0.1b
	Beta div	0.52a	0.54b	0.63b
	Mean number of species	15.1 \pm 3.1a	11.2 \pm 5.3a	7.1 \pm 2.5b
2012	Density (10 ³ individuals·m ⁻²)	20.1 \pm 12.9a	8.4 \pm 4.6a	2.4 \pm 2.2b
	Shannon diversity index	2.1 \pm 0.3a	2.0 \pm 0.3a	1.7 \pm 0.3
	Evenness index	0.8 \pm 0.1	0.8 \pm 0.1	0.9 \pm 0.1a
	Beta div	0.55a	0.74ab	0.74a
2013	Mean number of species	10.7 \pm 5.4ab	9.7 \pm 1.9a	8.2 \pm 4.1b
	Density (10 ³ individuals·m ⁻²)	7.5 \pm 2.1ab	3.3 \pm 2.6ab	3.3 \pm 2.7b
	Shannon diversity index	1.6 \pm 0.7a	1.9 \pm 0.6a	1.7 \pm 0.6
	Evenness index	0.7 \pm 0.2	0.9 \pm 0.1	0.8 \pm 0.2a
2013	Beta div	0.53a	0.86a	0.63b
	Mean number of species	7.6 \pm 2.8b	4.2 \pm 2b	9.2 \pm 3.1ab
	Density (10 ³ individuals·m ⁻²)	4.4 \pm 3.3b	1.7 \pm 1.8b	4.1 \pm 2.6b
	Shannon diversity index	1.6 \pm 0.4a	1.0 \pm 0.5b	1.7 \pm 0.4
	Evenness index	0.8 \pm 0.2	0.8 \pm 0.2	0.8 \pm 0.1a

In arable soils, the diversity and the density were lower in 2011 than in previous years (10 species and $8 \cdot 10^3$ individuals·m⁻² in 2010 versus 7 species and $2 \cdot 10^3$ individuals·m⁻² in 2011). After 2011, the diversity and the density increased progressively up to 9 species and $4 \cdot 10^3$ individuals·m⁻² in 2013. Evenness and beta diversity fluctuated along the years but no clear significant differences were noticed.

Neither year nor land use nor their interaction effect was observed for functional indices (Table 7).

In the same way, no significant difference was observed on functional indices among the years except for the forest land use which had a functional richness increase in 2011 compared to other years (Table 8).

3.2. Community composition: taxonomic approach and trait-based approach

An NMDS was performed on the Collembola community's taxonomic composition of the Meuse area. No clear pattern was highlighted by the three NMDS on the community composition of the three land uses according to the year (Fig. S2).

We also studied the variations of the nine most frequent species in each land use among the years (Table 9). In forests, the three most frequent species were *Folsomia quadrioculata* (Tullberg, 1871), *Isotomiella minor* (Schaeffer, 1896), *Mesaphorura* sp. and *Parisotoma notabilis* (Schaeffer, 1896). In 2011, two other species joined this group: *Lepidocyrtus cyaneus* Tullberg, 1871/*Lepidocyrtus lanuginosus* (Gmelin, 1788) and *Pseudosinella alba* (Packard, 1873) identified in 90 % of the forest sampled site. In the other years, their frequency varied between 17 % and 67 %.

In grasslands, *I. minor* and *Mesaphorura* sp. were the most frequent species over the four years. *Mesaphorura* sp. decreased from 100 % of frequency in 2010 to 33 % in 2013. *I. minor* decreased quickly in 2011 with a recorded presence in 25 % of the sites only, contrary to its greater frequency in the following years (>50 %).

In arable lands, only *P. notabilis* was particularly frequent over the 5 years, even though its frequency decreased drastically in 2011 (only 37 % versus 60 % and more in the other years). 2011 seemed to be a special year concerning the composition of dominant species in arable lands. In particular, *Entomobrya lanuginosa* (Nicolet, 1841), which was infrequent in the other years, was found in 75 % of the sites in 2011, while the most frequent species in the other years (e.g. *Isotoma viridis* Bourlet, 1839, *P. alba* or *Mesaphorura* sp.) were present in <44 % of the sites in 2011.

In forest, *Isotomiella minor* (Schaeffer, 1896), *Mesaphorura* sp. and *Folsomia quadrioculata* (Tullberg, 1871) were the most frequent species over the five years. However, as for arable lands, the last two species frequency decreased drastically in 2011.

In arable land, functional traits discriminated among the five years

Table 7

Results of generalized linear mixed models testing year, land use and their interaction effects on functional indices. No significant model was demonstrated. Y = Year, L = Land use.

	df	F	Pvalue
Functional richness			
Year	4	0.06	1.00
Land use	2	0.01	1.00
Y * L	7	0.05	1.00
Functional divergence			
Year	4	0.03	1.00
Land use	2	0.04	0.96
Y * L	7	0.02	1.00
Functional evenness			
Year	4	0.07	1.00
Land use	2	0.18	0.84
Y * L	7	0.06	0.99

Table 8

Functional diversity indices (mean +/- standard deviation) of Collembola in the 3 land uses according to the year (Functional richness, Functional evenness, Function divergence). Lower case letters indicate significant differences among the years (alpha = 0.05).

		Forest (n = 47)	Grassland (n = 20)	Arable land (n = 77)
2009	Fric	0.001 ± 0.001ab		0.18 ± 0.04
	FEve	0.52 ± 0.11ab		0.62 ± 0.16
	Fdiv	0.77 ± 0.15		0.77 ± 0.1
2010	Fric	0.001 ± 0.001ab	0.20 ± 0.02	0.20 ± 0.05
	FEve	0.64 ± 0.06ab	0.58 ± 0.22	0.66 ± 0.1
	Fdiv	0.83 ± 0.10	0.78 ± 0.10	0.81 ± 0.1
2011	Fric	0.004 ± 0.002a	0.18 ± 0.04	0.14 ± 0.06
	FEve	0.57 ± 0.09ab	0.68 ± 0.05	0.76 ± 0.08
	Fdiv	0.86 ± 0.09	0.79 ± 0.11	0.82 ± 0.05
2012	Fric	0.001 ± 0.002ab	0.15 ± 0.07	0.15 ± 0.07
	FEve	0.52 ± 0.09b	0.76 ± 0.10	0.72 ± 0.1
	Fdiv	0.70 ± 0.21	0.82 ± 0.07	0.76 ± 0.15
2013	Fric	0.001 ± 0.001b	0.11 ± 0.05	0.17 ± 0.07
	FEve	0.69 ± 0.13a	0.63 ± 0.23	0.70 ± 0.08
	Fdiv	0.76 ± 0.14	0.89 ± 0.1	0.78 ± 0.1

along axis 1 and 2 (ANOSIM, P = 0.001, Fig. 3 a,b). The year 2011 was notably opposed to the other years on axis 1 and 2. The axis 1 (32 %) was associated with the following traits: number of ocelli, furcula length, reproduction mode, PAO, scales and trichobothria presence. Axis 2 (20 %) was associated with ecomorphosis and body size over 3 mm. Also, there were significant differences of CWM among the years with a higher representation of individuals with 8 + 8 ocelli (66 % in 2011 vs 18 % in 2009), sexual reproduction (66 % in 2011 vs 18 % in 2009) and without scales (63 % in 2011 vs 88 % in 2009) and PAO (49 % in 2011 vs 20 % in 2009).

The year of sampling did not affect the functional composition of collembolan communities in forests. On the PCA (Fig. 3 c,d), Axis 1 (33 %) was associated with number of ocelli, furcula length, pigmentation and reproduction mode, whereas axis 2 (19 %) was associated with scales, ecomorphosis and PAO.

In grasslands, functional traits were significantly discriminated over the four years along axis 1 (ANOSIM, bray distance, P = 0.009, Fig. 3 e, f): 2011, 2012, 2010 and finally 2013 on the left of axis 1. Axis 1 (34 %) was associated with several functional traits: number of ocelli, furcula length, body size, PAO presence and reproduction mode. Axis 2 (18 %) was associated with ecomorphosis and body shape without distinction between the years. There were significant differences of CWM among the years, especially between 2013 and 2011 with a higher representation of individuals with sexual reproduction in 2011 (85 %) compared to 2013 (63 %), and long furcula in 2011 (87 %) compared to 2013 (41 %) and a bigger body size (>2 mm) in 2011 compared to 2013.

4. Discussion

In this study, we investigated the Collembola community dynamics over five years, including an extreme drought event (year 2011), at the regional scale (Meuse, France) in different land use types. We found that (1) the extreme drought modified the taxonomic and functional compositions of Collembola communities. We confirmed (2) that the land use modulated the effects of the extreme drought year event on Collembola richness and densities, this one being stronger in agricultural systems compared to forests.

These observations are contrary to previous studies that noticed weak effects of climate change on the structure of Collembola (Makkonen et al., 2011; Yin et al., 2020). Collembola are often considered drought tolerant because they are able to go into diapause or anhydrobiosis (Beladjal et al., 2024; Bonfanti et al., 2023). However, this sub-lethal effect is often demonstrated in studies with moderate drought, not in the case of extreme events (Bonfanti et al., 2022). Jucevica and Melecis (2006) concluded that an increase in temperature

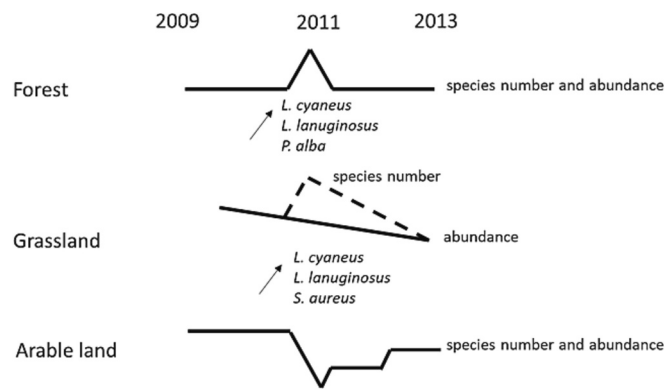


Fig. 4. Schematic representation of Collembola communities' responses to an extreme drought in 2011.

(Thompson et al., 2009), and/or a resilience capacity to face this extreme drought event year. The tree canopy could buffer the climatic variations. (ii) In grasslands, 2011 induced an increase in species richness followed by a strong decrease in species richness and abundance in 2012 and 2013 with values lower than in 2010. As for forests, the increase in 2011 in grasslands could be associated to the presence of new species or an increase of “move” species such as *L. cyaneus* or *L. lanuginosus*. These modifications of species frequency could also be observed on functional Collembola communities with a greater number of individuals with a long furcula, ocelli, sexual reproduction and also a bigger size in 2011 compared to the other years. These created new biotic interactions, which seem unfavourable for Collembola communities with a decrease of species/abundances in the following years. No resilience or resistance was observed in grasslands in the time frame studied. (iii) In arable lands, 2011 involved a decrease of taxonomic and functional indices followed by a slight increase in the following years. This pattern corresponds to our hypothesis considering that an extreme drought event involves a decrease of taxonomic and functional indices. In contrast to the other two land uses, “move” or “change” species were affected in the same way. The ability of arable land to return slightly to a pre-condition state advocated in favour of a resilience in arable lands.

Thus, the biodiversity of Collembola severely decreased in arable lands and in grasslands in 2011. Even though, in the case of the arable lands, we observed a resilience, the very low biodiversity frequently observed in this land use (Joimel et al., 2017) combined with the time needed to recover to its initial state, raises questions about the sustainability of the arable land system, especially if climatic events are more frequent in the coming years. Moreover, the strong Collembola density decrease in grasslands after 2011 adds concerns about the ability of Collembola communities to resist climate change. In contrast, forests appear to be a more stable ecosystem compared to grasslands. Indeed, they remain in a similar state within bounds, that is, they are capable of maintaining a dynamic equilibrium in time while resisting change (Thompson et al., 2009). In summary, these findings suggest that the negative effects of climate change could be intensified by land use type and more specifically by intensive management.

More generally, this regional-scale study addressed the need for multiple sampling efforts throughout the year and over several years (Eisenhauer et al., 2019; Siebert et al., 2019), using a trait-based approach to better understand how soil biodiversity and ecological functions respond to climate change (Yin et al., 2020). This type of long-term observatory is more common in the case of physicochemical studies but is rarer for biodiversity. The ongoing development of national programmes on soil biodiversity monitoring should be encouraged. However, attention should be paid to the construction of these programmes which are often based on stratified sampling around a grid. As land use has such an effect on the soil biodiversity response, it appears necessary to consider the different land uses.

Finally, this event of 2011 was classified as an “extreme event” with reference to 1981–2010 norms which are representative of the average climate over a period of time around the 1990s. However, these norms are no longer representative of the ‘current’ climate in the context of climate change, particularly in terms of temperature. Also, in the beginning of 2022, in accordance with the World Meteorology Organisation, Météo-France undertook an operation to update the reference norms for the period 1991–2020. It will replace the 1981–2010 reference period. It can therefore be concluded that what was extreme in 2011 will become the norm in the coming years with consequent effects on soil communities.

5. Conclusion

We conclude that an extreme drought could negatively affected Collembola communities by decreasing their density and taxonomic diversity and modifying their species and functional composition. Our findings also reveal that this effect could be short (arable land), long (grassland) or even no effect could be observed (forest) depending on the land use. The diversity of Collembola communities may be considered as an indicator of the resilience of the ecosystems facing extreme climatic events. Especially, functional indices in addition of taxonomical indices could be useful in order to better understand the relationship between climate change and soil fauna. The varying responses could be due to the stability of forest ecosystems, less perturbed by human activities than agricultural land uses and due to its pedoclimatic conditions (higher humidity and more organic matter). Urban land use, subject to high levels of perturbation, need to be incorporated in the observatory of soil biodiversity.

Future studies need to carry on the functional exploration in integrating trait measures in order to determine (i) the effects on soil functioning and (ii) the adaptations of Collembola individuals to climate change.

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CRediT authorship contribution statement

Sophie Joimel: Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Jonathan Bonfanti:** Writing – review & editing, Writing – original draft. **Julie Bahri:** Methodology, Investigation. **Pierre Ganault:** Writing – review & editing, Writing – original draft. **Alain Rakoto:** Investigation. **Paul-Olivier Redon:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Jérôme Cortet:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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