

Effect of different crop management practices on soil Collembola assemblages: A 4-year follow-up



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ARTICLE INFO

Keywords:

Springtails
Functional approach
Conservation agriculture
Temporal dynamic
Tillage

ABSTRACT

Soil biota are a major component of agroecosystems, playing a decisive role in ecosystem services with synergistic effects on crop production. The conservation of their diversity has become a key component of a strategy towards agricultural sustainability. Over four years (2010–2014), under the “SOil Functional diversity as an Indicator of sustainable management of Agroecosystems” (SOFIA) project, we followed soil Collembola assemblages in response to the set-up of 5 cropping systems differing in crop rotations (annual or perennial), rate of N fertilization, and in tillage intensity (annual ploughing vs. shallow). Our results demonstrated that shifting from a conventional to conservation cropping system had a strong positive effect upon species richness and density of Collembola. Specifically, all treatments with a reduction in intensity of soil tillage fostered Collembola assemblages. At the end of our study, density and species richness were 3 to 4 times higher in reduced tillage (RT) than in conventional tillage (CT). Nevertheless, differentiation between the assemblages only occurred after 2 years but steadily increased until 4 years. At the last sampling date, all treatments contained significantly different Collembola assemblages (Anosim with Bray-Curtis distance). In parallel, we noticed shifts in the functional structure of the assemblages, even if globally, all life-forms were promoted under reduced tillage. However, contrary to our expectations, euedaphic Collembola were not promoted by restitution of crop residues. Our study over several years under field conditions showed that Collembola assemblages were more sensitive to tillage intensity than to either residue management or N fertilization. Clearly, conservation agriculture can foster one of the numerous services provided by the soil compartment, namely the soil biodiversity and therefore improve soil quality and health.

1. Introduction

Conservation agriculture aims at developing sustainable agricultural systems that pursue crop production while greatly mitigating their negative environmental impacts (Bommarco et al., 2013; Hobbs, 2007). To do so, agronomical practices must integrate ecological processes in order to rely more efficiently on agroecosystem self-regulation (Altieri, 1999; Wezel et al., 2014). Sustainable systems are generally based on decreasing soil disturbance by reducing tillage intensity, decreasing N fertilisation, and increasing restitution of crop residues to restore soil organic matter content (Michels et al., 1995; Scheunemann et al., 2015b).

One of the major processes taking place in soil and linked to plant production is the decomposition of organic matter and subsequent

nutrient cycling performed by soil organisms (de Graaff et al., 2015; Kibblewhite et al., 2008; Van Der Heijden et al., 2008). Within agroecosystems, beside soil microbial communities, Collembola is one of the most abundant groups of organisms. They have been shown to significantly influence belowground processes such as organic matter decomposition rate, N mineralisation, soil respiration or leaching of dissolved organic carbon (Filser, 2002) and were shown in turn to impact plant performance (Forey et al., 2015). Most of these effects are indirect, *i.e.* acting *via* alterations in microbial activities (Moore, 1988; Verhoef and Brussaard, 1990; Visser, 1985) and by transporting fungal propagules (Lussenhop, 1992; Seastedt, 1984). In turn, the Collembola critically depend on microbial communities fuelled by plant litter and root exudates (Moore et al., 2003; Schneider and Maraun, 2009). Due to their notable contribution in shaping soil microbial communities,

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Table 1

Description of the 5 investigated treatments of the SOERE ACBB located in Estrées-Mons, France, according to three main practices: soil tillage, crop residue management, and N fertilization rate.

Code	Treatment	Soil tillage Depth in cm	Crop residue management	N Fertilisation rate (kgN ha ⁻¹ yr ⁻¹)
CT	Conventional tillage	Annual ploughing 25	Returned (mouldboard ploughing)	134
CT-RN	Conventional tillage and reduced nitrogen	Annual ploughing 25	Returned (mouldboard ploughing)	43
RT	Reduced tillage	Shallow tillage 8	Returned (Disk ploughing)	134
RT-RR	Reduced tillage and residue removal	Shallow tillage 8	Exported (Hay baler)	134
P-BC	Perennial and bioenergy crop	Ploughing before culture 25	Exported (Hay baler)	134

Collembola are considered to play an important role in biological control of fungal plant pathogens (Klironomos and Kendrick, 1995; Lartey et al., 1994; Wolfarth et al., 2013). Collembola species are usually aggregated in three different life forms (epedaphic, hemiedaphic, and euedaphic) that closely relate to both dispersal ability and various functional attributes such as reproduction, mobility, and metabolic activity (Gisin, 1943) and therefore to biodemographic strategies. These life forms can be assimilated to functional groups. Aggregation to life forms or functional groups is a convenient way to detect changes in components of soil biota with broadly similar ecologies (Chauvat et al., 2003).

In general, positive effects of new conservation agricultural practices on Collembola communities have been observed (Cortet et al., 2002; Dittmer and Schrader, 2000; Petersen, 2002; Winter et al., 1990) but may depend on the soil depth considered (See Petersen, 2002). According to a compilation of the results of 106 studies done by Wardle (1995), Collembola are usually slightly stimulated when shifting from conventional toward no-tillage management, probably due to a stress-release. Furthermore, the restitution of crop residues (organic matter), was shown to significantly influence microclimatic conditions and increase trophic resources for decomposers (Axelsen and Kristensen, 2000; Kladvik, 2001), including Collembola, but see Ngosong et al., 2009). However, several studies revealed contradictory patterns with either no or negative effect of conservation practices on soil Collembola compared to conventional management (Cole et al., 2008; Holland, 2004; Postma-Blaauw et al., 2010; Scheunemann et al., 2015b; Tsiafouli et al., 2015; van Capelle et al., 2012).

Only few studies have so far focused on the dynamics of the different Collembola functional groups according to changes in agricultural practices. This approach could refine our understanding of Collembola responses to environmental changes (Chauvat et al., 2014a) and the subsequent consequences on ecological processes (Petersen, 2002). Furthermore, studies generally compared single agricultural practices, e.g. tillage type, N fertilisation rate or residues management. The effect of combining these different practices has little been addressed. Both, resource supply and physical disturbance are considered to be key determinants of biological diversity in aboveground systems (Cole et al., 2008; Lawton and Kinne, 2000).

In the present study, we monitored Collembola assemblages over four years in response to different practices varying according to crop rotations (annual vs perennial), the rate of N fertilization (low vs high), tillage (deep vs reduced), and crop residues management (restitution vs removal). The main objective of this study was to follow the differentiation of Collembola assemblages between agricultural practices over time. We hypothesized that (1a) decreasing soil mechanical disturbance will increase abundance and richness of the whole Collembola assemblage, (1b) deep living species to be favored by a reduction of tillage intensity. (2a) Reducing trophic resources through exportation of crop residues (i.e. removal) or lower N fertilization negatively impact Collembola assemblages; (2b) soil living species will mainly suffer from reducing the amount of organic matter and N entering the system. (3) Dissimilarity in Collembola assemblages composition increases with time-differentiation of agricultural practices.

2. Materials and methods

2.1. Site description

The study was conducted on the experimental platform SOERE-ACBB (Systèmes d'Observation et d'Expérimentation pour la Recherche en Environnement-Agrosystèmes Cycles Biogéochimiques et Biodiversité), located at Estrées-Mons (Northern France; 49.873 N, 3.032 E) and managed by the INRA (Institut National de la Recherche Agronomique). Soil is a typical LUVISOL (clay = 187 ± 31 g kg⁻¹, silt = 744 ± 34 g kg⁻¹, sand = 69 ± 21 g kg⁻¹, pH in water = 8.20 ± 0.10, organic C = 10.40 ± 0.80 g kg⁻¹, and total N = 1.04 ± 0.05 g kg⁻¹), climate is temperate with an annual average rainfall of 678 mm and an average annual temperature of 10.8 °C. The site characteristics were fully described by Coudrain et al. (2016).

2.2. Experimental design

The experiment was established on a 11 ha field and initiated by setting up a six-year rotation composed of spring pea (*Pisum sativum*, L.), winter wheat (*Triticum aestivum*, L.), rapeseed (*Brassica napus*, L.), spring barley (*Hordeum vulgare*, L.), maize (*Zea mays*, L.), winter wheat. A specific treatment was dedicated to switchgrass (*Panicum virgatum*, L.), a perennial crop used as bioenergy crop. The design consisted of 4 randomized blocks of 6 plots (24 plots in total, each plot was 85 m long and 48 m wide). Prior to the setting of the experiment (y + 0), all the plots were managed under conventional tillage (CT, see below). In spring 2010, 6 different treatments/practices were established according to different crop rotations (annual and bioenergy crop rotations), rate of N fertilization (reference rate vs. one third of reference rate), crop residue management (returned vs. removed), soil tillage (full-inversion ploughing vs. reduced tillage) (Table 1). Only five treatments (20 plots) were investigated in the present study: CT (conventional tillage); CT-RN (conventional tillage and reduced N fertilization); RT (reduced tillage); RT-RR (reduced tillage and crop residues removal); P-BC (perennial and bioenergy crop). For detailed information see to Table 1.

The mean amount of C returned through aerial residues was estimated to range between 1.6 and 3.2 t C ha⁻¹ yr⁻¹ in the exported vs. the returned crop residue treatments, respectively. Over the full rotation, the mean fertilization rate (reference) was 134 kg N ha⁻¹ yr⁻¹ except for the treatment RN that received only 43 kg N ha⁻¹ yr⁻¹.

2.3. Sampling, extraction and identification of collembola

Soil samples were collected in March 2010 (y + 0) before the set-up of the experiment, then in March 2012 (y + 2), 2013 (y + 3), and 2014 (y + 4) at the start of the vegetation season. In each of the 20 experimental plots, 3 soil samples (at the Northeast, Central, Southwest of each plot) were collected (60 sampling points in total) by means of soil corers (diameter 5 cm). A single core included the organic layer and the top 5 cm of the mineral horizon. We focused on the topsoil (0–5 cm) as more than 90% of the Collembola are to be found within this layer in

this experimental site (Coulibaly & Chauvat unpubl.). In the laboratory, Collembola were extracted during two weeks using the Berlèse-Tullgren device (Tullgren, 1918) that creates a temperature gradient over soil core, crumbled into a plastic sieve with 2 mm suspended over a collecting vessel containing 70% alcohol. Individuals (Collembola) collected in alcohol were counted and identified following identification keys (Gisin, 1960; Hopkin, 2007). However, some individuals were identified to genera when species identification was not possible. Finally, all species were allocated to one of three different life-forms, i.e. epedaphic, hemiedaphic, euedaphic (Gisin, 1943). These life-forms differ in fundamental ecological properties (including reproduction, vertical distribution, and metabolic activity; cf. Petersen, (2002) and can thus be considered as different functional groups.

2.4. Soil chemical properties and microbial communities

Initial soil physico-chemical parameters and their spatial variability were measured in January 2010 in the upper layer (0–20 cm). Details concerning methods and protocols are available in Coudrain et al. (2016). At each of the 60 sampling points in $y + 2$, $y + 3$, and $y + 4$, five comparative soil cores were taken, then pooled to obtain one sample per plot for each year. Soil samples were placed in plastic containers, stored in cool boxes at 4 °C and transported to the laboratory for microbial or chemical analyses. In the laboratory, soil samples were sieved at 2 mm and stored at 4 °C during few days, until further analyses.

Total organic carbon concentration (TOC) was measured for each sieved soil sample using an elemental analyser (NA 1500, Carlo Erba, Milan, Italy). Microbial biomass carbon (MBC or C_{biom}) was determined using the fumigation-extraction method described by (Vance et al., 1987). The extraction of dissolved organic C (DOC) from soil samples either fumigated with chloroform or not, was performed with 40 mL of K₂SO₄ 0.03 M (soil-solution 1:4, agitation 30 min, 20 °C) and the concentration of DOC in extracts was analysed with a C-analyser (1010, O.I. analytical, Globalspec, NY, USA). The amount of C in microbial biomass was calculated as the difference in DOC contents between fumigated and unfumigated samples, with a correction factor KEC of 0.38 (Vance et al., 1987). C mineralization was measured in standardized conditions using C–CO₂ emitted from soils during a 72 h-incubation at 15 °C and was used as a proxy of soil heterotrophic microbial activity. To do so, moist soil samples (42 g equivalent dry soil at 18.6 g H₂O 100 g⁻¹ soil) were placed in jars containing a beaker with water and a vial with 0.25 M NaOH solution to trap the CO₂ produced. The concentration of CO₂ trapped in the NaOH solution was measured by continuous flow colorimetry (Chaussod et al., 1986) using an auto-analyser (TRAACS 2000, Bran and Luebbe, Norderstedt, Germany). Soil pH_{H2O} was measured with soil diluted with demineralized water (1:2.5 w/w). Finally, standard sensors were used to continuously monitor soil temperature (TEMP) and humidity (HUM) over the project period.

2.5. Statistical analyses

For each plot and each year ($y + 0$ to $y + 4$), we calculated the mean Collembola density ($n = 3$) and species richness ($n = 3$). Density was expressed in number of individuals per square meter. Thereafter, the structure of Collembola communities was described by calculating the diversity index of Shannon (H') and the Evenness (J') Index. Furthermore, the density and species richness of each of the three functional groups were calculated to perform the different statistical analyses.

We were interested in differentiation of Collembola assemblages between treatments over time. Therefore, statistical analyses focused on the data collected for each date separately ($y + 0$, $y + 2$, $y + 3$, $y + 4$), because interannual variation within a single treatment was beyond the scope of our study. We, nevertheless, also performed analyses

to quantify changes between years for a single treatment.

To investigate the effect of agricultural practices on Collembola communities, soil abiotic and microbial parameters, we used Linear Mixed-Effects Models (LMM) with the descriptive variables of Collembola communities (total density; total species richness, density and species richness of each life form and the community diversity indices), or environmental parameters as response and the factor “treatments” (CT, CT-RN, P-BC, RT and RT-RR) as fixed categorical predictor, the factor “experimental blocks” (B1, B2, B3 and B4) as random categorical predictor. Significant differences between means were tested at a 5% rejection probability level using the Tukey HSD test. Normality and variance homogeneity were tested prior to statistical analyses.

Hypothesis of no difference in assemblage composition between treatments was tested using one-way ANOSIM based on the Bray-Curtis dissimilarity distance configuration (Clarke et al., 2006). If two groups of sampling units (treatments) are really different in their species composition, then compositional dissimilarities between the groups ought to be greater than those within the groups. ANOSIM was performed with 10000 permutations and Bonferroni's correction was applied *a posteriori*. In case of significant results, SIMPER analysis based on the Bray-Curtis dissimilarity distance was run to determine the species that contribute most in differentiating the two groups tested by ANOSIM. Finally, in order to visualize the pattern of species composition over all experimental treatments we used Non-metric multi-dimensional scaling (NMDS) computed on Bray-Curtis similarity matrix using yearly average values for each treatment.

We finally performed a Redundancy Analysis (RDA) to depict relationships between Collembola community variables as response matrix (Y) and environmental variables as explanatory matrix (X). The response matrix consisted of total density of Collembola, total species richness, density and richness of each of the three life forms. Data were transformed prior analysis to follow the normal distribution based on Gaussian or Normal distribution (data normed weighted averages). Explanatory matrix contained microbial biomass carbon (C_{biom}), metabolic activity (CO₂), soil water content (HUM), Soil temperature (TEMP), and pH_{water}. With redundancy analysis, the components extracted from X are such that they are as much as possible correlated with the variables of Y and vice versa.

ANOSIM, SIMPER and NMDS analyses were performed with the free PAST 3.14 software. Univariate statistical analyses and RDA were performed using R software (Team, 2015) with the libraries ade4 (Dray and Dufour, 2007), lme4 (Bates et al., 2014), MuMIn (Bartoń, 2013), multcomp (Hothorn et al., 2008), car (Fox and Weisberg, 2010) and vegan (Oksanen et al., 2013).

3. Results

3.1. Community structure indices

At the onset of the experimental setup (before the introduction of agronomic treatments) ($y + 0$), we recorded on average over all plots 4.60 ± 0.99 species and 1585 ± 757 individuals m

Table 2

Results of Linear Mixed-Effects Models (LMM) of the effect of year (y + 2, y + 3 and y + 4) on total density, species richness of Collembola assemblages for each agricultural treatment (CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal). The tests values are given. Chisq: Chi-squared, *p*: *p*-value, R²: variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at α = 0.05. ****p* < 0.001, ***p* < 0.01, **p* < 0.05, ns *p* > 0.05.

	LMM outputs		
	Chisq	<i>p</i>	R ² (%)
CT			
Total density	15.0	***	67.7
Total species richness	5.25	ns	32.3
CT-RN			
Total density	21.5	***	71.9
Total species richness	17.3	***	68.0
RT			
Total density	5.15	ns	35.5
Total species richness	8.91	*	63.9
RT-RR			
Total density	4.59	ns	29.5
Total species richness	9.75	**	65.7
P-BC			
Total density	55.7	***	83.5
Total species richness	11.1	**	50.2

found regarding abundance of Collembola between the last two years. Both abundance and species richness of Collembola in the treatment P-BC were significantly impacted by the factor time with a consistent pattern of higher values in y + 4 compared to the other years (Table 2 and Fig. 1).

3.1.2. Treatment effect within each year

After 2 years (y + 2), only the total density differed significantly between treatments (Table 3), with about 2-fold higher values in RT-RR than in CT (7193 and 3243 individuals m⁻², respectively). The three other treatments showed intermediate values (Fig. 2a). After 3 years (y

Table 3

Results of Linear Mixed-Effects Models (LMM) of the effect of treatment on total density, species richness, Shannon index and evenness of Collembola assemblages sampled at three different sampling dates (y + 2, y + 3 and y + 4). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. The tests values are given. Chisq: Chi-squared, *p*: *p*-value, R²: variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at α = 0.05. ****p* < 0.001, ***p* < 0.01, **p* < 0.05, ns *p* > 0.05.

	LMM outputs		
	Chisq	<i>p</i>	R ² (%)
y + 2			
Total density	36.0	***	65.4
Total species richness	7.77	ns	29.0
Shannon (H')	3.76	ns	16.5
Evenness (J')	4.71	ns	19.7
y + 3			
Total density	69.7	***	78.6
Total species richness	29.6	***	60.9
Shannon (H')	20.5	***	54.5
Evenness (J')	10.8	*	36.3
y + 4			
Total density	71.7	***	80.0
Total species richness	27.4	***	59.0
Shannon (H')	11.4	*	37.5
Evenness (J')	6.63	ns	25.9

+ 3), all community indices were influenced by experimental treatments (Table 3). The Collembola density ranged from ca 1440 to 6580 individuals m⁻² (in CT and RT-RR, respectively). On average, 3-fold more individuals were collected in RT and RT-RR than in CT, CT-RN and P-BC (5563 and 1515 individuals m⁻²; Fig. 2b). The total species richness and the Shannon index displayed the same pattern, being significantly higher in RT and RT-RR compared to CT and CT-RN. P-BC showed an intermediate richness value (Figs. 2 b, 3 b). The evenness was significantly higher in CT-RN (0.97 ± 0.06) compared to RT-RR

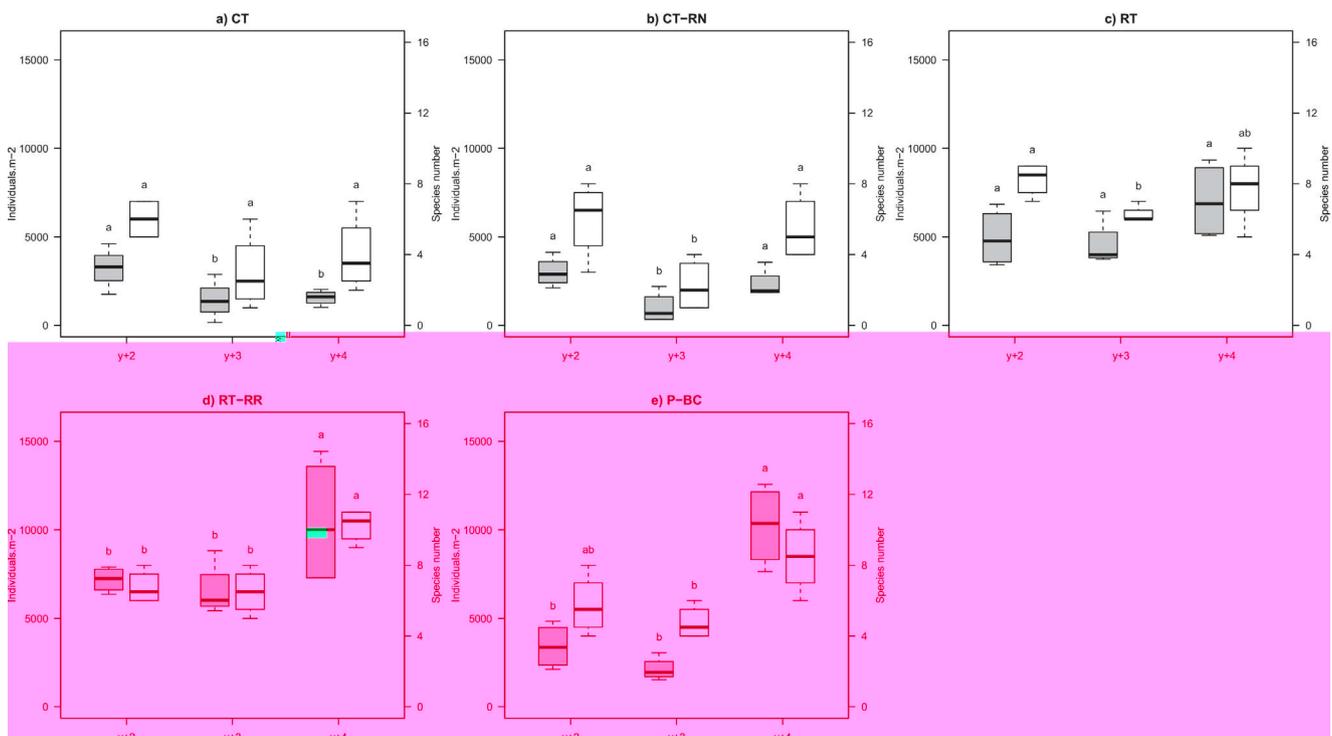


Fig. 1. Total density (grey boxplots) and species richness (white boxplots) of Collembola assemblages between years (y + 2: 2012, y + 3: 2013 and y + 4: 2014) for five different agricultural treatments (North of France). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at α = 0.05%.

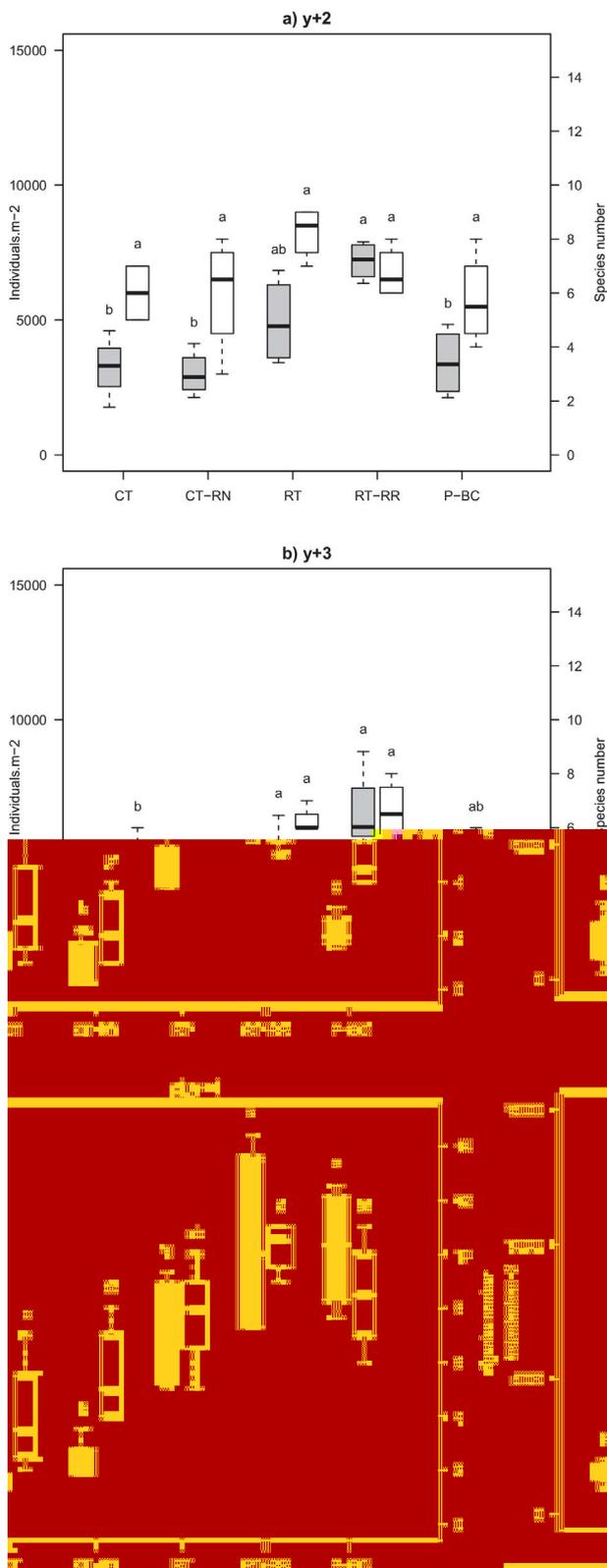


Fig. 2. Total density (grey boxplots) and species richness (white boxplots) of Collembola assemblages of five different agricultural treatments (North of France) over a 4-year period (2a: y + 2: 2012. 2b: y + 3: 2013 and 2c: y + 4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at $\alpha=0.05\%$.

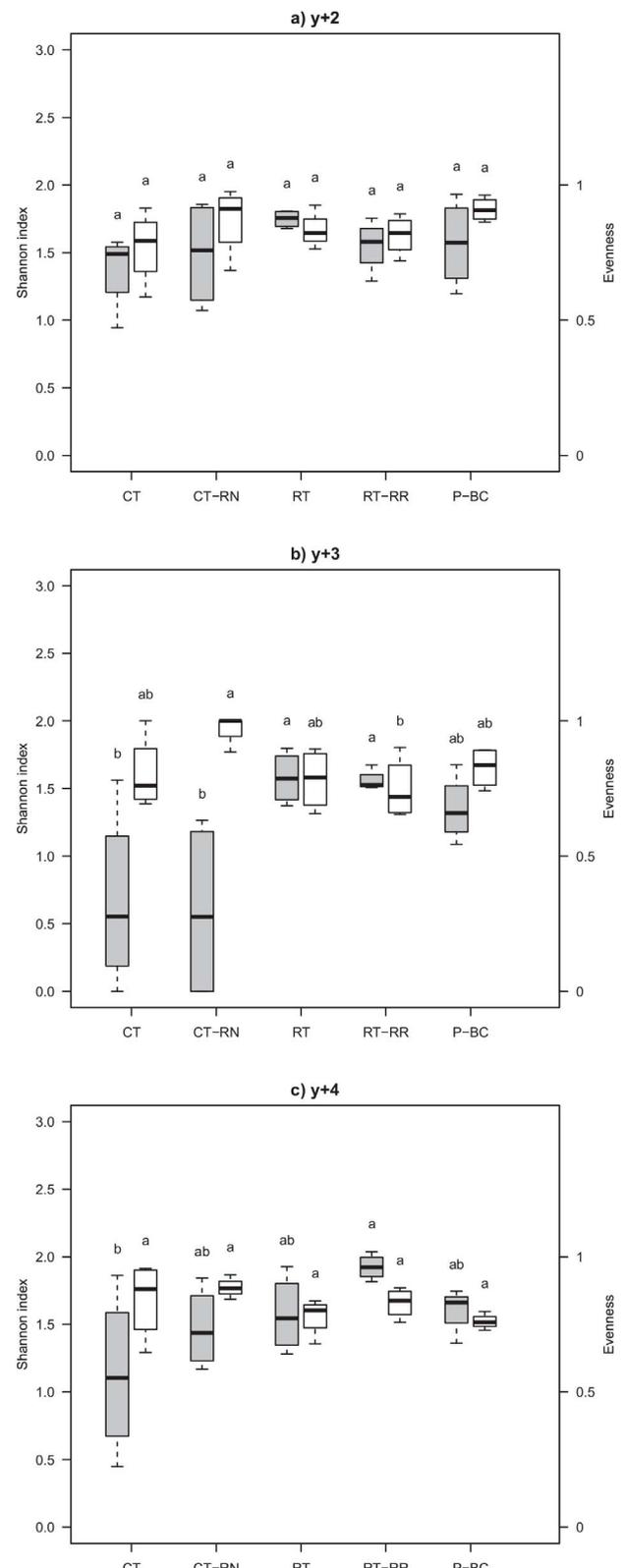


Fig. 3. Shannon index (grey boxplots) and Evenness (white boxplots) of Collembola assemblages of five different agricultural treatments (North of France) followed over 4 years (3a: y + 2: 2012. 3b: y + 3: 2013 and 3c: y + 4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at $\alpha=0.05\%$.

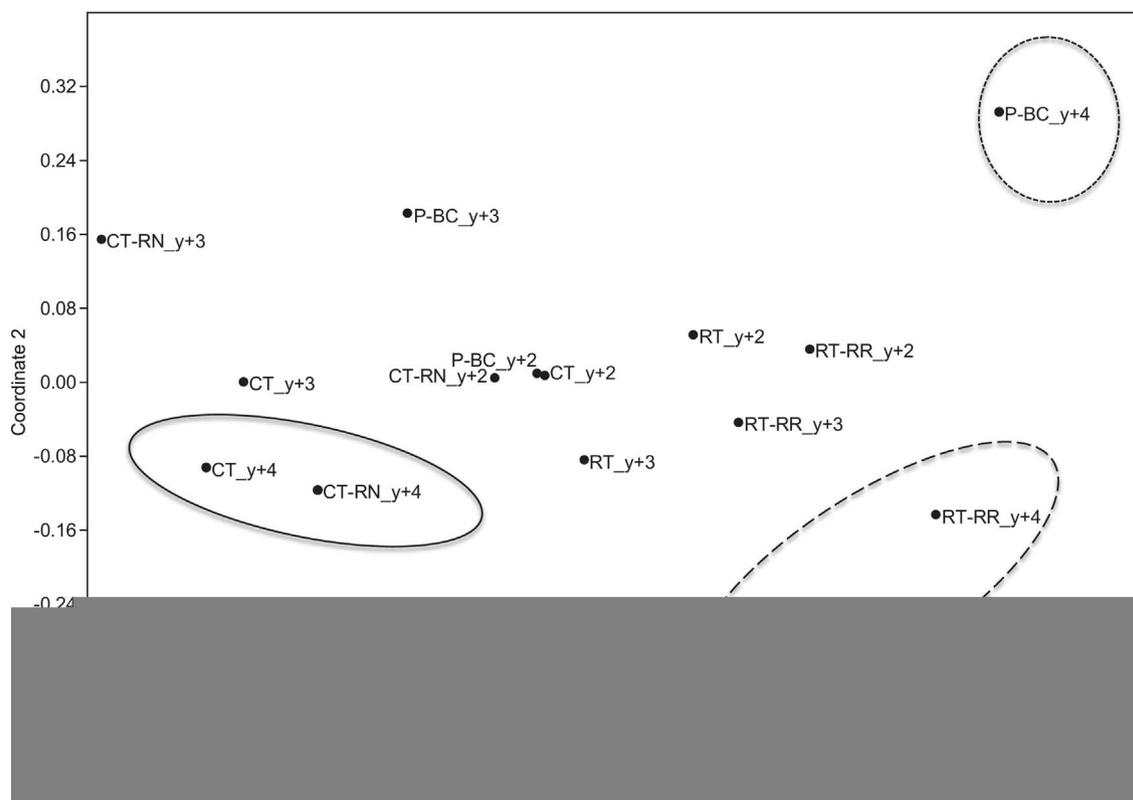


Fig. 4. Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity indices derived from abundance of collembolan species recorded in five different agricultural practices (North of France) across a 4-year period (y + 2: 2012, y + 3: 2013 and y + 4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal.

(0.75 ± 0.11), the other treatments being intermediate (Fig. 3b). After 4 years (y + 4), all indices, except the evenness, significantly differed between treatments (Table 3). The density ranged from 1952 to 9242 individuals m^{-2} (in CT and CT-RN vs. RT-RR and P-BC; Fig. 2c). Species richness and Shannon index likely responded to the treatments, with maximum values in RT-RR and minimum values in CT, the other treatments exhibiting intermediate values (Figs. 2 c, 3 c).

3.2. Community composition

NMDS ordination of the experimental treatments over the different years (y + 2, y + 3, y + 4) revealed a clear temporal differentiation between CT and CT-RN on one side and both RT and RT-RR on the other side of the first axis. P-BC became at y + 4 quite isolated according to the second axis. Dissimilarities between treatments increased over time as distances between them in the NMDS increased (Fig. 4).

ANOSIM analyses showed significant differences in species composition after 3 and 4 years but not after 2 years (Table 4). After 3 years, composition differed in RT-RR from CT, CT-RN and P-BC, and the latter two differed from RT. This pattern was mainly due to the contribution of two species. *Parisotoma notabilis* dominated in CT and RT while *Protaphorura armata* was dominant in CT-RN and RT-RR (Appendix A – Table A1). After 4 years, differences between assemblages were stronger, and only assemblages under conventional tillage (CT and CT-RN) did not differ from each other. A different set of species contributed to assemblages' dissimilarity. For instance, *Mesaphorura* sp. and *Sminthurinus elegans* mostly contributed to discriminate P-BC from treatments under conventional tillage. *Megalothorax minimus* differentiated RT, CT and CT-RN. Finally, *P. notabilis* and *Isotoma anglicana* participated to discriminate RT-RR from CT-RN, CT and RT (Appendix A – Table A2).

Table 4

Results of ANOSIM analyses between collembolan assemblages within five different agricultural treatments (North of France) after 3 (y + 3) and 4 years (y + 4) following experimental set-up. CT: Conventional tillage; CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop. RT: Reduced tillage; RT-RR: Reduced tillage and crop residues removal. *P*-value and *R*-values (within brackets) are given. For clarity, significant results are in bold.

	CT	CT-RN	RT	RT-RR	P-BC
y + 3					
CT		0.42 (0.02)	0.12 (0.13)	0.03 (0.29)	0.17 (0.18)
CT-RN			0.03 (0.55)	0.03 (0.61)	0.15 (0.14)
RT				0.34 (0.02)	0.03 (0.70)
RT-RR					0.02 (0.84)
P-BC					
y + 4					
CT		0.77 (0.14)	0.03 (0.81)	0.03 (0.87)	0.03 (0.97)
CT-RN			0.02 (0.59)	0.03 (0.65)	0.03 (0.89)
RT				0.03 (0.50)	0.03 (0.99)
RT-RR					0.03 (0.84)
P-BC					

3.3. Functional groups

After 2 years, only euedaphic density showed significant differences between treatments (Table 5), with twice as many individuals found in RT-RR than in CT and CT-RN (3214 and 1223 individuals m^{-2} , respectively). The other treatments presented intermediate values (Fig. 5).

After 3 years, the density of each of the three functional groups was significantly influenced by the treatments (Table 5). On average, euedaphic density was almost 38 times higher in RT and RT-RR (average values of 3217 individuals m^{-2}) than in other treatments (average values of 85 individuals m^{-2}). Similarly, hemiedaphic Collembola were

Table 5

Results of Linear Mixed-Effects Models (LMM) of the effect of the factor treatment on the density and species richness of the three functional groups after 2 (y + 2), 3 (y + 3) and 4 years (y + 4). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Chisq: Chi-square value. *p*: *p*-value. R²: variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at α = 0.05. ****p* < 0.001. ***p* < 0.01. **p* < 0.05. ns *p* > 0.05.

	LMM outputs		
	Chisq	<i>p</i>	R ² (%)
y + 2			
Density			
Epedaphic	3.66	ns	16.2
Hemiedaphic	8.56	ns	31.1
Euedaphic	20.0	***	53.7
Species richness			
Epedaphic	1.59	ns	7.72
Hemiedaphic	6.86	ns	26.5
Euedaphic	6.61	ns	36.4
y + 3			
Density			
Epedaphic	21.0	***	52.5
Hemiedaphic	26.3	***	59.9
Euedaphic	15.2	**	46.1
Species richness			
Epedaphic	30.3	***	61.5
Hemiedaphic	8.87	ns	56.4
Euedaphic	11.3	*	44.4
y + 4			
Density			
Epedaphic	19.8	***	51.0
Hemiedaphic	50.8	***	72.8
Euedaphic	44.5	***	74.4
Species richness			
Epedaphic	15.4	**	44.7
Hemiedaphic	17.4	**	47.7
Euedaphic	17.9	**	48.5

approximately 3.8 times more abundant in RT and RT-RR (average values of 1655 individuals m⁻²) than in CT, CT-RN and P-BC (average values of 439 individuals m⁻²). Euedaphic density also ranged from minimum values in CT and CT-RN (average values of 638 individuals m⁻²) to a maximum in RT-RR (3400 individuals m⁻²). In parallel to the density, the number of epedaphic species in RT-RR was 5.5 times higher than in CT, CT-RN and P-BC. RT had an intermediate value. The number of euedaphic species in RT was 2.4 times greater than in CT-

RN. The 3 other treatments had intermediate values (Fig. 5).

After 4 years, both the density and species richness of each of the three functional groups were significantly influenced by experimental treatments (Table 5). On average, epedaphic density in RT-RR and P-BC were about 10 times higher than in CT (1677 vs. 170 individuals m⁻²), CT had the lower epedaphic species richness compared to all other treatments. Hemiedaphic density ranged from 700 to 3170 individuals m⁻² (average values of CT and CT-RN vs RT, RT-RR and P-BC), in parallel, the number of hemiedaphic species in RT-RR was 2.3 times higher than in CT and CT-RN. RT and P-BC exhibiting intermediate values. Finally, euedaphic density displayed the same pattern as the hemiedaphic with significantly more individuals and species in P-BC, RT and RT-RR than in CT and CT-RN (Fig. 5).

3.4. Environmental parameters

From y + 2 to y + 4, microbial biomass (Cbiom) and activity of the microflora (CO2) significantly differed between treatments (Appendix C – Table C1), with maximum values in P-BC and minimum values in CT and CT-RN. Soil moisture (Hum) and pHwater showed significant differences only after 3 years. Lower soil moisture values were found in CT-RN compared to other treatments (CT exhibiting intermediate value) and at the same time, pH values were higher in CT-RN than in CT, the other treatments being intermediate. Soil temperature was significantly influenced by the treatments at y + 2 and y + 4, with always minimum values in P-BC. At y + 3, one month prior to our sampling, the average soil temperature did not differ between the treatments and was of 3.78 °C considering all treatments together.

The proportion of the total variance in the RDA (Fig. 6), which is explained by all environmental parameters, is 67%. The first axis accounted for 60% of variance and the second only for a further 5%. Basically, treatments under conventional tillage were separated from the treatments under reduced tillage along the first axis, with the latter correlating to high values of all collembolan parameters. Abundance and richness of euedaphic species were related to higher values of soil humidity (HUM), microbial C biomass (Cbiom) and microbial activity (CO2), while high values of abundance and richness of epedaphic Collembola were correlated to higher values of soil temperature (TEMP).

4. Discussion

We followed 5 different crop practices commonly used in Western

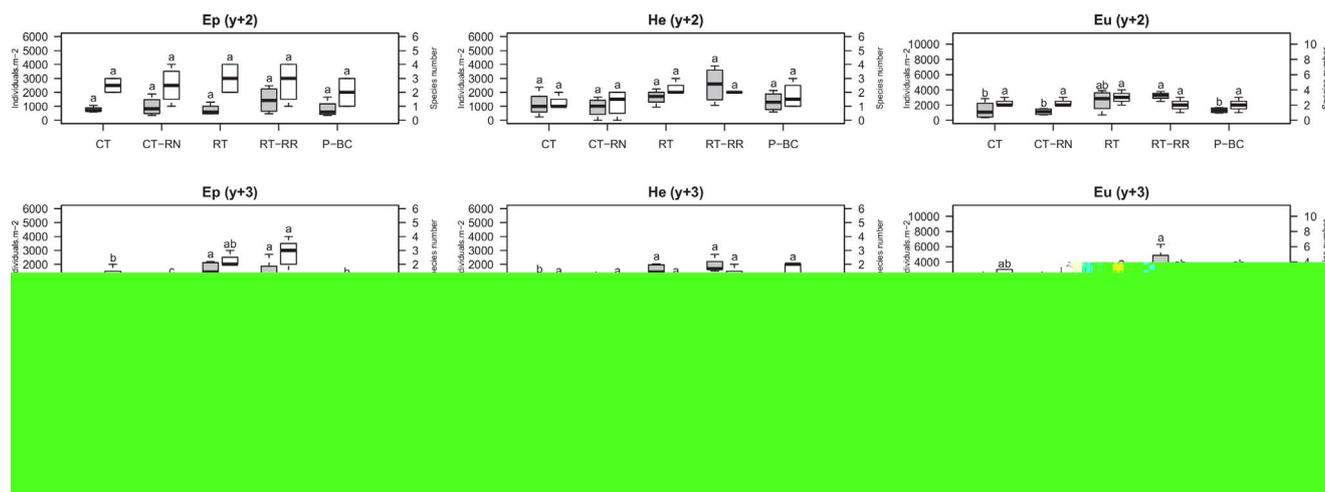


Fig. 5. Density (grey boxplots) and species richness (white boxplots) of the three Collembola functional groups recorded in five different agricultural treatments across a 4-year period (y + 2, y + 3 and y + 4). Ep: Epedaphic, He: Hemiedaphic, Eu: Euedaphic. CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters within a single parameter denote significant differences between treatments at α = 0.05% (Turkey’s HSD).

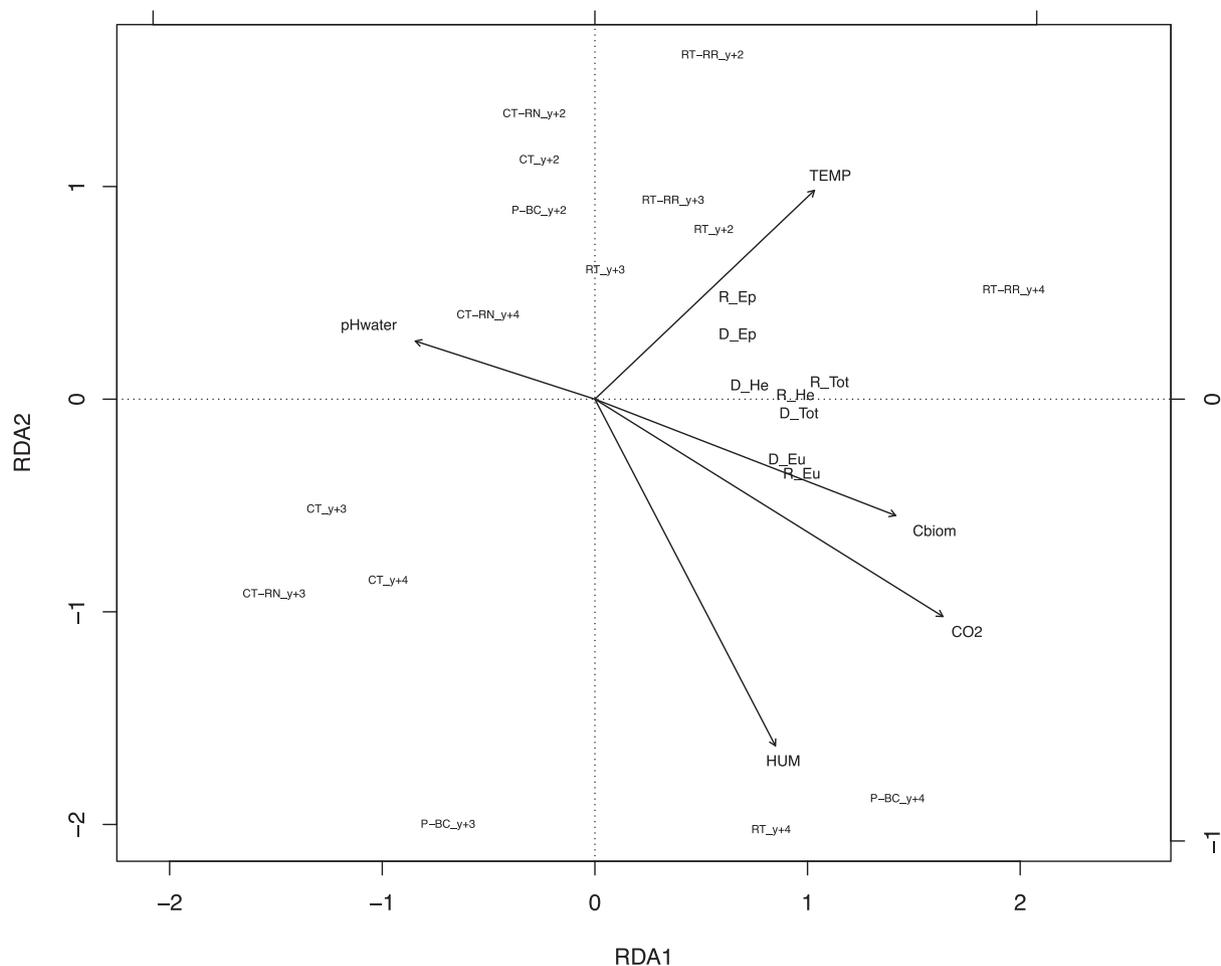


Fig. 6. Redundancy analysis (RDA) based on Total density of Collembola (D_{tot}), total species richness (R_{tot}), density and richness of each of the three life forms (D_{Ep} , D_{He} , D_{Eu} , R_{Ep} , R_{He} , R_{Eu}), microbial C biomass (Cbiom), microbial activity (CO₂), soil moisture (HUM), soil temperature (TEMP) and soil pH (pHwater). All variables were measured in five different agricultural treatments (north of France) 2 to 4 years (y + 2: 2012, y + 3: 2013 and y + 4: 2014) after experimental set-up. CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal.

Europe. Since all the studied plots were previously for at least 15 years managed under conventional tillage (CT), this offered us the opportunity to evaluate if shifting from CT towards less intensive management may produce changes in soil Collembola assemblages by minimizing disturbances due to soil tillage in particular. Furthermore we could over a 4-year-period follow the differentiation of the Collembola assemblages within and between the treatments.

Overall, the mean density and species richness of soil Collembola found in our study (ranging from 168 to 14430 individuals m^{-2} and from 1 to 11 species, respectively) are in the range of other European studies focusing on agricultural land (Bosch-Serra et al., 2014; Chauvat et al., 2014a; Petersen, 2002; Scheunemann et al., 2015a; van Capelle et al., 2012). Low values of abundance and species richness were noticeable after 3 years (y + 3) in almost all treatments. This may be due to a severe winter in 2013 with soil (5 cm depth) mean temperature, within the sampling site, during the month before sampling of around 3 °C compared to average temperatures of 7 and 8 °C in comparative period of 2012 and 2014, respectively. It is well known that among abiotic factors, temperature has a direct effect on activity, fecundity and mortality of collembolans (Christiansen, 1964; Eaton et al., 2004). Under field conditions, the correlation between collembolans and temperature is usually hard to establish or is only weakly confirmed. But for example, Wolters (1998) and Bedano et al. (2006), found that Collembola density was negatively correlated with soil and/or air temperature.

4.1. Soil mechanical disturbance

Our results showed a general increase in collembolan density and species richness with reduction of tillage intensity which is in accordance with a number of previous studies (Brennan et al., 2006; Petersen, 2002; Wardle, 1995) and confirms our first hypothesis. But this is in contradiction to the findings of van Capelle et al. (2012), who recently in a meta-analysis on German data found no difference in abundance of Collembola between conventional tillage and reduced tillage and even a higher number of Collembola in convention tillage compared to no-tillage systems. However, they found this pattern to be strongly dependent of soil type. For example, in silty soils, as in our study, they rather found reduced tillage to foster Collembola abundance (+47%) compared to conventional tillage. In our study, we recorded a much higher stimulation of Collembola individual numbers between CT and RT after 4 years (+400%). This agrees well with a general view that soil biota are usually inhibited by cultivation. In their meta-analysis, van Capelle et al. (2012) showed that total earthworm abundance, biomass, and species diversity were increased significantly in tillage systems with lower tillage intensity. Nakamoto et al. (2006) found the same results on the numbers of nematodes, but Didden et al. (1994) indicate that enchytraeids are unaffected by tillage due to their small body size and their great reproductive rates. Generally, larger organisms are more sensitive to tillage practices than smaller ones (Wardle, 1995). Within soil fauna, Collembola are considered to be a fast

responsive group (r-strategist) to environmental changes (Butcher et al., 1971; Chauvat et al., 2003; Dunger, 1975; Kaczmarek, 1975; Klironomos and Kendrick, 1995; Ponge, 1983).

In our case, according to the NMDS and the RDA results (Fig. 4 and Fig. 6), tillage type (conventional vs. reduced) is the first factor driving the fate of collembolan assemblages in terms of species composition and relative abundance. Indeed we observed in $y + 4$ a very clear separation between three clusters (Fig. 4), each one with a different dominating species, one made of the two CT treatments dominated by *P. notabilis*, a second one made of the two RT treatments dominated by *M. minimus*, and the third one with the P-BC alone with *Mesaphorura* sp. *M. minimus* and *Mesaphorura* sp. are the main species contributing for composition dissimilarities between the treatments. Both species are rather small and live deep in the soil. Their respective abundance increased over time in reduced tillage (RT) or in perennial crop (P-BC or no tillage) treatments compared to the treatments under conventional tillage. Probably, reducing physical disturbance in deep soil layers alleviates constraints on them and allow population growth over time. They also may benefit from a more stable resource supply (fungal mycelium) in those treatments with a lower mechanical disturbance.

The dissimilarity in species composition between tillage conventional and reduced tillage treatments was not visible at a functional level. Surprisingly the proportion (relative abundance) of the three collembolan functional groups did not really differ between conventional (CT and CT-RN) and reduced tillage (RT and RT-RR) treatments after $y + 4$ (see Appendix B – Table B1). This is partly in contradiction with the findings of Sabatini et al. (1997), but rather in accordance with the meta-analysis of van Capelle et al. (2012) concluding that all three functional groups were equally promoted under reduced tillage in silty soils.

4.2. Management of crop residues and N fertilization

Contrary to our hypothesis, the other components of management, either “nitrogen input reduction” and “restitution/exportation of crop residues” did not favour soil living Collembola, either hemiedaphic or euedaphic.

For crop residues management, no difference in density or species richness was found between RT-RR and RT for both hemi- and euedaphic during the study ($y + 2$ at $y + 4$, Fig. 4). However, relative abundance of euedaphic Collembola species in $y + 4$ dropped by 22 points when removing the crop residues (i.e. from RT to RT-RR, Appendix B-Table B1), but this was due to a single species, *M. minimus* with a relative abundance decreasing from 41.6% to 14.2% in RT and RT-RR, respectively (Appendix B-Table B1). In a recent study, Scheunemann et al. (2015a) found that in arable soil, shoot residues only form an additional resource of minor importance to soil fauna compared to the predominant importance of root-derived resources, suggesting that removal of shoot residues should not strongly impact Collembola. On the other hand, the restitution of residues, specifically the superficially burying into the soil of residues using disk ploughing, causes an additional mechanical disturbance that may impact Collembola assemblages especially soil living species. Our results support this assertion with the relative abundance of three dominant soil living species, namely *P. notabilis*, *Mesaphorura* sp., *P. armata*, that decreased in RT compared to RT-RR from $y + 3$ to $y + 4$ (Appendix B – Table B1). Furthermore, Brennan et al. (2006) found the addition of crop residues to also decrease the abundance of two euedaphic Collembola species: *Mesaphorura krausbaueri*, *Supraphorura furcifera*, and one hemiedaphic species: *Friesea truncata*. They suggest that the presence of crop residues on the soil surface may lead to an increase in predatory arthropods, as found by Scheunemann et al. (2015b) for Gamasid mites, and therefore a higher top-down regulation on soil Collembola. We believe that both mechanical disturbances linked to burying of crop residues and an increase in top-down regulation, counterbalance the well-known positive effect of beneficial resources provided by crop

residues to decomposers (Cochran et al., 1994; Hall and Hedlund, 1999).

Also our results (Fig. 5) showed that density and diversity parameters did not differ significantly between the perennial crop (P-BC with exportation of crop residues) and both reduced tillage treatments RT (with restitution of crop residues) and RT-RR (with exportation of crop residues). However, at the functional level, P-BC showed relative abundances of functional groups much more similar to those observed in RT than those in RT-RR, especially for epedaphic and euedaphic Collembola. Perennial habitats, even with exportation of residues likely provide resources that are unavailable in annual crops between harvesting and planting, such as root turnover and exudation (Bianchi et al., 2006). Our RDA results support this assertion, by showing a correlation between euedaphic Collembola abundance and richness and microbial biomass (Cbiom). The positive effect of energy crops on the microbial biomass (Appendix C – Table C1) may explain the marked increase of euedaphic species as they are known to be rather bottom-up controlled by trophic resources (Henneron et al., 2016; Schneider and Maraun, 2009).

For N fertilization, our results showed no impact of reducing N mineral input on both density and species richness of Collembola (CT vs. CT-RN, Please refer to Fig. 2). Under field conditions, correlations between Collembola and total N are usually weak (Filser, 2002). But we could have anticipated a change in basal microbial groups following N reduction that would have scaled-up till Collembola. This is apparently not the case, since even microbial biomass (Cbiom) and activity of the microflora were low in these treatments (Appendix C – Table C1). Our results are comparable to those of Ngosong et al. (2009), who indicate that Collembola density was not influenced by N fertilization rate. Villenave et al. (2010) found that mineral nitrogen fertilization had little impact on free-living nematodes and that only plant-feeding nematodes increased mostly with increased mineral fertilization, the other groups of nematodes showed no difference. Potter et al. (1985) indicated a highly significant linear decrease in earthworm density and biomass as annual rates of N fertilization increased. These authors found that mites were unaffected by N fertilization. While few studies have considered consequences of lowering N application on soil biota, current evidence indicates only a weak effect at a short-term at least.

4.3. Differentiation with time

In our study, two years after the start of the experiment, surprisingly few differences were noticeable between the treatments. Keeping in mind that all plots were under conventional tillage prior to our experiment, it seems that at least two to three years were necessary for Collembola species to colonize plots that were converted into different management. As suggested by several authors (Auclerc et al., 2009; Ims et al., 2004), colonization rate may strongly depend on surrounding landscape. Differences in assemblages across treatments increased afterwards with time as we hypothesized. Finally, four years seemed not enough to obtain stabilized assemblages across the treatments, as differentiation between the treatments seems still on its way. It is highly probable looking at the results of the NMDS (Fig. 4) that collembolan assemblages will continue to diverge in the next years according to the different treatments. Time seems, therefore, an important aspect when considering the response of Collembola to agricultural practices. Time may, together with the soil type (van Capelle et al., 2012) and the surrounding landscape (Auclerc et al., 2009; Ims et al., 2004) explained the discrepancies found in the literature about the response of Collembola to different tillage intensities. Focusing on ecomorphological groups allowed us to show that functional groups responded differently to the agricultural management, contributing unequally to the differentiation over time. For instance, the euedaphic species still increased after four years in the more conservative treatment (P-BC). Finally, we demonstrated that the species richness of epedaphic Collembola rapidly and strongly changed already after 2 years, which was not the case for

epedaphic ones. This is in line with the better abilities of epedaphic species to disperse and colonize (Chauvat et al., 2014b).

5. Conclusion

This study over several years under field conditions showed that Collembola assemblages were more sensitive to tillage intensity than to either residue management or N fertilization. This demonstrates the impact of mechanical disturbance on the dynamics of collembolan assemblages. Differentiation of Collembola assemblages between cropping systems increased with time and may not reach a maximum even after 4 years. Thus, long-term studies are essential in assessing temporal responses of soil biota to cropping systems, especially according to the

natural backdrop of temporal variation (Wardle et al., 1999). Finally, our functional approach showed complex responses of soil Collembola to agricultural practices and therefore pleads in favour of improving our knowledge of relationships between soil biota and functions performed.

Acknowledgements

The present study was funded through the SOFIA project (ANR Agrobiosphere, ANR- 11-AGRO-0004), the Agrobiof project (GRR VASI). SFM Coulibaly obtained a grant from the Région Haute-Normandie through the GRR TERA – SCALE. We thank all members of the SOFIA project, from the SOERE ACBB, and from the Ecodiv lab for technical assistance and fruitful discussions.

Appendix A

Table A1

Contribution of the first five Collembola species to the dissimilarity between assemblages of treatments in $y + 3$. Cont%: Contribution percentage to dissimilarity. Cum%: Cumulative percentage of contribution to dissimilarity. CT: Conventional tillage; CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop. RT: Reduced tillage; RT-RR: Reduced tillage and crop residues removal.

Taxa	CT vs.		CT-RN vs.		P-BC vs.	
	RT-RR		RT	RT-RR	RT	RT-RR
	Cont%		Cont%	Cont%	Cont%	Cont%
<i>Protaphorura armata</i>	30.0		18.8	25.6	16.8	21.4
<i>Parisotoma notabilis</i>	23.8		26.6	27.8	28.7	30.9
<i>Mesaphorura sp</i>	12.2		–	12.8	11.0	11.8
<i>Megalothorax minimus</i>	10.3		12.8	10.6		9.85
<i>Lepidocyrtus violaceus</i>	7.60		16.5	7.96	16.0	–
<i>Isotomurus unifasciatus</i>	–		7.22	–	7.03	7.92
cum%	83.9		81.9	84.8	79.5	81.9

Table A2

Contribution of the first five Collembola species to the dissimilarity between assemblages of treatments in $y + 4$. Cont%: Contribution percentage to dissimilarity. Cum%: Cumulative percentage of contribution to dissimilarity. CT: Conventional tillage; CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop. RT: Reduced tillage; RT-RR: Reduced tillage and crop residues removal.

Taxa	CT vs.			CT-RN vs.			RT vs.		P-BC vs.
	RT	RT-RR	P-BC	RT	RT-RR	P-BC	RT-RR	P-BC	RT-RR
	Cont%	Cont%	Cont%	Cont%	Cont%	Cont%	Cont%	Cont%	Cont%
<i>Megalothorax minimus</i>	39.1	10.9	–	37.9	12.3	–	19.3	19.2	7.37
<i>Parisotoma notabilis</i>	19.9	25.4	6.42	19.5	25.3	6.76	19.7	10.6	15.5
<i>Protaphorura armata</i>	8.03	8.70	7.67	6.99	8.50	7.50	7.49	–	–
<i>Sphaeridia pumilis</i>	6.48	–	–	6.18	–	–	–	–	–
<i>Mesaphorura sp</i>	6.39	9.82	40.8	5.56	8.44	38.8	6.92	29.1	23.5
<i>Sminthurinus elegans</i>	–	–	15.8	–	–	15.0	–	11.1	8.56
<i>Paratullbergia callipygos</i>	–	–	9.34	–	–	9.40	–	7.16	–
<i>Isotoma anglicana</i>	–	19.6	–	–	19.6	–	19.3	–	12.7
cum%	80.0	74.5	80.1	76.1	74.1	77.4	72.7	77.1	67.7

Table B1

Species list, relative abundance (values in%) and total abundances of Collembola in

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