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Collembola taxonomic and functional diversity in conventional, organic and conservation cropping systems

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Abstract

Intensive agriculture has been demonstrated to be a main threat to soil biodiversity through physical and chemical disturbances of soil. Alternative systems based on lower disturbances may help to promote soil biodiversity and its role in soil functioning. However, the effects of alternative systems on soil biodiversity are still poorly understood, especially regarding soil mesofauna. In this study, we aimed to assess the effects of alternative cropping systems and practice intensity on the taxonomic and functional diversity of Collembola. Collembola were sampled for two consecutive years in 21 fields (3 plots per field) under conventional or alternative systems, namely conservation or organic systems either stable (≥ 7 years) or in transition (≤ 3 years). Indicators and indices were computed to characterize separately tillage, pesticide treatments and organic fertilization in each field. Collembola species and functional traits were investigated. Functional diversity of Collembola was assessed using species traits (i.e. traits from the literature) and by conducting length measurements directly on collected Collembola individuals (body, head, leg, antenna and furca length). Collembola diversity was highly variable between and within cropping systems and years. Species richness was notably higher in conservation than in conventional systems in the second year of the study. More specifically, low

tillage and high pesticide treatment intensities increased taxonomic and functional diversity and affected species with traits adapted to the surface (i.e. scales, trichobothria). Measured Collembola body length additionally revealed the presence of larger individuals under low tillage and high pesticide treatment intensities, with similar results for other length traits. Overall, our results revealed that 1) taxonomic and functional diversity are complementary to understand the effects of agricultural practices and systems on Collembola and 2) measurement of body length is relevant to assess the effects of disturbances on the local Collembola community.

Key words: Collembola, functional traits, body length, conservation agriculture, organic farming, tillage.

1. Introduction

Soil biodiversity plays an essential role in the functioning and sustainability of agroecosystems [1]. However, intensive agriculture was identified as a main threat for soil biodiversity in Europe [2,3]. Intensive systems indeed rely on strong physical and chemical disturbances of soil, which may select organisms that are able to develop under changing conditions, namely species with a short life cycle, high reproduction capacity, and with a body size on average lower than in other ecosystem types [3–5]. Alternative cropping systems, such as organic and conservation agriculture, aim to decrease physical or chemical disturbances of soil to increase the sustainability of cropping systems. Yet, compared to aboveground biodiversity, few studies investigated the effect of alternative systems on the diversity of soil organisms.

Among soil organisms, microarthropods and in particular Collembola are good bioindicators of soil biodiversity as a large number of species can be recovered in a small amount of soil and as they are well-documented in terms of species identification and functional traits in temperate areas [6,7]. In addition, they are considered to be good bioindicators of soil disturbances [8,9]. Collembola play a

main role in soil functioning through their influence on soil organic matter decomposition [10,11], nutrient dynamics [12], soil structure formation [6,13] and regulation of microbial populations [14]. Collembolan taxonomic and functional diversities are lower in agroecosystems than in any other ecosystems [15,16]. In particular, intensive cropping systems are reported to have a low collembolan species diversity [6]. However, few studies report the effects of alternative cropping systems on collembolan diversity. The knowledge gap is especially important regarding conservation systems [17] and transitional alternative systems [18,19]. Collembolan species diversity was alternatively reported to be higher [19,20] or similar in organic compared to conventional systems [21–23]. In contrast, despite a very low number of studies, conservation systems were reported to show no significant difference in collembolan species diversity compared to conventional systems [24,25]. Reduced and no-tillage systems were reported to have variable effects on collembolan species diversity [26,27]. Studies assessing the effect of the transition toward alternative systems mostly focused on the transition toward organic systems. They reported little change in the community composition of Collembola [18] and an increase in collembolan species richness during the first years of transition from conventional to organic systems [19]. In addition, individual agricultural practices were demonstrated to influence Collembola density [28,29] but less studies report the effects of different practices on Collembola diversity [30,31]. Furthermore, practice intensity indicators were observed to be relevant to assess cropping system effects on collembolan density and species richness (Chassain et al., submitted).

The responses of soil organisms to disturbances, such as the ones caused by agricultural practices, are increasingly investigated using functional traits [32–34] with recent studies focusing on Collembola [15,35,36]. Functional traits allow characterizing individuals through their intrinsic properties (i.e. morphological, physiological, phenological or behavioral), with the aim to better estimate their responses to disturbances (i.e. response traits) or their relations to soil functions (i.e. effect traits). They are reported to complement the taxonomic approach to describe the diversity of soil organisms [33]. The assessment of functional traits within a community of soil invertebrates is often performed

by attributing an average trait value at the species level (i.e. one trait value per species). These average species traits are extracted from database computing information from the literature (e.g. BETSI database). Functional traits can also be measured directly on collected individuals [37,38]. Most studies rely on traits at the species level as large datasets are available and as trait measurement is time consuming. However, values of continuous traits (e.g. body length) may strongly vary between individuals of the same species due to local disturbances. In addition, the effects of cropping systems or practice intensity on collembolan traits and functional diversity are still poorly investigated.

In that context, the objectives of this study were to characterize the effects of alternative and transitional cropping systems and of practice intensity on collembolan taxonomic and functional trait diversity. Collembola traits were characterized both at the species level (i.e. average traits based on the literature) and individual level (i.e. measured body, head, leg, antenna and furca length on collected organisms). We hypothesized that both taxonomic and functional diversity will be higher under alternative than under conventional systems, and that they will differ between stable and transitional systems. In addition, we expected that species traits will vary depending on the intensity of practices, with for instance larger Collembola species being the most sensitive to intensive tillage. Lastly, traits directly measured on individuals were presumed to provide more precise information on the influence of disturbances caused by practices on the Collembola community than species traits retrieved from the literature.

2. Materials and methods

2.1 Study sites and experimental design

The study was conducted over 21 fields located in the Paris basin, France (Table 1). In this area, the climate is temperate with mean annual precipitations of 600 to 700 mm and a mean annual temperature of 11°C. All samplings were performed in autumn, from October 19th to December 2nd in

2020 and from October 25th to November 22nd in 2021. Fields were cropped with winter wheat in 2020-2021 and with various crops or cover crops in 2021-2022 (Table 1). Soils were silty or clayed, with a pH ranging from 5.6 to 8.1 at 0-10 cm depth (Table 1).

Fields belonging to the same cropping system were considered as pseudo-replicates (i.e. three to six replicated fields per system). On each field, three plots were defined at the corner of a 271 m² triangle (i.e. spaced from each other by 25 m) located 25 m apart from the field margins. Studied cropping systems were namely i) stable systems established since seven to more than 20 years in conventional (Conv, n = 6 fields), organic (OA, n = 3) or conservation agriculture (CA, n = 3), and ii) systems in transition since 2 to 3 years from conventional to conservation (Conv-CA, n = 3), conventional to organic (Conv-OA, n = 3) or conservation to organic agriculture (CA-OA, n = 3) (Table 1). Organic systems are based on the ban of synthetic inputs [39], while soil conservation systems are defined as systems relying on no-tillage, permanent soil cover and diversification of the crop rotation [40].

Information on agricultural practices applied to each field was collected by conducting farmer's survey. Using this information, indicators and composite indices of practice intensity adapted from Büchi et al. [41] were computed (Table S1). Effects of various practices on Collembola diversity were assessed using composite indexes of tillage intensity (Itill) and of pesticide treatment intensity (Itreat), and a primary indicator of the number of organic matter inputs over 5 years (nbOrg) (Table 1, Fig. S1).

2.2 Collembola sampling and identification

Soil cores (5.6 cm in diameter, 4 cm high) were used to sample Collembola on the three plots of each field. They were kept at 4°C no longer than 8 days before extraction. Collembola were extracted using MacFayden extractor and following the NF/ISO 23611-2 norm (8 days of extraction under a gradient of temperature with a progressive increase from 25°C to 45°C).

Collembola were sorted under binocular and identified at the species level using phase-contrast microscope and identification keys [42–44]. They were grouped into eco-morphological groups

(euedaphic, hemiedaphic, epedaphic) [45]. Densities were obtained by dividing the abundance by the area of soil extraction (0.0025 m²). Collembolan species diversity was estimated using species richness, Shannon index and Pielou's evenness index.

2.3 Collembola functional traits

Collembolan species traits were selected in order to understand the responses of species to disturbances caused by cropping practices. We selected eight morphological traits with two to three trait attributes: body length (< 1.5 mm, > 1.5 mm), body shape (cylindrical, spherical), furca type (long, short/absent), number of ocelli (0, 1-5, ≥ 6), and presence/absence of post-antennal organ (i.e. PAO), pigmentation, scales and trichobothria. These traits were used as they could be related to distribution in soil and dispersal abilities [46]. We also took into account the reproduction type (sexual, parthenogenetic) and ability for ecomorphosis (presence, absence) as they could be good indicators of the recovery or resistance facing disturbances. Indeed, the reproduction type represents the ability of Collembola to recolonize an area after disturbances (e.g. tillage) as parthenogenetic populations have a higher ability to recover after being disturbed. The motion strategy was represented by the furca presence/absence and size, which determine the ability to jump and to escape predators. All traits for Collembola species were collected from the BETSI database (CESAB/FRB) containing data extracted from the literature [33]. Using species traits, we calculated the functional richness (FRic), which represents the volume of the functional space occupied by the community, and the functional evenness (FEve) which corresponds to the regularity of the distribution of species density in this volume [47].

Additionally, length traits were directly measured on collected Collembola individuals to account for actual traits of the local community. Lengths of body, head, leg, antenna and furca were measured using Flexacam C1 camera on DM2000 microscope (Leica) and the Leica Application Suite X software.

Up to 10 individuals per species and per sample were measured. Lengths were measured along the main axis of each element, taking into account inflexion points (Fig. 1).

Two measurements were performed for the body length: 1) total length from the posterior end of the abdomen to the head between the antennae, 2) headless length from the posterior end of the abdomen to the anterior end of the first thoracic segment. As both measurements were highly correlated (Spearman correlation, $cor = 0.99$, $P < 0.001$ in 2020 and 2021), we decided to keep the total length including head, hereafter called body length (Fig. 1). Head length is the maximum diagonal length from top of head to the labrum. Leg length is the average length of both posterior legs (i.e. third pair of legs) from claw tip to top part of coxae. Antenna length corresponds to the length of all antenna segments. Lastly, furca length comprises the length of manubrium, dens and mucro.

2.4 Statistical analyses

The effects of cropping systems and years on collembolan species community composition were assessed at the field level (average value for the three plots of each field) by performing a principal coordinates analysis (PCoA) using Bray-Curtis distance, which allowed looking at the dissimilarities between communities. It was followed by a permutational analysis of similarities (ANOSIM) to test for significant differences between systems and years.

For each species trait, the community-weighted mean (CWM) was calculated as the average trait values weighted by the density of species in the community [48]. A PCA was performed on CWM to assess the functional composition of Collembola communities at the field level (average value for the three plots of each field).

The responses of Collembola density, diversity and traits to cropping systems and practice intensity were assessed at the plot level. For measured individual traits, each Collembola individual was considered as a data point. The normality and homogeneity of variances were first tested with a Shapiro-Wilk test ($\alpha > 0.05$) and a Bartlett test ($\alpha > 0.05$). Generalized linear mixed-effects models

(GLMM) were then applied with a fixed effect for management factors (cropping systems, *ltill*, *ltreat* or *nbOrg*) and a random effect for fields. Negative binomial distribution with linear parametrization was fitted for densities, species richness, species traits and measured individual traits, and Gaussian distribution was fitted for diversity indexes (Shannon, Pielou's evenness, *FRic* and *FEve*). Tukey post-hoc tests were then performed when comparing different systems.

All the analyses were performed using R software version 3.6.3 (R Development Core Team 2020) and the *stats* (R Development Core Team 2020), *ade4* [49], *vegan* [50], *FD* [51], *glmmTMB* [52] and *multcomp* [53] packages.

3. Results

3.1 Effects of cropping systems on collembolan species richness and community composition

The total number of collected Collembola species was 30 in 2020 and 43 in 2021. Collembolan species richness and Shannon index were higher in Conv, CA and Conv-CA than in Conv-OA in 2020 (Fig. 2a.1, Table S2) whereas species richness was higher in CA than in Conv and CA-OA in 2021 (Fig. 2a.2). Collembolan species richness increased as tillage intensity decreased (Fig. 2a.3) and as pesticide treatment intensity increased (Fig. 2a.4) in both years, and as organic matter inputs decreased in 2020 (Fig. 2a.5). Shannon index increased as tillage intensity decreased in both years and as pesticide treatment intensity increased in 2020 (Table S3). Evenness index was similar in all systems in both years (Table S2) and was not influenced by practice intensity (Table S3).

Hemiedaphic species had a higher density in Conv, CA and Conv-CA than in Conv-OA in 2020, and in CA than in Conv, Conv-OA and CA-OA in 2021 (Table S2). Euedaphic species had a higher density in OA than in Conv in 2021 (Table S2). In addition, a higher density of epedaphic and hemiedaphic species were observed as tillage intensity decreased and as pesticide treatment intensity increased in 2020, with similar effects of tillage intensity in 2021 (Table S3).

The Collembola community composition was significantly different in 2020 and 2021 (Fig. 3a). Conventional and conservation systems had similar communities, differing significantly from communities in organic systems in 2020 (Fig. 3b), but not in 2021 (Fig. 3c). Differences between communities in 2020 were related to the absence or low occurrence of several species in organic systems (Table S4). *Pseudosinella alba* (Packard, 1873) and *Isotomurus palustris* (Muller, 1776) species were collected in all systems in both years (Table S4). Two species were collected exclusively in 2020 against 15 species in 2021, including 12 species occurring in one field only. Despite differences in densities, we did not find species representative of the different cropping systems.

Collembola species that were significantly influenced by practice intensity all had a higher density as tillage intensity decreased and pesticide treatment intensity increased (Table 2). In particular, significantly higher densities of *Lepidocyrtus cyaneus* Tullberg, 1871 and *Sminthurinus elegans* (Fitch, 1863) were observed under low tillage intensity in both years, with a similar trend for *I. palustris* (Table 2). Densities of *L. cyaneus* and *P. alba* increased as pesticide treatment intensity increased in 2020 only (Table 2a). In addition, an increase in the number of organic matter inputs had a negative effect on the density of *L. cyaneus* in 2020 (Table 2a).

3.2 Effects of cropping systems on collembolan species traits and community composition

Collembola functional richness was on average similar in 2020 and in 2021. It was significantly higher in CA than in CA-OA in 2021 (Fig. 2b.2), but we found no difference between systems in 2020 (Fig. 2b.1, Table S2). Functional evenness was similar in all systems in both years (Table S2). Functional richness and evenness could not be calculated for Conv-OA plots in 2020 as the number of species in each plot was too low (i.e. one or two species), hence the functional richness was estimated as close to zero. Moreover, functional richness increased as tillage intensity decreased in 2021 (Fig. 2b.3) and as pesticide treatment intensity increased in 2020 (Fig. 2b.4, Table S3). Functional richness and evenness

increased and decreased respectively as the number of organic matter inputs decreased in 2020 (Fig. 2b.5, Table S3).

Functional communities did not differ significantly between cropping systems according to PCA based on CWM of collembolan species traits (Fig. S2). In addition, we found no significant difference in traits CWM between systems in 2020, whereas several significant differences were observed in 2021 (Table S5). We observed a higher representation of species without ocelli in OA than in Conv, CA and Conv-OA and less species with pigmentation in OA than in Conv and Conv-OA (Table S5). In addition, less species with a cylindrical body shape were collected in CA-OA than in all other systems (Table S5). Moreover, in Conv, we observed less species with ecomorphosis ability than in CA and less species with trichobothria than in Conv-CA and CA-OA (Table S5).

As tillage intensity increased, we observed a lower representation of Collembola species with scales and trichobothria in both years (Table 3), and additionally with pigmentation in 2020 (Table 3a) and ecomorphosis abilities in 2021 (Table 3b). Contrastingly, as pesticide treatment intensity increased, we observed a higher representation of Collembola with cylindrical body shape in both years (Table 3) and with scales in 2020 (Table 3a). In addition, an increase in organic matter inputs was related to less species without ocelli, with scales, cylindrical body shape and ecomorphosis ability in 2020 (Table 3a).

3.3 Effects of cropping systems on measured Collembola length traits

Collected Collembola had an average body length of $768 \pm 479 \mu\text{m}$ (186-2573 μm) in 2020 and $888 \pm 502 \mu\text{m}$ (204-5179 μm) in 2021. Comparing the mean body length of species obtained from our measurements and from the literature, we observed that measured individuals of several Collembola species were smaller or belonged to the lower range of body lengths reported in the literature (Table S6).

Mean measured length traits showed no significant difference between systems in 2020 nor between years. However, in 2021, measured body length was significantly larger in CA than in Conv, OA and CA-

OA and furca length was smaller in OA than in Conv, CA and Conv-OA (Table S5). In addition, distribution of collembolan length traits differed regarding cropping systems and years (Fig. 4). Body length distribution differed between Conv, CA and OA (Fig. 4). A higher share of small Collembola was observed in CA and OA than in Conv in 2020, and inversely in Conv and OA than in CA in 2021. In addition, body length was similar in Conv-CA and Conv in 2020 but not in 2021 (Fig. 4). Furthermore, Conv-OA trait distribution looks more like OA in 2021 than in 2020, while CA-OA followed a similar pattern in both years that does not resemble CA nor OA. The few collected Collembola in Conv-OA in 2020 were less than 1 mm long with only one individual above 2.5 mm. Head, antenna and leg lengths did not bring further information (Fig. 4). Furca length was variable in all systems and allowed to observe that all individuals had a furca in OA in 2020 and in Conv-OA and CA-OA in 2021 (i.e. absence of some poduromorpha species) (Fig. 4).

Overall, measured traits were impacted by pesticide treatment intensity and by the number of organic matter inputs in 2020 (Table 4a) and by tillage intensity in 2021 (Table 4b). In 2020, body, head, leg and antenna length increased as pesticide treatment intensity increased and organic matter inputs decreased (Table 4a). In 2021, body length followed a similar tendency regarding treatment intensity, while body and head length decreased significantly as tillage intensity increased (Table 4b).

A diagram illustrating the relations between cropping systems, practice intensity and Collembola population parameters and traits is given Figure S3.

4. Discussion

4.1 Taxonomic and functional responses of Collembola diversity to cropping systems

Collembolan species diversity was influenced by cropping systems and practice intensity with the significance of the observed effects depending on years. As in previous studies, we found no significant difference in collembolan species diversity between stable conservation and conventional systems in

2020 [24,25] nor between stable organic and conventional systems in both years [21,23]. However, species diversity was significantly higher under conservation systems in 2021. This was mostly explained by the absence of tillage, which had a positive effect on Collembola diversity.

We found no species representing the different cropping systems, however *L. cyaneus* could be a good representative of the effects of tillage and pesticide treatments. Indeed, the density of several Collembola species tended to be affected by tillage and pesticide treatment intensity, but *L. cyaneus* was abundant in all systems and showed significant responses to practices in both years. However, species are subjected to spatio-temporal dynamics. In addition, previous studies rarely reported the abundance of similar species, or do not reach this level of identification, which limits the determination of indicators species.

The functional approach of diversity brought additional insight to the taxonomic approach on the effects of cropping systems on Collembola, as reported in previous studies for various land-use types [33,54,55]. Differences were mostly observed by looking at traits separately rather than by observing functional indices or functional community composition.

Collembolan species and functional richness were both very low in recent organic systems in 2020, but this was mostly an effect of the very low abundance of Collembola in the samples. At the community level, collembolan species composition differed between organic and conservation systems, but this could again be explained by the absence or low occurrence of several species in organic systems. In contrast, functional trait composition was not significantly different between cropping systems, the latter having a poor influence on species traits.

Several species traits responded to tillage or pesticide treatment intensities. Morphological traits observed under low tillage intensity (i.e. presence of scales, trichobothria and pigmentation) and high pesticide treatment intensity (i.e. cylindrical body shape and presence of scales) correspond to Collembola living at the soil surface and in open habitats [34]. This is in agreement with the effects we observed for epedaphic and hemiedaphic Collembola, and for instance for *L. cyaneus* (i.e. epedaphic species, with scales, trichobothria and pigmentation), *S. elegans* (i.e. epedaphic species, with

trichobothria, pigmentation and cylindrical shape) or *P. alba* (i.e. hemiedaphic species, with scales). All of this supports the fact that tillage represents a main disturbance for the Collembola community, in particular for surface species presenting specific traits. These species may be more sensitive to physical injuries caused by tillage, and deprived of food as organic matter is buried owing to morphological characteristics not adapted to forage deeper in soil. In contrast, no effects of tillage nor pesticides was observed for traits corresponding to Collembola living deeper in soil (i.e. absence of ocelli, presence of PAO, parthenogenetic reproduction) [34]. Similarly, we observed no effect on euedaphic Collembola, which presented a low density following a general trend in croplands [35]. However, the additional input and mixing of organic matter deep in soil might have a negative impact on all Collembola ecomorphological groups. First, as it decreases their access to food as the top soil, where Collembola mostly reside, will be devoid of organic matter. Then, as it often comes with deep soil tillage that have detrimental effects on collembolan density and diversity. Therefore, the observed negative effect of an increase in the number organic matter inputs on Collembola species or traits could be related to the negative effect of tillage (i.e. confounding effect).

4.2 Measurements of Collembola length traits in cropping systems

All measured Collembola length traits were highly correlated and tended to have a similar response to practice intensity, although they may show different distributions depending on cropping systems. Appendages (head, leg, antenna, furca) length did not provide further information compared to body length. In addition, body length is the easiest length to measure on Collembola. Therefore, body length measurement seems to be sufficient to assess change in Collembola length traits within cropping systems. However, further investigations are required to confirm if length traits are responding differently to disturbances under other ecosystem types (e.g. grazing in grassland).

While species traits from the literature provide an average trait value for each species using data from various pedoclimatic contexts, individual traits measured on collected Collembola additionally take

into account the variability among individuals of the same species and this in a specific context. Thus, our measurements of Collembola length traits support the fact that cropping systems host individuals with a relatively small body length compared to the average values observed under various ecosystems [3–5]. This being said, trait measurement is especially relevant for traits that can greatly vary between individuals of a species (e.g. length traits), whereas traits from the literature are relevant for features that are less subjected to change between individuals (e.g. shape, presence/absence of furca, pigmentation or scales). In this study, we found that measurements of individual traits bring additional information to species traits. Indeed, we did not observe significant effect of cropping systems on body length using species traits, while traits measured on collected individuals demonstrated a significant effect of practice intensity on body length, and other length traits, in both years. Overall, Collembola tended to be larger and to have larger appendages under low tillage and high pesticide treatment intensities. This is consistent with our initial hypothesis on the impact of physical disturbances on larger Collembola. However, observed benefits of pesticides are surprising as they are reported to have deleterious impacts on Collembola. In particular, insecticides and fungicides were reported respectively to increase mortality and to decrease reproduction of Collembola [56]. We suggest that the observed size increase of Collembola in our study can be related to a lower proportion of juveniles due to a lower reproduction. Comparatively, the effect of herbicides on Collembola could be of a much lesser extent, but they could cause disturbances to the ecosystem which might have indirectly stimulated Collembola. Predators were notably reported to decrease under high treatment intensity [57,58], and a low predation pressure may accelerate recolonization of fields by large and highly mobile Collembola.

Furthermore, measured traits helped to observe intra-specific variations between years, which could reveal some climatic or management effects. Larger mean body length observed in 2021 is partly due to the presence of larger species such as *Orchesella villosa* (Geoffroy, 1762), which was absent in 2020, and of larger *Lepidocyrtus lignorum* (Fabricius, 1793) individuals in 2021 than in 2020. Trait measurements of a specific species would be highly relevant when a species dominates all fields within

a study and is present at a high density. It was not the case here, and we did not observe any significant change in length traits at the species level.

5. Conclusion

Alternative cropping systems could increase Collembola diversity, even if their effects vary greatly between fields and years. Taxonomic and functional trait approaches of diversity bring complementary insight on the way Collembola communities are influenced by cropping systems and practice intensity. We therefore encourage their combined use in order to assess the diversity of Collembola in cropping systems. Moreover, collembolan species traits available in existing databases and individual traits measured in the specific context of the study are both useful to observe how communities respond to soil disturbances. Measurement of length traits is especially relevant to assess more accurately the effect of practices on the local Collembola community. However, because all measured length traits followed the same trends, and as trait measurement is undoubtedly time consuming, we suggest future studies in agricultural areas to concentrate their effort first and foremost on body length measurements.

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Table 1. Parameters of the 21 fields of the study. Age corresponds to the number of years since conversion to the current system in 2020. Values of indexes of tillage intensity (Itill) and pesticide treatment intensity (Itreat) are normalized between 0 and 1. Soil properties are given at 0-10 cm depth.

Field	System	Age	Crop		Itill		Itreat		nbOrg		Clay	Silt	Sand	SOM	pH
			2020	2021	2020	2021	2020	2021	2020	2021	g.kg ⁻¹	g.kg ⁻¹	g.kg ⁻¹	g.kg ⁻¹	
A1	Conv-CA	3	wheat	wheat	0.1	0.1	0.8	1	0	0	151.3	474.3	55.7	19.5	6.8
A2	CA	17	wheat	cover	0	0	0.7	0.8	1	1	210.3	381.3	118.7	33.5	6.3
A3	OA	20	wheat	wheat	0.4	0.7	0	0	3	3	157.7	409	196.3	17.5	6.5
A4	OA	19	wheat	bare	0.9	0.7	0	0	6	6	426.3	236.7	93.3	34.4	7.9
A5	Conv	20	wheat	barley	0.3	0.3	0.5	0.8	1	1	206	448	52	24.5	6.8
A6	CA-OA	2	wheat	bare	0.7	0.5	0	0	3	4	277.3	377.7	28.7	21	6.6
A7	Conv-OA	2	wheat	rye	0.8	0.9	0	0	3	3	172.3	481.3	63	22.3	6.6
A8	CA	7	wheat	mustard	0.1	0	0.2	0.2	0	0	192.7	363.7	182.7	24	5.6
A9	Conv	20	wheat	rapeseed	0.9	0.8	0.4	0.8	0	0	208	402.3	187.3	18.5	6.8
A10	Conv	20	wheat	alfalfa	0.4	0.1	1	0.9	0	0	219.7	441.7	46.7	20.9	7.2
A11	OA	20	wheat	cover	0.8	0.7	0	0	6	6	252.7	350	120.3	27	7.3
A12	Conv	20	wheat	cover	0.5	0.5	0.6	0.6	2	2	221.3	352	164.3	23.3	7.4
A13	CA-OA	2	wheat	rye, lentil	0.3	0.3	0	0.1	2	3	248.3	411.7	75.3	33.4	6.9
A14	Conv-CA	3	wheat	cover	0.1	0	0.8	0.5	1	1	175	385	119.7	32	6.8
A15	Conv-CA	3	wheat	wheat	0.1	0.1	0.8	0.8	2	2	193.3	395.3	91.7	28.1	7
A16	Conv	20	wheat	mustard	0.4	0.3	0.9	0.7	2	2	284.3	338	66.7	24.2	8.1
A17	CA	10	wheat	rapeseed	0	0	0.9	0.8	1	1	228	349	203.3	36.4	8.1
A18	Conv-OA	3	wheat	bare	0.7	0.5	0	0	3	3	195.7	454.7	68.3	23.9	6.8
A19	Conv-OA	2	wheat	clover	0.5	0.5	0	0	4	4	279.7	264	262	23.8	7.7
A20	CA-OA	2	wheat	cover	0.7	0.5	0	0	2	2	204	407	49.3	16.9	7.5
A21	Conv	20	wheat	barley	0.4	0.5	0.5	0.6	0	0	340	226.3	238	32.9	8

Conv: conventional agriculture, CA: conservation agriculture, OA: organic agriculture, Conv-CA: transition from conventional to conservation (≤ 3 years), Conv-OA: transition from conventional to organic (≤ 3 years), CA-OA: transition from conservation to organic (≤ 3 years), Itill: tillage intensity index, Itreat: pesticide treatment intensity index, nbOrg: number of organic matter inputs over 5 years, SOM: soil organic matter, BD: bulk density.

Table 2. Effects of practice intensity on collembolan species density in (a) 2020 and (b) 2021. z-values and *P*-values were obtained using GLMM with a negative binomial distribution. Positive and negative z-values indicate respectively an increase and a decrease in Collembola density as practice intensity increases. Bold values indicate significant effects (*P* < 0.05 *, < 0.01 **, < 0.001 ***). Results are only reported for Collembola species among the most frequent.

	ltill		ltreat		nbOrg	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>
(a) 2020						
<i>C. thermophilus</i>	-1.70	0.089	1.10	0.271	-1.12	0.263
<i>I. palustris</i>	-1.85	0.064	1.70	0.089	-1.44	0.149
<i>I. viridis</i>	-0.51	0.610	1.63	0.102	-0.64	0.523
<i>L. cyaneus</i>	-2.67	0.008**	3.72	<0.001***	-2.42	0.015*
<i>M. macrochaeta</i>	-0.90	0.368	0.17	0.862	-0.76	0.449
<i>P. alba</i>	-1.26	0.206	3.05	0.002**	-1.09	0.275
<i>P. armata</i>	-0.48	0.633	1.49	0.136	-0.81	0.418
<i>S. elegans</i>	-1.97	0.049*	1.93	0.054	-1.75	0.081
(b) 2021						
<i>C. thermophilus</i>	-1.17	0.242	0.46	0.648	-1.17	0.241
<i>I. palustris</i>	-2.80	0.005**	1.19	0.233	-1.38	0.166
<i>I. viridis</i>	-2.41	0.016*	0.98	0.327	-1.59	0.113
<i>L. cyaneus</i>	-2.88	0.004**	1.00	0.317	-0.78	0.435
<i>M. macrochaeta</i>	-0.84	0.402	0.89	0.375	-0.32	0.749
<i>P. alba</i>	-1.59	0.112	1.08	0.279	0.17	0.862
<i>P. armata</i>	-0.62	0.534	1.00	0.315	-0.23	0.820
<i>S. elegans</i>	-2.41	0.016*	1.58	0.115	-0.42	0.676

ltill: tillage intensity index, ltreat: pesticide treatment intensity index, nbOrg: nb of organic matter inputs (5 y).

Table 3. Effects of practice intensity on collembolan species traits in (a) 2020 and (b) 2021. z-values and *P*-values were obtained using GLMM with a negative binomial distribution. Positive and negative z-values indicate respectively an increase and a decrease in the trait representation as practice intensity increases. Bold values indicate significant effect ($P < 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$). Only attributes of species traits showing a significant or strong relation to at least one indicator are reported.

	Itill		Itreat		nbOrg	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>
(a) 2020						
Body length <1.5 mm	-0.37	0.715	-0.30	0.765	0.99	0.324
Ocelli absent	-0.24	0.813	1.42	0.155	-2.34	0.019*
Scales present	-2.58	0.009**	4.76	<0.001***	-2.44	0.015*
Trichobothria present	-2.62	0.009**	1.10	0.273	-0.45	0.651
Cylindrical body shape	0.02	0.984	3.14	0.002**	-1.99	0.047*
Pigmentation present	-2.38	0.017*	0.42	0.673	0.41	0.684
Ecomorphosis present	-0.69	0.493	1.47	0.142	-2.19	0.029*
(b) 2021						
Body length <1.5 mm	0.38	0.706	-1.37	0.169	0.59	0.557
Ocelli absent	-0.49	0.625	-0.21	0.837	0.57	0.567
Scales present	-2.69	0.007**	-0.02	0.981	0.45	0.652
Trichobothria present	-3.59	<0.001***	-0.48	0.630	1.03	0.304
Cylindrical body shape	-0.64	0.524	2.51	0.012*	-1.44	0.149
Pigmentation present	0.35	0.723	0.25	0.805	-1.61	0.107
Ecomorphosis present	-4.76	<0.001***	1.44	0.148	-1.10	0.270

Itill: tillage intensity index, Itreat: pesticide treatment intensity index, nbOrg: nb of organic matter inputs (5 y).

Table 4. Effects of practice intensity on measured length traits of Collembola in (a) 2020 and (b) 2021. z-values and P-values were obtained using GLMM with a negative binomial distribution. Positive and negative z-values indicate respectively an increase and a decrease of the length as practice intensity increases. Bold values indicate significant effects ($P < 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$).

	I _{till}		I _{treat}		nbOrg	
	z	P	z	P	z	P
(a) 2020						
Body length	-0.73	0.468	2.51	0.012*	-2.09	0.036*
Head length	-0.71	0.480	2.05	0.040*	-1.72	0.085*
Leg length	-1.29	0.196	2.93	0.003*	-1.99	0.047*
Antenna length	-1.46	0.144	3.03	0.002**	-1.94	0.052
Furca length	-0.49	0.623	0.35	0.727	-0.10	0.920
(b) 2021						
Body length	-2.73	0.006**	1.9	0.058	-1.10	0.270
Head length	-3.07	0.002**	1.39	0.163	-0.47	0.636
Leg length	-1.67	0.095	1.07	0.286	-0.18	0.858
Antenna length	-1.92	0.054	1.12	0.261	-0.26	0.794
Furca length	-1.93	0.053	1.05	0.294	-1.64	0.100

I_{till}: tillage intensity index, I_{treat}: pesticide treatment intensity index, nbOrg: nb of organic matter inputs (5 y).

Figure 1. Measurements of length traits on Collembola. Red arrows represent the position of the different length measurements.

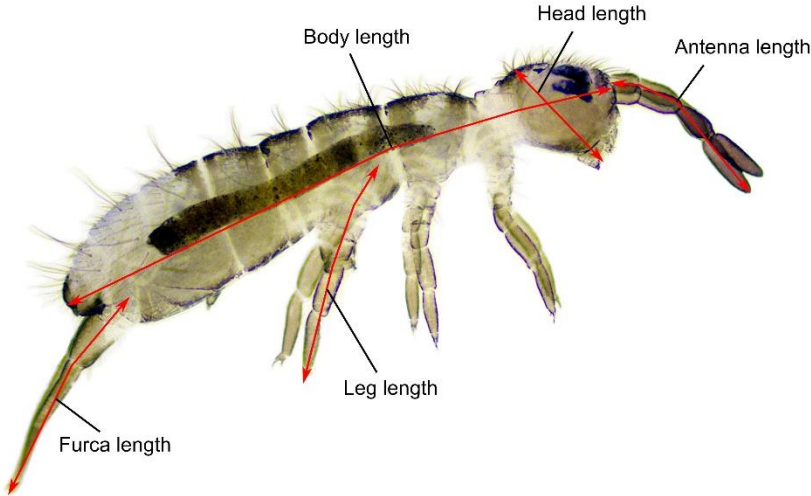


Figure 2. Effect of cropping systems and practice intensity on collembolan (a) species richness and (b) functional richness in 2020 and 2021. Significant differences between systems are represented with different lower-case letters and significant effects of intensity indicators are reported for each year ($P < 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$), all according to the results of GLMM with negative binomial (species richness) or Gaussian (functional richness) distribution. Conv, CA and OA: conventional, conservation and organic agriculture, Conv-CA, Conv-OA and CA-OA: initial-recent system transitions, Itill: tillage intensity, Itreat: pesticide treatment intensity, nbOrg: number of organic matter inputs over 5 years.

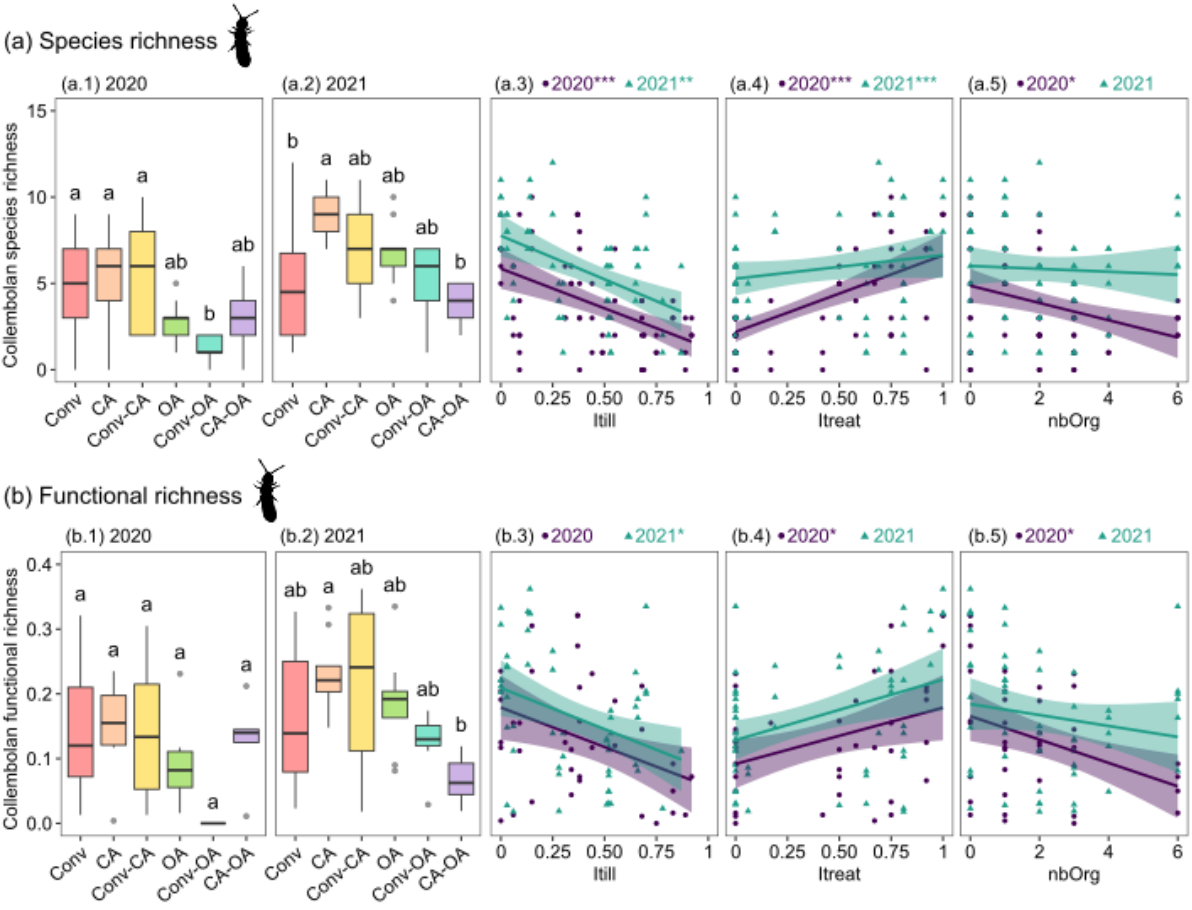


Figure 3. Principal coordinate analysis of collembolan species community (a) in 2020 and 2021 (ANOSIM year: $R = 0.130$, $P = 0.005$; ANOSIM system: $R = 0.135$, $P = 0.016$), and in the different cropping systems (b) in 2020 (ANOSIM system: $R = 0.241$, $P = 0.021$) and (c) in 2021 (ANOSIM system: $R = 0.078$, $P = 0.231$). Conv, CA and OA: conventional, conservation and organic agriculture, Conv-CA, Conv-OA and CA-OA: initial-recent system transitions.

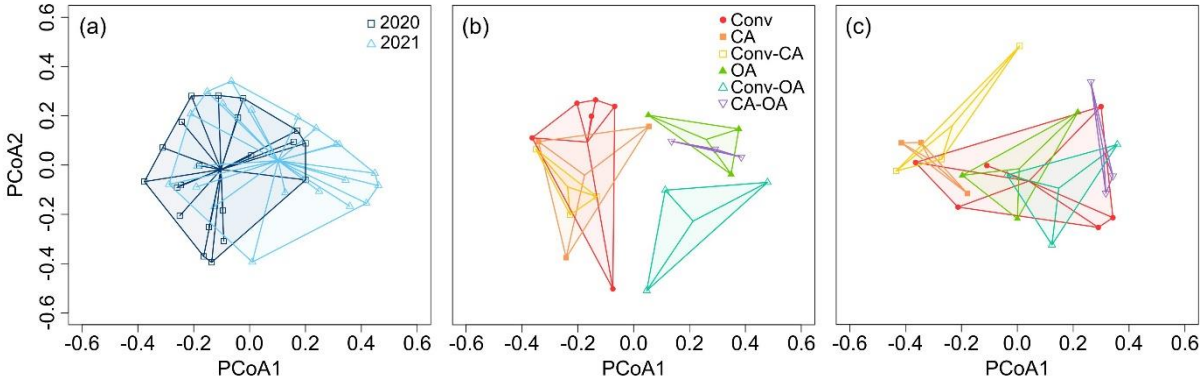


Figure 4. Distribution of length traits measured on Collembola individuals in the different cropping systems in 2020 and 2021. Values are presented as violin plots. Width of violin represents the number of individuals presenting trait of a given length. Conv, CA and OA: conventional, conservation and organic agriculture, Conv-CA, Conv-OA and CA-OA: initial-recent system transitions.

