



## Land use modulates the effects of climate change on density but not community composition of Collembola



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### ABSTRACT

Collembola are highly abundant and diverse soil animals and play key roles in litter decomposition and nutrient cycling. Given their functional significance, it is important to understand their responses to human-induced global changes, such as climate change and land-use intensification. Here, we utilized an experimental field study, to test the interactive effects of climate (ambient vs. future) and land use (five land-use regimes, from extensively-used meadow to conventional farming) on three eco-morphological life forms of Collembola: epedaphic, hemiedaphic, and euedaphic species. We found that the effects of climate change on Collembola density were modulated by land use, and that the responses of different life forms to climate × land use interaction differed in magnitude and/or direction. The densities of total and hemiedaphic Collembola significantly decreased under organic farming and marginally increased in grasslands under future climatic conditions, whereas epedaphic Collembola tended to decrease their density with climate change in grasslands. In contrast, the density of euedaphic Collembola significantly increased with climate change in intensively-used grasslands. Further, we found that grasslands (especially extensively-used meadow) support the most abundant Collembola communities, with high species richness but low evenness. Multivariate analyses revealed independent effects of climate change and land-use intensification on Collembola community composition. Together, our findings indicate that the effects of climate change on Collembola communities depend on their life forms and land-use types. Surface-dwelling Collembola are more vulnerable to land use and climate change than those living in deeper soil layers. This may slow down the process of soil-surface litter decomposition in a changing world.

### 1. Introduction

Climate change and land-use intensification are two of the most pervasive global environmental changes, which are threatening the biodiversity and functioning of terrestrial ecosystems (Sala et al., 2000). However, the impacts of these global changes and their potential interactions are mostly studied for aboveground communities, and we still know less about the responses of below-ground communities (Bokhorst et al., 2012). Soil fauna communities are remarkably

abundant and diverse. They play crucial roles in soils, which regulate multiple ecosystem functions and determine how these ecosystems respond to global changes, such as climate and land use (Bardgett and Van Der Putten, 2014). Among them, Collembola are one of the most abundant invertebrate decomposer groups in almost all terrestrial ecosystems, with densities often reaching thousands of individuals per square meter (Hopkin, 1997). They greatly contribute to litter decomposition through fragmentation or via stimulating microbial activity by grazing (Hanlon, 1981). Moreover, Collembola often occupy a key

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position in soil food webs, as they are not only consumers of microorganisms (Thakur and Geisen, 2019; Turnbull and Lindo, 2015), but also prey of predators, such as centipedes and predatory mites (Turnbull and Lindo, 2015; Yin et al., 2019b). Due to their high sensitivity to environmental changes, Collembola are often used as indicators to assess environmental degradation and soil quality (Frampton, 1997; Hågvar and Klanderud, 2009).

The dynamics and assemblage of Collembola communities are closely related to environmental conditions (Chernova and Kuznetsova, 2000; Makkonen et al., 2011). Kardol et al. (2011) found that the density and species richness of Collembola were positively related to soil moisture content and were negatively related to soil temperature (due to warming-related reductions in soil moisture content). Therefore, both warming and desiccation can negatively affect Collembola communities (particularly euedaphic species, Krab et al., 2010). Different species are likely to differ in response to these environmental factors (McGeoch et al., 2006), which could alter their community structure (Bokhorst et al., 2008; Pollierer and Scheu, 2017). Again, temperature and moisture have also been shown to explain most of the variation in community composition of soil microarthropods (Kardol et al., 2011) and their activity (Thakur et al., 2018). However, many previous studies investigated the effects of temperature and moisture separately on Collembola communities. Though, in most regions, future climate is characterized by the combination of higher temperatures and altered precipitation patterns (Dale et al., 2001; IPCC, 2018). Therefore, studies are urgently needed to explore their combined effects under realistic climate scenarios (Korell et al., 2019). Besides, the changes in land-use type and management intensity are also considered as primary factors determining Collembola community composition (Hopkin, 1997; Lavelle, 1997). Understanding these effects of global changes on Collembola is thus essential to develop and implement effective measures to conserve their community and ecosystem functioning (Sousa et al., 2006).

Collembola species occupy distinct spatial habitats within the soil (Rusek, 1998), and are accordingly grouped into three main life forms (Hopkin, 1997). First, species dwelling on the surface of the soil are epedaphic Collembola with relatively large body size and fast dispersal ability. Second, species dwelling in the soil are euedaphic Collembola with relatively small body size and low dispersal ability, and third, species showing intermediate characteristic between epedaphic and euedaphic species are called hemiedaphic Collembola. These life forms of Collembola exert distinct roles in the soil. For example, epedaphic species tend to initiate the earlier stages of decomposition (with higher litter C to N ratios), while euedaphic species (by dwelling in the deeper layers of the organic soil horizon with lower soil C to N ratios) become active during the later stages of decomposition (Krab et al., 2010). Moreover, different life forms may differ in their responses to climate change and land-use intensification, which may subsequently result in shifts in the structure of Collembola communities (Auclerc et al., 2009), and thereby the functioning of ecosystems (Briones et al., 2009). However, it is still poorly known how global change drivers affect different life forms of Collembola.

Temperature differences determined by soil layers are indicative for the thermal niches of soil organisms living therein (Lieferting and Ellers, 2008). Euedaphic species occupy comparatively stable environments, therefore they have been shown to be more negatively affected by fluctuating temperature regimes and extreme weather events compared to hemiedaphic and epedaphic species (Bokhorst et al., 2012; Holmstrup et al., 2018). Tsiafouli et al. (2005) showed that the desiccation intolerance of Collembola was related to their body size, cutaneous respiration, and relatively thin exoskeleton. Therefore, Collembola with smaller body size, such as euedaphic species, have higher surface area to volume ratios and are particularly vulnerable to desiccation (Krab et al., 2010). Additionally, different life forms of Collembola may differ in response to intensive land use (Pollierer and Scheu, 2017), but until now, there is no consensus on potential differences. For example, Ponge et al. (2006) suggested that euedaphic

species, due to their limited active dispersal, may suffer more from land-use intensification, compared to hemiedaphic and epedaphic species. By contrast, Ellers et al. (2018) showed stronger effects of intensive land use on epedaphic than euedaphic Collembola. Furthermore, land-use types characterized by higher plant diversity can favor Collembola communities (Querner et al., 2018), but these effects might differ among Collembola life forms with more pronounced effects on soil-dwelling species than on epedaphic species (Eisenhauer et al., 2011).

Given that both climate change and land-use intensification can negatively influence Collembola communities and may differentially influence specific life forms of Collembola, it is plausible that climate-change effects are dependent on land-use type and/or management intensity (Walter et al., 2013; Yin et al., 2019a). In fact, land-use effects can further cause shifts in microclimate (i.e., temperature and moisture), which may modulate climate-change effects on soil organisms (Petersen, 2011). Intensive land use, often with low biodiversity, may intensify detrimental climate-change effects. By contrast, extensive land use, with relatively high biodiversity, may buffer these detrimental effects, since systems with high diversity often have higher resistance to combat adverse environmental conditions (de Mazancourt et al., 2013; Goldenberg et al., 2018; Siebert et al., 2019). Therefore, exploring the potential interactive effects of climate and land use is crucial to predict how Collembola communities and their functions may be influenced and could be maintained under future conditions.

Here, we utilized the Global Change Experimental Facility (GCEF; Schädler et al., 2019) to investigate the single and interactive effects of climate change and land-use intensification on Collembola communities. In this experimental platform, a future climate scenario for Central Germany in the years of 2070–2100 is simulated by increased air and soil temperatures (+0.6 °C vs. ambient) and altered precipitation (−20% in summer and +10% in spring/autumn vs. ambient). In addition, five land-use regimes with two croplands (conventional farming and organic farming) and three grasslands (intensively-used meadow, extensively-used meadow and extensively-used pasture) were set up. The aim of this study was to explore the effects of climate change on the density, species richness, and community composition of Collembola, and how these effects are altered by land-use type (croplands vs. grasslands) and management intensity. We tested four hypotheses: (1) climate change will decrease the densities and species richness of Collembola communities, especially for euedaphic (soil-dwelling) species; whereas epedaphic (surface-dwelling) and hemiedaphic (intermediate between epedaphic and euedaphic) species may be influenced to a lower extent. (2) Grasslands and extensively-managed fields will have higher densities and species richness of Collembola than croplands and intensively-managed fields. More specifically, epedaphic Collembola species will be more vulnerable to land-use intensification than euedaphic Collembola. (3) Climate-change effects on the densities and species richness of Collembola communities will be modulated by land-use type/management intensity. Specifically, the detrimental climate-change effects will be intensified in croplands and/or under intensive management, with the most pronounced effects on epedaphic and hemiedaphic Collembola; whereas detrimental climate-change effects will be modest in grasslands and/or under extensive management, with the most pronounced effects for euedaphic Collembola. (4) Interactive effects of climate and land use will alter the community composition of Collembola, as driven by the distinct responses of Collembola species with different life forms. Investigating how Collembola communities respond to the interactive effects of climate change and land-use intensification will allow us to better predict the responses of soil communities and the processes they drive (i.e., litter decomposition and nutrient cycling) to global change.

## 2. Materials and methods

### 2.1. Study site

The study site is located at the field research station of the Helmholtz-Centre for Environmental Research (UFZ) in Bad Lauchstädt, Saxony-Anhalt, Germany (51° 23' 30N, 11° 52' 49E, 116 m a.s.l.), which was a former arable land (with the last crop cultivation in 2011). The soil type of this study site belongs to Haplic Chernozem, which is based upon carbonic loess substrate. The humus layer reaches down to a soil depth of more than 40 cm. Within the upper 15 cm, the soil is characterized by high concentrations of total carbon (1.71%–2.09%) and total nitrogen (0.15%–0.18%), as well as high water storage density (1.35 g/cm<sup>3</sup>) (WRB, 2006), which provides a habitat with generally favorable conditions for soil organisms with a neutral pH (~7.0) and low susceptibility to drought (Altermann et al., 2005).

### 2.2. Experimental set-up

The Global Change Experimental Facility (GCEF, Schädler et al., 2019) was established in 2013 as an experimental platform for ecologists to investigate the interacting effects of climate and land use on multiple ecosystem processes. The two experimental treatments were implemented using a split-plot design with climate as main-plot factor (n = 10) and land use as sub-plot factor (n = 50). Specifically, each of the ten main-plots was divided into five sub-plots (16 m × 24 m), resulting in 50 sub-plots in total (Fig. S1a). Half of the main-plots are subjected to ambient climate conditions, while the other half main-plots are subjected to future climate conditions (Fig. S1b).

The climate treatments were first applied in 2014 (initiating the temperature treatment in spring; and initiating precipitation treatment in summer). The main-plots with future climate have steel construction (5 m height) with an irrigation system as well as mobile roofs and side panels that can be closed via rain sensors/timers. The main-plots with ambient climate also have steel constructions to control for potential side effects of the infrastructure, i.e., microclimatic effects. The climate treatments were chosen based on a consensus scenario across several dynamic models for Central Germany for 2070–2100, which include higher inter-annual rainfall variability with longer drought periods over summer and increased precipitation in spring and fall (Jacob and Podzun, 1997; Rockel et al., 2008). The mean projection across the different scenarios is an increase of mean temperature across all seasons by around ~1 °C. For precipitation, mean values of the 12 projections resulted in an experimental treatment consisting of a ~9% increase in spring (March–May) and autumn (September–November) and a ~21% decrease in summer (June–August).

For our future climate treatment, shelters were automatically closed from sundown to sunrise to increase night temperature (Beier et al., 2004). During our experiment, the roofs were active from 22nd March to 29th November in 2016. The night closing during these periods increased the mean daily air temperature at 5 cm-height by 0.55 °C, as well as the mean daily soil temperature in 1 cm- and 15 cm-depth by 0.62 °C and 0.50 °C, respectively. With the irrigation system we added around ~110% of ambient rainfall to the main-plots with future climate in spring and autumn. Additionally, the rain sensors associated with the irrigation system were used to control precipitation on the main-plots with future climate to ~80% of ambient rainfall in summer (from May to August). As a result, precipitation was increased by 9.2%–13.6% in spring and autumn and decreased by 19.7%–21.0% in summer in 2016.

Within each main-plot, the five sub-plots were randomly assigned to one of the five land-use regimes: (1) conventional farming (CF, cropland), (2) organic farming (OF, cropland), (3) intensively-used meadow (IM, grassland), (4) extensively-used meadow (EM, grassland), and (5) extensively-used pasture with sheep grazing (EP, grassland; Fig. S1c). Before the establishment of the land-use treatments, oat was planted in 2013 to homogenize the plots. Each land-use treatment represents a

**Table 1**

Results (F-values) of split-plot generalized linear mixed models (type III sum of squares) testing the effects of climate, land use, and their interaction on (a) density and (b) species richness of total, epedaphic, hemiedaphic, and euedaphic Collembola, as well as (c) diversity indices (Pielou's evenness, Simpson dominance and Shannon-wiener diversity) of Collembola communities. \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

Effects	Df	a) Density			
		Total Collembola	Epedaphic Collembola	Hemiedaphic Collembola	Euedaphic Collembola
Climate (C)	1,8	0.26	0.05	0.54	0.15
Land use (L)	4,32	495.2***	280.74***	126.37***	3.21*
C × L	4,32	12.28***	3.17*	26.65***	19.66***
Effects	Df	b) Species richness			
		Total Collembola	Epedaphic Collembola	Hemiedaphic Collembola	Euedaphic Collembola
Climate (C)	1,8	0.93	0.08	1.03	0.33
Land use (L)	4,32	15.69***	18.61***	2.77*	0.22
C × L	4,32	0.81	0.8	0.47	0.57
Effects	Df	c) Diversity indices			
		Shannon-wiener diversity	Pielou's evenness	Simpson dominance	
Climate (C)	1,8	0.33	0.00	2.01	
Land use (L)	4,32	0.98	5.69**	0.6	
C × L	4,32	1.93	0.03	1.15	

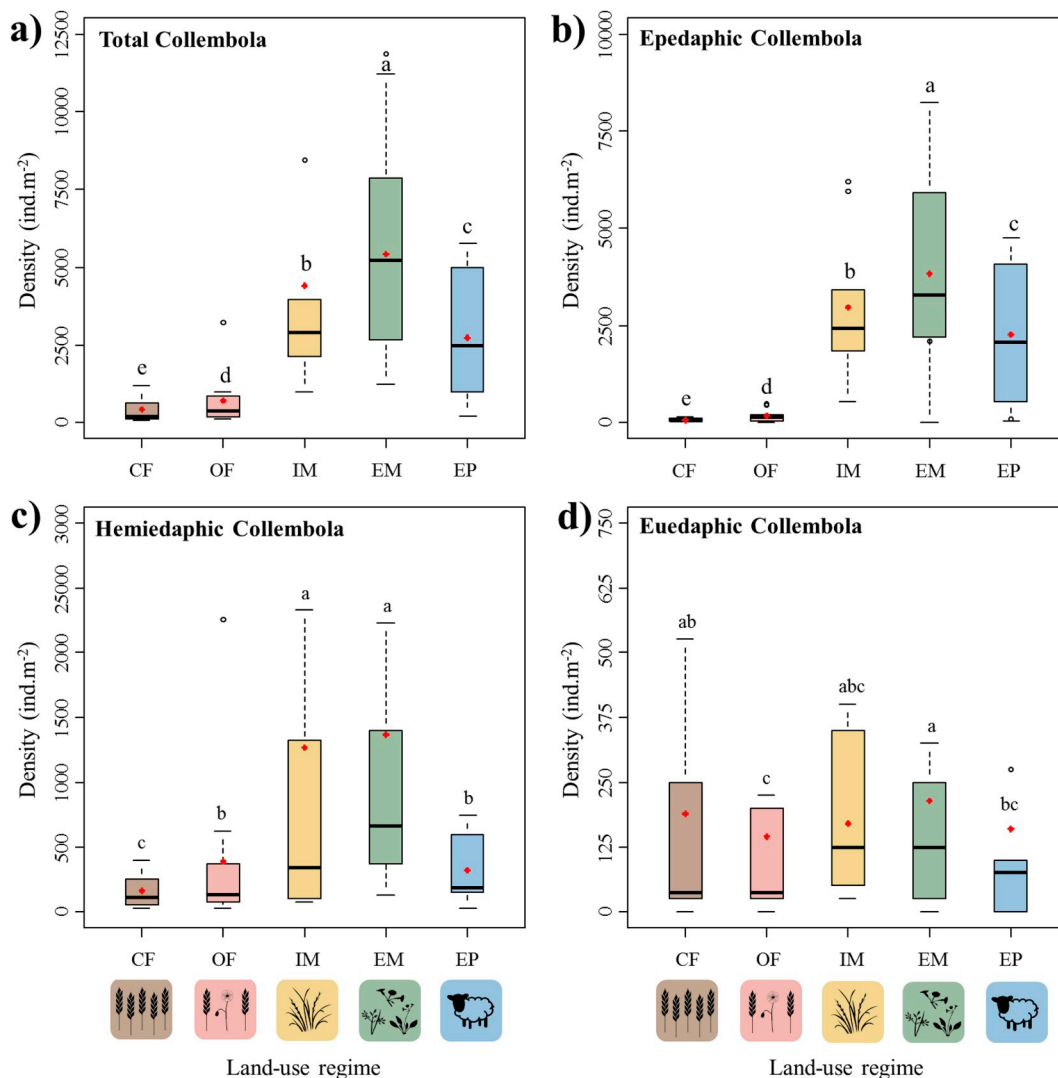
common local management type that entails multiple aspects of above-ground vegetation diversity and composition, management intervals, and fertilization (Schädler et al., 2019). In brief, under conventional farming a typical crop rotation (winter rape-winter wheat-winter barley) was established while allowing the use of the usual mineral fertilizers and pesticides whereas under organic farming fertilization is exclusively realized by replacing rape by legumes (alternating alfalfa and white clover) and most pesticides are not allowed. The intensively used grassland was established from a seed mixture of 4 forage grasses and is moderately fertilized and mown four times per year. The extensively used grasslands are established from a mixture of about 60 grassland species from different local populations and are mown two times per year (meadows) or grazed by sheep three times per year (pastures). While the two extensively-used grasslands contained  $53.1 \pm 2.0$  plant species per 9 m<sup>2</sup>, the intensively-used grassland had  $10.1 \pm 3.6$  plant species per 9 m<sup>2</sup> (mean ± SD for 2015–2017). The land-use treatments were established in autumn 2013 and spring 2014 (extensively used grasslands) by sowing. To avoid edge effects, a buffer zone of 4.5 m at the northern and southern sides and 2 m at the eastern and western sides of the subplots is generally excluded from any measurements. For further details on experimental design and the plant species pools and sowing densities see Schädler et al. (2019).

### 2.3. Collembola sampling, extraction, and identification

To investigate Collembola communities, two soil cores (Ø 16 cm, 5 cm length) were taken at a distance of more than 2.5 m along a 15 m × 0.6 m transect from each sub-plot (Fig. S1d) in October 2016. Within 10 days, Collembola were extracted from the soil cores using a Kempson heat extractor by gradually increasing the temperature. The extracted Collembola were preserved in ethanol (70%) and identified to species level and classified into three life-form groups, epedaphic, hemiedaphic, and euedaphic (specific species with basic description see Table S1, Dunger and Schlitt, 2011; Fjellberg, 2007; Hopkin, 1997, 2007, Pomorski, 1998; Potatov, 2001) using a VHX-Digital Microscope (Japan).

### 2.4. Statistical analysis

Individual numbers (abundance), density, and species richness were



**Fig. 1.** Effects of land use on densities of (a) total, (b) epedaphic, (c) hemiedaphic and (d) euedaphic Collembola. Boxplots show the median (horizontal line), the mean (red dot), first and third quartile (rectangle), 1.5 × interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes by Post hoc Tukey's HSD tests at  $P < 0.05$ . Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture (by sheep grazing). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

determined for each sub-plot. We further calculated the diversity indices, i.e., Shannon-Wiener diversity ( $H'$ ), Pielou's evenness ( $J'$ ), and Simpson dominance ( $c$ ).

Shannon-Wiener diversity

$$H' = \sum_{i=1}^N Pi \ln Pi$$

Pielou's evenness:

$$J' = H' / \ln N$$

Simpson dominance:

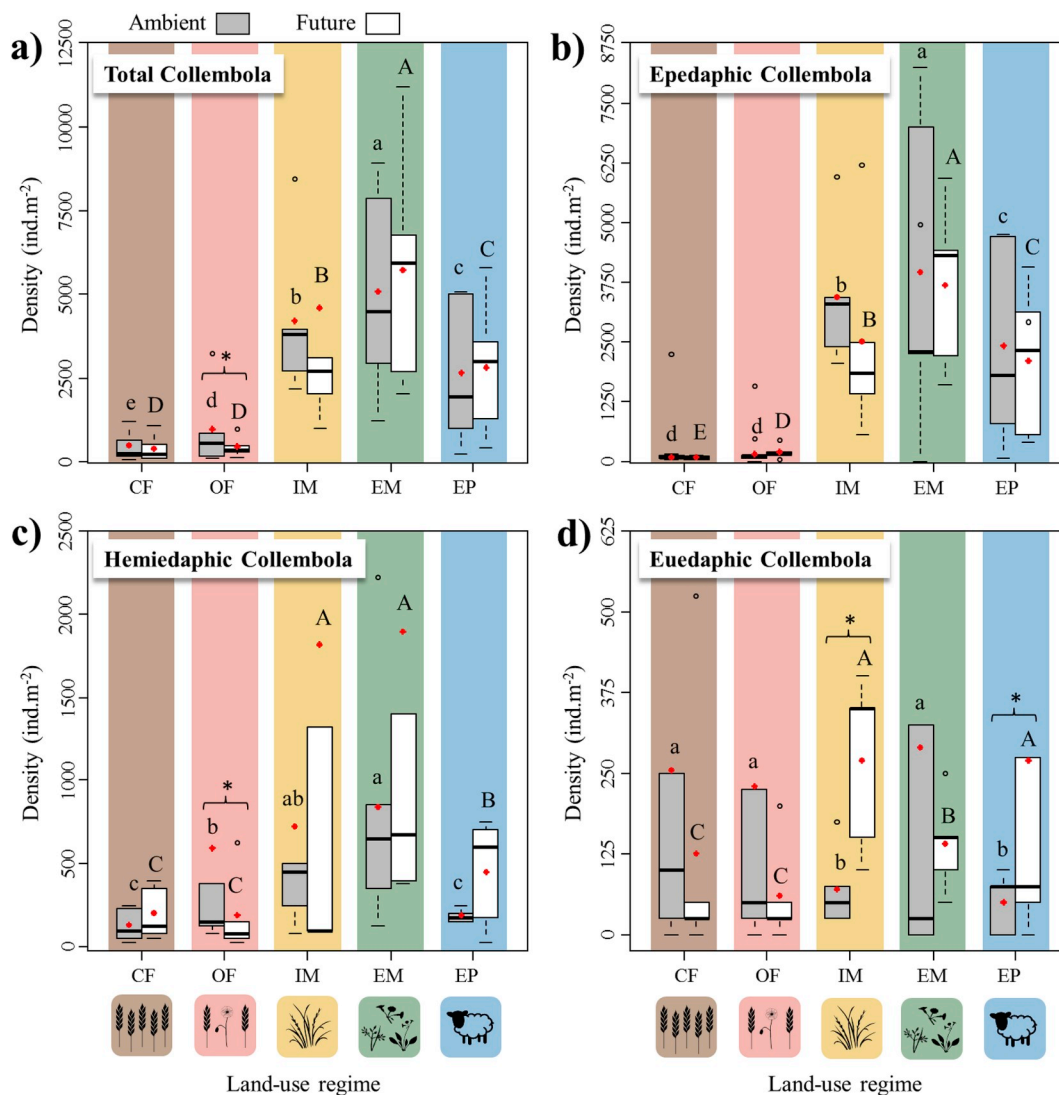
$$c = \sum (Pi)^2$$

where  $N$  represents total number of species and  $Pi = ni/N$  represents the relative ratio on abundance of the  $i$ th species ( $ni$ ) to total abundance ( $N$ ).

All response variables were analyzed in relation to climate and land use using a split-plot generalized linear mixed models (GLMM) with Type III sum of squares (PROC MIXED, SAS University Edition v9.4). The effects of climate (two levels) were analyzed at the main-plot level,

and the effects of land use (5 levels) and its interaction with climate were tested at the sub-plot level. Count data were analyzed assuming Poisson-distributed residuals with the log-link function. There was no indication of overdispersion of data, and assuming alternative distributions (including negative binomial) resulted in inferior model fit (assessed via Akaike Information Criterion). When the ANOVAs indicated significant treatment effects, post-hoc Tukey's HSD tests were conducted to test for differences among the respective levels within factors.

To analyze the relationships between Collembola community composition and the two experimental factors (climate, 2 levels and land use, 5 categories), redundancy analyses-RDA (Rao, 1964; van den Wollenberg, 1977) with permutation tests (permutation number: 999) were carried out using abundance data (R 2.1.4.2. package vegan, Oksanen et al., 2015). We checked for linear relationships in the data sets (Euclidean metric; prerequisite for this method) by detrended correspondence analyses (DCA) and identifying the respective longest gradient. As these were always lower than 3, the use of linear methods was considered appropriate (Lepš; Šmilauer, 2003). Additionally, we used scores of RDA axis 1 as a proxy for 'community composition'. Pairwise Pearson's correlation was tested between the community



**Fig. 2.** Interactive effects of climate and land use on densities of (a) total, (b) edaphic, (c) hemiedaphic, and (d) euedaphic Collembola. Boxplots show the median (horizontal line), the mean (red dot), first and third quartile (rectangle),  $1.5 \times$  interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters and capital letters represent significant differences between land-use regimes under ambient and future climate scenarios, respectively identified by Post hoc Tukey's HSD tests at  $P < 0.05$ . Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture (by sheep grazing). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

composition of Collembola and the densities and species richness of total, epedaphic, hemiedaphic, and euedaphic Collembola.

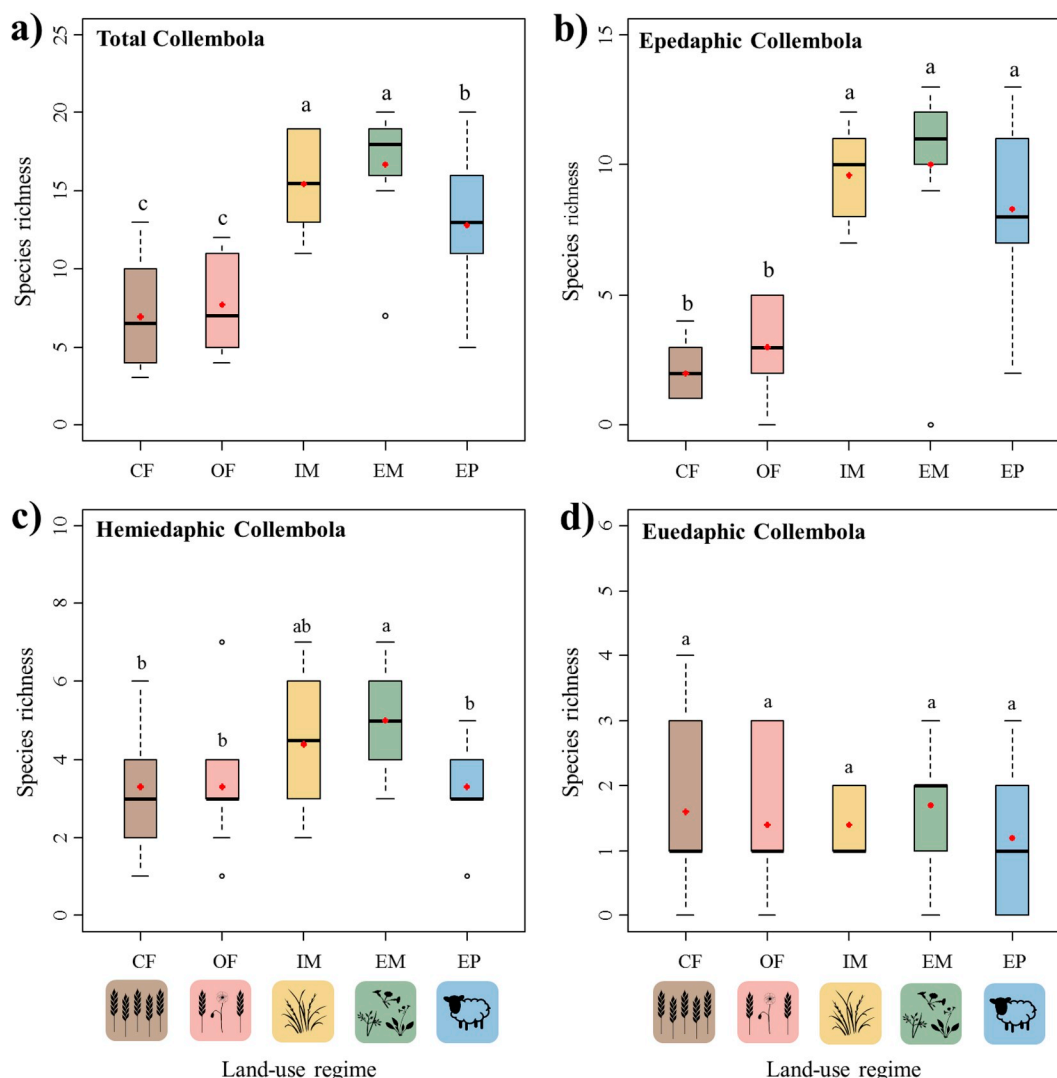
### 3. Results

#### 3.1. Population density

Overall, the densities of Collembola communities were significantly influenced by land use (Table 1a; Fig. 1). Specifically, the density of total Collembola significantly decreased from the extensively-used meadow to conventional farming, with generally higher densities in grasslands (EM > IM > EP) compared to croplands (OF > CF; Fig. 1a). Epedaphic Collembola followed the same pattern as total Collembola (Fig. 1b). In contrast, hemiedaphic Collembola showed a slightly different pattern, with highest densities in intensively- and extensively-used meadows, followed by organic croplands and extensively-used pasture and lowest densities under conventional farming (Fig. 1c). Euedaphic Collembola responded differently between

croplands (CF > OF), and differently among grasslands (meadows > EP; Fig. 1d) but with lower overall differences.

Moreover, these land-use effects were modulated by climate, with a significant interaction effect on densities of Collembola communities (Table 1a). Future climate significantly decreased (by 56%) the density of total Collembola under organic farming, while future climate tended to increase the density of total Collembola in grasslands (Fig. 2a). The responses of different life forms of Collembola to these interactive effects varied in direction and magnitude (Fig. 2b–d). The density of epedaphic Collembola had no consistent significant effects of climate (Fig. 2b). The density of hemiedaphic Collembola was significantly decreased (by 77%) in organic farming, but tended to increase in grasslands under future climatic conditions (Fig. 2c). By contrast, the density of euedaphic Collembola increased significantly with climate change in intensively-used meadows and extensively-used pastures (Fig. 2d). Additionally, the responses of individual species of epedaphic, hemiedaphic, and euedaphic Collembola to the effects of climate and land use were highly variable (Tables S2–4).



**Fig. 3.** Effects of land use on the species richness of (a) total, (b) edaphic, (c) hemiedaphic and (d) euedaphic Collembola. Boxplots show the median (horizontal line), the mean (red dot), first and third quartile (rectangle),  $1.5 \times$  interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes identified by Post hoc Tukey's HSD tests at  $P < 0.05$ . Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture (by sheep grazing). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 3.2. Species richness

Land-use regime significantly affected the Collembola species richness, whereas climate change did not (Table 1b). Total Collembola species richness was highest in intensively- and extensively-used meadows, followed by extensively-used pasture, and the two types of croplands (Fig. 3a). The responses of the different life forms of Collembola to these land-use effects were different in magnitude, although similar in direction. Specifically, the species richness of epedaphic Collembola was found to be significantly higher in the three types of grasslands than in the croplands (Fig. 2b). The species richness of hemiedaphic Collembola was significantly higher in the extensively-used meadow than in the two croplands and extensively-used pasture (Fig. 2c). The species richness of euedaphic Collembola was not significantly affected by land use (Table 1b; Fig. 2d).

### 3.3. Diversity indices

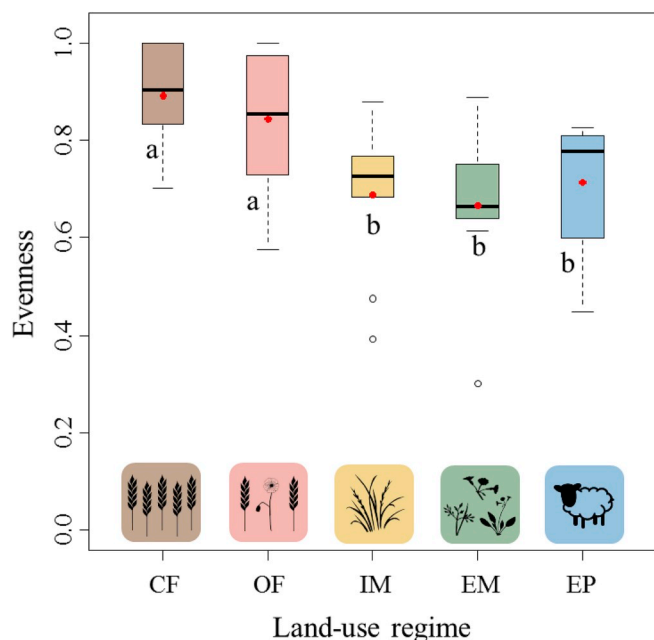
Pielou's evenness of Collembola was significantly affected by land use but not by climate, with substantially higher evenness in the two croplands compared to the three grasslands (Table 1c; Fig. 4). No

significant climate and land-use effect on Simpson dominance and Shannon-Wiener diversity was found (Table 1c).

### 3.4. Community composition

Climate change and land use significantly and independently affected the community composition of Collembola, no interaction effects were detected (Table 2). About 20% of the total variance in the data set was explained by the five constrained RDA axes (Table S5). Therein, the first RDA axis explained  $\sim 49\%$  of the variance (Table 2; Fig. 5), among which the extensively-used meadow explained mostly (Table S6), and *Isotoma viridis* had the highest species score (Table S7). The second RDA axis accounted for  $\sim 24\%$  of the variance (Table 2; Fig. 5), among which the intensively-used meadow explained mostly (Table S6), and *Sminthurus niger* had the highest species score (Table S7).

In addition, the community composition of Collembola (= RDA axis 1) was significantly correlated with the densities and species richness of total, epedaphic, and hemiedaphic Collembola, but not the density and species richness of euedaphic Collembola (Fig. S2).



**Fig. 4.** Effects of land use on evenness of Collembola communities. Boxplots show the median (horizontal line), the mean (red dot), first and third quartile (rectangle),  $1.5 \times$  interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes by Post hoc Tukey's HSD tests at  $P < 0.05$ . Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture (by sheep grazing). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 2**

ANOVA table of permutation tests for the effects of climate, land use, and their interaction on community composition of Collembola, as well as the five RDA axes. Significant effects are indicated in bold font. Var: the constraining variance.

	Df	Var	F-value	P-value
Climate effects	1	1.34	2.05	<b>0.009</b>
Land-use effects	4	5.87	2.44	<b>0.001</b>
Climate $\times$ land use interaction	4	178.4	0.56	0.903
RDA 1	1	3.55	5.43	<b>0.001</b>
RDA 2	1	1.73	2.64	<b>0.012</b>
RDA 3	1	1.03	1.58	0.308
RDA 4	1	0.5	0.76	0.976
RDA 5	1	0.41	0.63	0.893

## 4. Discussion

In this study, we tested the interactive effects of climate change and land use on the responses of Collembola communities. We found that (1) climate change alone did not significantly decrease the densities and species richness of Collembola communities; (2) land-use type significantly influenced Collembola communities, generally with higher densities and species richness in grasslands than in croplands; (3) climate-change effects on densities of Collembola communities varied among land-use regimes and among the three life forms, as indicated by significant interactive effects of the two global change drivers; and (4) effects of climate change and land-use intensification on Collembola community composition were independent from each other. Moreover, shifts in community composition of Collembola were significantly correlated with the shifts in densities and species richness of epedaphic and hemiedaphic Collembola but not euedaphic Collembola. Together, we showed that different Collembola life forms vary in responses to changing environmental conditions, and species more associated to the

soil surface may be more vulnerable to these changes than species living deeper in the soil. This is likely to slow down the litter decomposition at soil surface under intensive land use and future climate conditions.

### 4.1. Weak effects of climate change on the structure of Collembola communities

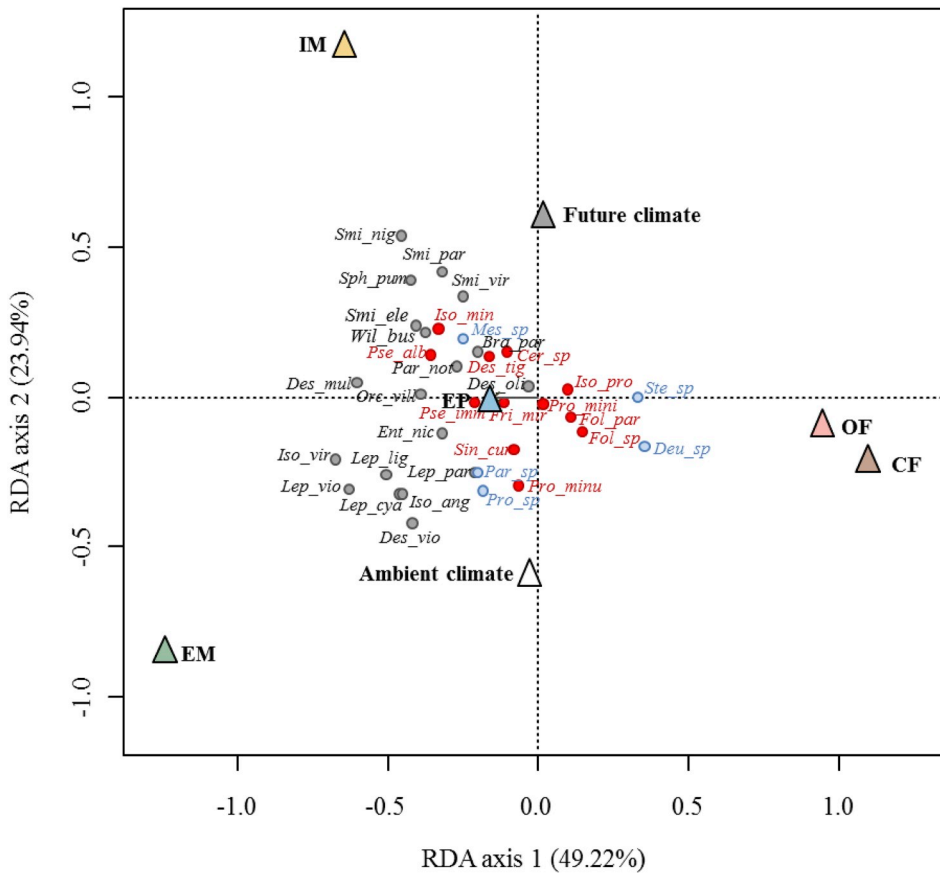
Previous studies have shown negative effects of climate change on Collembola (Kardol et al., 2011; Krab et al., 2013; Makkonen et al., 2011; Petersen et al., 2011; Sjrursen et al., 2005; Xu et al., 2012). However, contrary to our first hypothesis, we did not find any main effects of climate change on the densities and species richness of Collembola communities. The weak effects of climate change in our study could be related to the season of fauna sampling (i.e., autumn), when the climate manipulation consists of elevated temperature and higher precipitation. These climatic conditions may have counteracted potential effects of previous summer drought. This assumption is supported by Hodkinson et al. (1998), who showed that desiccation (rather than increased temperature) may drive declines of Collembola communities especially in the dry season (i.e., summer). Moreover, our previous study showed that soil fauna-driven litter decomposition decreased in summer, but not in other seasons (Yin et al., 2019a). Therefore, the climate-change effects on Collembola communities may vary among seasons, and more studies are needed with multiple samplings across the year and during several years for understanding seasonal variations in soil invertebrate animals (Eisenhauer et al., 2018; Siebert et al., 2019). This would reveal if intra-annual effects of changed precipitation and temperature patterns would result in neutral long-term climate-change effects.

### 4.2. Significant land-use effects on the structure of Collembola communities

Our findings largely support our second hypothesis that grasslands and extensively-managed fields will have higher densities and species richness of Collembola than croplands and intensively-managed fields, and that epedaphic Collembola species will be more vulnerable to land-use intensification than euedaphic Collembola. Specifically, we found that the density of total Collembola in grasslands can reach up to 5000 ind.  $m^{-2}$ , which was several times higher than the total Collembola density in croplands (conventional farming had especially low values of density with less than 1000 ind.  $m^{-2}$ ). This finding is supported by Sousa et al. (2006), who found that the densities of Collembola were significantly higher in grasslands (meadows and pastures) than in croplands across Europe. Additionally, we also found that the species richness of total Collembola was significantly higher in the three grasslands ( $15 \pm 4$ ) compared to the two croplands ( $7.3 \pm 3.1$ ). This result is in line with several previous studies (Alvarez et al., 2000; Heisler and Kaiser, 1995; Sousa et al., 2006), which indicated that land use with lower plant species richness and/or more frequent disturbances related to intensive management may cause a decrease in Collembola species richness. In further support of our second hypothesis, we also found that the effects of land use on Collembola were stronger for epedaphic species than for the other life forms. This finding suggests that epedaphic species may be particularly vulnerable to intensive land use, as they are more directly affected by changes in soil surface conditions such as differences in vegetation composition (Querner et al., 2018).

### 4.3. Land use-modulated climate effects on densities of Collembola communities

In support of our third hypothesis, climate-change effects were modulated by land-use type/intensity, particularly for Collembola densities. More specifically, our results showed that future climate decreased the density of total Collembola in croplands, especially in the organic farming treatment; while it tended to increase the total density



**Fig. 5.** Species-treatment plot resulting from redundancy analyses (RDA) of Collembola community composition. About 20% of the total variance in the data set was explained by the five constrained RDA axes. Therein RDA axis 1 and 2 explained ~49% and ~24% of this variance respectively. Treatments included are climate (Ambient and Future) and land-use regimes (CF, OF, IM, EM and EP). Epedaphic species are in black, Hemiedaphic species in red, and Euedaphic species in blue. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture (by sheep grazing), and for Collembolan species: *Bra\_par* = *Brachystomella parvula*, *Cer\_sp* = *Ceratophysella* sp., *Des\_mul* = *Desoria multisetis*, *Des\_oli* = *Desoria olivacea*, *Des\_tigr* = *Desoria tigrina*, *Des\_vio* = *Desoria violacea*, *Deu\_sp* = *Deuteraphorura* sp., *Ent\_nic* = *Entomobrya nicoletti*, *Fol\_ang* = *Folsomides angularis*, *Fol\_par* = *Folsomides parvulus*, *Fol\_sp* = *Folsomia* sp., *Fri\_mir* = *Frieesia mirabilis*, *Iso\_ang* = *Isotoma anglicana*, *Iso\_vir* = *Isotoma viridis*, *Iso\_min* = *Isotomiella minor*, *Iso\_pro* = *Isotomodes productus*, *Lep\_cya* = *Lepidocyrtus cyaneus*, *Lep\_lig* = *Lepidocyrtus lignorum*, *Lep\_par* = *Lepidocyrtus paradoxus*, *Lep\_vio* = *Lepidocyrtus violacea*, *Mes\_sp* = *Mesaphorura* sp., *Orc\_vill* = *Orchesella villosa*, *Par\_not* = *Parisotoma notabilis*, *Par\_sp* = *Paratullbergia* sp., *Pro\_minu* = *Proisotoma minuta*, *Pro\_sp* = *Protaphorura* sp., *Pse\_alb* = *Pseudosinella alba*, *Pse\_imm* = *Pseudosinella immaculata*, *Sin\_cur* = *Sinella curviseta*, *Smi\_ele* = *Sminthurinus elegans*, *Smi\_nig* = *Sminthurus niger*, *Smi\_par* = *Sminthurus parvulus*, *Smi\_vir* = *Sminthurinus viridis*, *Sph\_pum* = *Sphaeridia pumilis*, *Ste\_sp* = *Stenaphorura* sp., *Wil\_bus* = *Willowsia buski*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

*Sminthurus parvulus*, *Smi\_vir* = *Sminthurinus viridis*, *Sph\_pum* = *Sphaeridia pumilis*, *Ste\_sp* = *Stenaphorura* sp., *Wil\_bus* = *Willowsia buski*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

in the three grasslands. This finding is somehow supported by some other studies (Isbell et al., 2017; Oliver et al., 2016), which suggest that intensive land use may aggravate climate-change effects on insect diversity and agroecosystems functioning due to higher disturbance and lower above- and below-ground biodiversity. Accordingly, detrimental climate-change effects could be intensified in croplands. Furthermore, the densities of different life forms varied in response to the interactive effects of climate and land use. More specifically, we found that epedaphic Collembola were not affected by the interaction of both factors. By contrast, the density of hemiedaphic Collembola significantly decreased with climate change in organic farming, whereas the density of euedaphic Collembola significantly increased in intensively-used grasslands. These results give us a new perspective that highly variable effects of climate change on Collembola communities depend on their life form and land-use type. Moreover, these findings partly support the other part of our third hypothesis, postulating that detrimental climate-change effects would be intensified by croplands and/or intensive management, with the most pronounced responses for epedaphic and hemiedaphic Collembola; whereas detrimental climate-change effects would be alleviated by grasslands and/or extensive management, with the most pronounced responses for euedaphic Collembola.

#### 4.4. Independent effects of climate and land use on community composition of Collembola

In contrast to our fourth hypothesis, we did not find any interactive effects of climate and land use on the community composition of Collembola. However, we found significant but independent effects of climate change and land-use intensification. Specifically, croplands

could lead to a less diverse community assemblage by particularly affecting soil surface-dwelling species. By contrast, ambient climate and grasslands (especially extensively-used meadow) supported a more diverse Collembola community. Together, these findings indicate rather consistent climate-change effects on Collembola species across land-use regimes. The independent climate and land-use effects on Collembola community composition are supported by an unpublished study in our experiment, where we demonstrated that climate change and land-use intensification independently decreased the total biomass of soil microarthropods due to i) climate change-induced reduction of their mean body size, and ii) land use-induced decreases of their densities. A better understanding of global change effects on the community composition of Collembola may help to predict how soil ecosystems will function in a changing world (Yin et al., 2019a).

## 5. Conclusion

We conclude that climate change and land-use type conversion from grasslands to croplands could negatively affect Collembola communities by decreasing their density and diversity. Moreover, our findings reveal that different global-change drivers can vary in their effects on Collembola communities through differential responses of Collembola life forms. These varying responses of life forms may alter the soil ecosystem services they provide. For example, soil surface-litter decomposition, which is driven by soil surface-dwelling Collembola, may slow down in a changing world. Accordingly, future studies should focus on i) analyzing soil communities at different soil depths, ii) exploring their functional trait responses, and iii) assessing the soil processes at the corresponding soil depths. This can, for instance, be done



by measuring soil enzymes and microbial communities and/or placing root litterbags and other organic substrates at different soil depths. For that, Collembola life-form groups and their traits can be ideal for further exploration and in explaining soil ecological functions and processes in a changing world.

### Conflicts of interest

The authors declare no conflict of interest.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.107598>.

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