

RESEARCH ARTICLE

Minor changes in collembolan communities under different organic crop rotations and tillage regimes

Jan Hendrik Moos^{1,2}, Stefan Schrader², and Hans Marten Paulsen¹

Received: March 27, 2020
Revised: June 17, 2020
Revised: August 24, 2020
Accepted: September 10, 2020

HIGHLIGHTS

- Species richness and abundance of collembolans are not affected by tillage and crop rotations in organic farming systems.
- There is some evidence that the relative share of euedaphic collembolans is an indicator of management impacts.
- Collembolan communities are more influenced by crop type and crop cover than by specific crop rotations or differences in tillage regime.

KEYWORDS soil biodiversity, eco-morphological index (EMI), soil tillage, organic matter

Abstract

An aim of organic farming is to reduce negative impacts of agricultural management practices on physical, chemical, and biological soil properties. A growing number of organic farmers is trying out methods of reduced tillage to save costs, protect humus and to foster natural processes in the soil. Furthermore, techniques like increasing crop rotation diversity and reduced tillage are discussed under the topics of agroecology or ecological intensification also for implementation in non-organic farming systems.

The question arises as to whether these practices are positively impacting on soil ecosystems and which indicators can be used to describe these impacts. Collembolans are a widely distributed group of the soil mesofauna. They are mainly characterised as secondary decomposers feeding on fungi and other microorganisms. We investigated the influence of different long-term organic crop rotations (mixed farming with animal husbandry versus stockless arable) and the short term effects of two years of different tillage systems (conventional tillage versus reduced tillage) on the abundance, species richness, species composition, and selected species traits (life forms) of collembolan communities.

Although not significant, some trends are evident. Species composition of collembolan communities responded to expected alterations in soil moisture mediated by different crop sequences and inter-annual effects rather than to different management practices. The proportion of euedaphic

collembolan individuals tended to increase in soil environments that offered more stable habitat conditions from increased availability of organic matter.

1 Introduction

Agriculture impacts directly and severely on soil biodiversity (Orgiazzi et al., 2016). Negative effects are especially expected in intensively managed systems with simple cropping sequences (e.g. Eisenhauer, 2016). To foster sustainability, soil fertility, biodiversity and nutrient supply from the soil, organic farming uses diverse crop rotations, which include different leguminous crops, and rely on organic fertilisation. In organic mixed farming systems, crop nutrition relies on the application of livestock manure and the inclusion of forage and grain legumes. Besides mixed farming systems including animal husbandry, stockless arable cropping systems without manure input are used in organic farming. Their fertilisation is based on N-fixation by legumes and input of crop residues and green manure. In summary, that the main differences between crop rotations of organic farming systems with and without livestock keeping are the form of organic fertiliser used and the proportion of legumes.

Regardless of the fertilisation regime, a common feature of most organic crop rotations is the use of a mouldboard plough, mainly for weed management. As the negative impacts of regular ploughing for different soil functions are well known (Peigné et al., 2007), in recent years different approaches have

¹ Thünen Institute of Organic Farming, Westerau, Germany

² Thünen Institute of Biodiversity, Braunschweig, Germany

been presented to integrate reduced tillage practices into crop rotations in organic farming systems to enhance system sustainability (e.g. Mäder and Berner, 2012; Moos et al., 2016). In general, reducing tillage intensity has positive effects such as reducing the risk of soil erosion or increased macroporosity. Nevertheless, in organic farming, reducing the intensity of soil tillage is hindered by specific challenges such as increasing weed pressure, restricted N-availability, or restrictions in crop choice (Peigné et al., 2007).

The aim of our project was to investigate the influence of different management practices in organic cropping systems on the soil macro- and mesofauna. Complementing a report about effects on earthworms (Moos et al., 2016), this paper considers the influence of crops, crop rotations and tillage regimes on collembolans.

The investigation of widely distributed soil fauna groups such as earthworms and microarthropods, which hold key positions within soil food webs, can shed light on the impact of management practices on soil ecosystems. Collembolans are likely to be good indicators for soil conditions because they are widely distributed (Hopkin, 1997). Due to short life cycles of the species, composition and abundance of collembolan communities are expected to rapidly adapt to and reflect environmental changes. This response might be further enhanced through their function as secondary decomposers, feeding on fungi and microorganisms, which links them closer to the environment than predatory or herbivorous animals (Greenslade, 2007).

The influence of organic fertilisers on collembolan communities is still under debate. Platen and Glemnitz (2016) found a positive effect applying digestate from biogas production on collembolan abundance in a two-year field experiment. Kautz et al. (2006) showed a positive effect of annual applications of straw and green manure. Kanal (2004) also found a positive fertilisation effect when applying cattle manure but highlighted additional seasonal variations in abundance. In contrast, Pommeresche et al. (2017) described negative short-term effects of slurry application on collembolan abundance, with more negative effects for epigeic than endogeic species. None of the studies found any consistent effect on collembolan community composition. Therefore, the influence of organic fertilisation on characteristics of collembolan communities is at least mediated by the type of organic matter and the timing of application.

As for organic fertilisation, there are different results from examinations of the effects of tillage intensity on collembolan communities. Brennan et al. (2006) found that reduced tillage increases collembolan abundance, and Miyazawa et al. (2002) ascribed the related negative effect of conventional tillage on collembolan abundance to modified soil temperature, humidity and pore size distribution. In contrast, van Capelle et al. (2012) found a significant overall reduction in abundance and species diversity with decreasing tillage intensity. This result was however affected by interacting effects of soil texture and collembolan life-form. Negative effects of reduced tillage were shown for atmobiont and euedaphic species in loamy soils (van Capelle et al., 2012). Although euedaphic species are well adapted to live within the soil, they rely on the maintenance

of stable habitat conditions (Jeffery et al., 2010), especially on permanent pore space as they are not burrowing. On clay soils, reduced tillage can lead to a decrease in pore volume, which is likely to have a negative effect on euedaphic collembolans (e.g. Dittmer and Schrader, 2000).

Compared to euedaphic collembolans, hemiedaphic and atmobiont species are less dependent on the soil structure, as they inhabit the upper soil layer, the litter layer, or the soil surface. Other factors such as humidity near the soil surface and shading influence these life-forms (see above, c.f. Pommeresche et al., 2017). Thus, relative proportions of euedaphic, hemiedaphic and atmobiont species should indicate an impact of soil tillage intensity.

Besides fertilisation and tillage regimes, the characteristics of the cultivated crops influence soil conditions and thereby organisms inhabiting the soil. Different crop classes (e.g. cereals versus root crops) can influence evapotranspiration differently and thereby soil moisture and humidity on the soil surface. Legumes influence the soil specifically through their symbiosis with nitrogen fixing bacteria in root nodules. Some studies indicate positive effects of the presence of legumes on collembolan abundance and diversity in grassland due to increased microbial biomass, and higher litter quality (e.g. Sabais et al., 2011). For arable land, some studies have been conducted comparing the influence of simple crop rotations (without legumes) and more complex crop rotations (with legumes) on collembolan communities (Andrén and Lagerlöf, 1983; Jagers Op Akkerhuis et al., 1988). However, these studies did not give consistent results, with complex crop rotations having both positive and no effect on collembolan abundance.

In the study reported here, we examined how collembolan communities respond to different management practices in two organic arable crop rotations on the same experimental station, i.e. under comparable soil-climate and agro-technical conditions. Effects of tillage and crop rotation, as well as effects of crop classes and annual fluctuations (e.g. precipitation), on species richness, abundance, and life-form and species composition of collembolan communities were analysed. We focussed on the question which characteristics of collembolan communities are indicative of the effects of different crop rotations or tillage regimes in organic farming.

2 Material and methods

2.1 Study site

The study was conducted at the experimental station of the Thünen Institute of Organic Farming in Trenthorst/Wulmenau, Schleswig Holstein, northern Germany (53°46'N, 10°31'E). The site has been managed according to the EU Organic Standards 2092/91 and 834/2007 since conversion from conventional farming in 2001. The farming area is nearly flat and the soil conditions are homogeneous. The soils on the site are Stagnic Luvisols derived from boulder clay with silty-loamy texture and bulk densities of the topsoil between 1.3 to 1.5 Mg m⁻³. The Atlantic climate, with a mean annual precipitation of 700 mm, relatively well-distributed throughout the year and a mean annual temperature of 8.8°C, generally

offers favourable cropping conditions. Dry periods and low temperatures can limit N-mineralisation in the heavy soils in early spring. The C:N-ratio of about 10 lies in a range which is typical for high yielding agricultural land (Blume et al., 2010). According to German fertilisation recommendations, soils are sufficiently supplied with P, K, and Mg. The apparent soil pH of 6.3 to 6.5 is typical for arable land in temperate regions.

Within the experimental station, four crop rotations were established: livestock I (LI), livestock II (LII), livestock III (LIII) and stockless (SL) (Figure 1). The crop rotations LI to LIII are part of mixed farming systems and have been designed to serve the needs of different livestock. Livestock manure (slurry and solid manure) from one central stock was applied to all fields of these three crop rotations. Furthermore, the crop rotations comprised similar elements (Table 1). Therefore, fields from the three rotations of the ‘mixed’ systems (LI, LII, LIII) can be seen as replicates when cultivated with identical crops. The stockless rotation (SL) differs from the livestock-based rotations (LI to LIII) in organic fertilisation and organic matter backflow through crop residues (c.f. 2.2).

Each field on the experimental station is identified by a unique field-code and includes one or two long-term monitoring plots (LTM-plot) of one hectare each (Figure 1). Generally, within each LTM-plot, four geo-referenced long-term sampling points (LTM-point) are located in a square at a distance of 60 m. Monitoring plots are stretched to cover one hectare in narrow fields and the LTM-points are then located in a zigzag with distances of 30 m (Figure 1). Soil sampling distances larger than 20 to 50 m assure the inclusion of spatial variability of chemical and physical soil parameters in this landscape (Haneklaus et al., 1998).

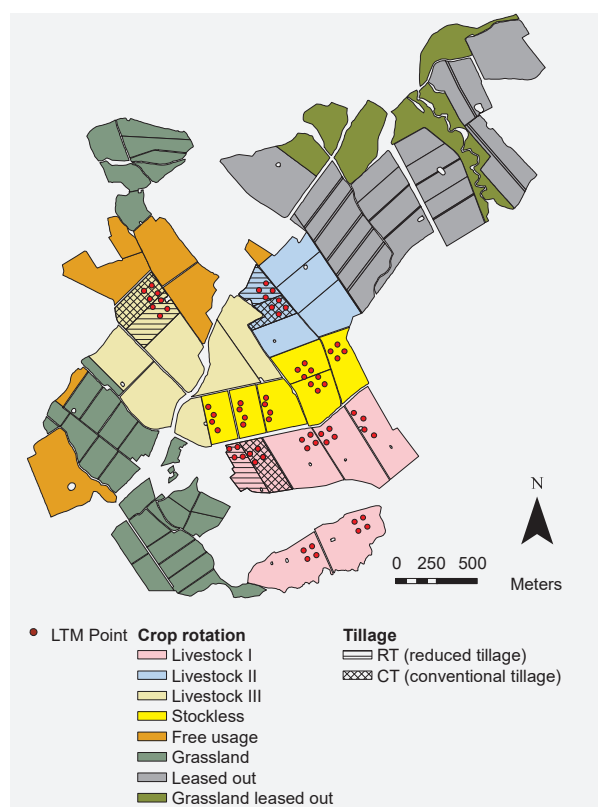


FIGURE 1 Map showing the experimental farm in Trenthorst/Wulmenau, Germany and the different farming systems realised within the farm. Red circles indicate the location of long-term monitoring (LTM) points used for this study.

TABLE 1

Crop rotations (livestock I, livestock II, livestock III, stockless) and average soil conditions within the upper 30 cm of soils in 2012 on the fields of the experimental farm in Trenthorst/Wulmenau. The crop rotations comprise five (livestock II), six (livestock I, stockless) or seven (livestock III) fields.

Crop rotation	Livestock I	Livestock II	Livestock III	Stockless
Crops	clover-grass	clover-grass	clover-grass	red clover
	clover-grass	maize	clover-grass	winter wheat
	maize	winter wheat	spring barley	spring barley
	winter wheat	field pea/spring barley	field pea/false flax	field pea
	field bean/oat	triticale	winter barley	winter rape
	triticale		field bean	triticale
		triticale		
pH	6.4 ± 0.1	6.4 ± 0.0	6.3 ± 0.1	6.5 ± 0.1
Nutrient content (mg 100g ⁻¹)				
P	7.0 ± 0.3	8.6 ± 0.4	6.1 ± 0.4	7.7 ± 0.3
K	11.9 ± 0.5	16.1 ± 0.8	13.0 ± 1.2	11.0 ± 0.4
Mg	10.3 ± 0.3	11.6 ± 0.2	11.8 ± 0.3	11.3 ± 0.3
Texture (g kg ⁻¹)				
Clay (< 2 µm)	23 ± 1	18 ± 2	24 ± 3	23 ± 1
Silt (2–50 µm)	35 ± 1	33 ± 3	40 ± 3	37 ± 0
Sand (50–2000 µm)	42 ± 2	48 ± 4	35 ± 2	39 ± 1

P and K: CAL extract (Schüller, 1969), Mg: CaCl₂ extract (Schachtschabel, 1954), Mean ± standard deviation.

The German Weather Service (DWD, Deutscher Wetterdienst) provided information about soil moisture for the years 2012 and 2014 (Figure 2). Water availability under winter wheat in the top 30 cm was calculated for soil and weather conditions at the experimental station using the AMBAV model (Löpmeier, 1994).

2.2 Study design

To evaluate the influence of different management practices on collembolan communities in organic farming we compared (i) two crop rotations (livestock I versus stockless) and (ii) conventional tillage with mouldboard ploughing versus reduced tillage without mouldboard ploughing (Figure 1).

In (i) we evaluated the influence of one decade of different organic crop rotations on collembolan communities. The management of the crop rotations mainly differed in the share of forage legumes (Table 1), in the amount of plant material remaining on the fields (green mulch and straw) and in farmyard manure application (Table 2). We sampled all six fields of the livestock I (LI) and all six fields of the stockless (SL) rotation on 29 May 2012.

Since a crop rotation-independent influence of different crop classes (grains, legumes, forage crops) could not be excluded, this was also examined.

In (ii) we studied the effect of soil tillage on collembolan communities within a short-term experiment. Therefore, in summer 2012 we split one field from each of the LI, LII and LIII rotations (Figure 1). Afterwards in each of the three rotations, one field-half was managed with ploughing (CT: conventional tillage) and the other field-half without ploughing (RT: reduced tillage). Within our study, conventional and

TABLE 2

Characteristics of fertilisation and crop residue management on the fields of the livestock I and stockless rotation in the harvest years 2002 to 2012. For management measures the absolute number of events within 10 years is given.

	Livestock I	Stockless
N from organic fertilisers (kg ha ⁻¹ a ⁻¹)	39–62	–
Organic matter from organic fertilisers (kg ha ⁻¹ a ⁻¹)	954–1318	–
Liming (kg ha ⁻¹ a ⁻¹)	0–300	–
Plant residues remaining on the field (not clover-grass)	2–3	7–8
Years with clover-grass	2–4	1–2
Mulching of clover grass	0–3	1–4
Ploughing of clover-grass	1–2	1–2

reduced tillage were defined according to ASAE (2005). Conventional tillage included the use of a two-sided mouldboard plough, with a working depth of 25 to 30 cm, whereas no mouldboard plough was used in the field-halves managed with reduced tillage. In RT, tillage depth was a maximum of 15 cm without soil inversion. In RT, a chisel plough and a rotary harrow were used. Therefore, the reduced tillage regime in our study is rather intensive compared to much less intensive approaches like no-till. The two different tillage regimes were applied in two successive years. In 2012 before growing triticale and in 2013 before growing clover-grass. The soil management practices carried out are summarised in Table 3. We sampled the field-halves on 29 May 2012

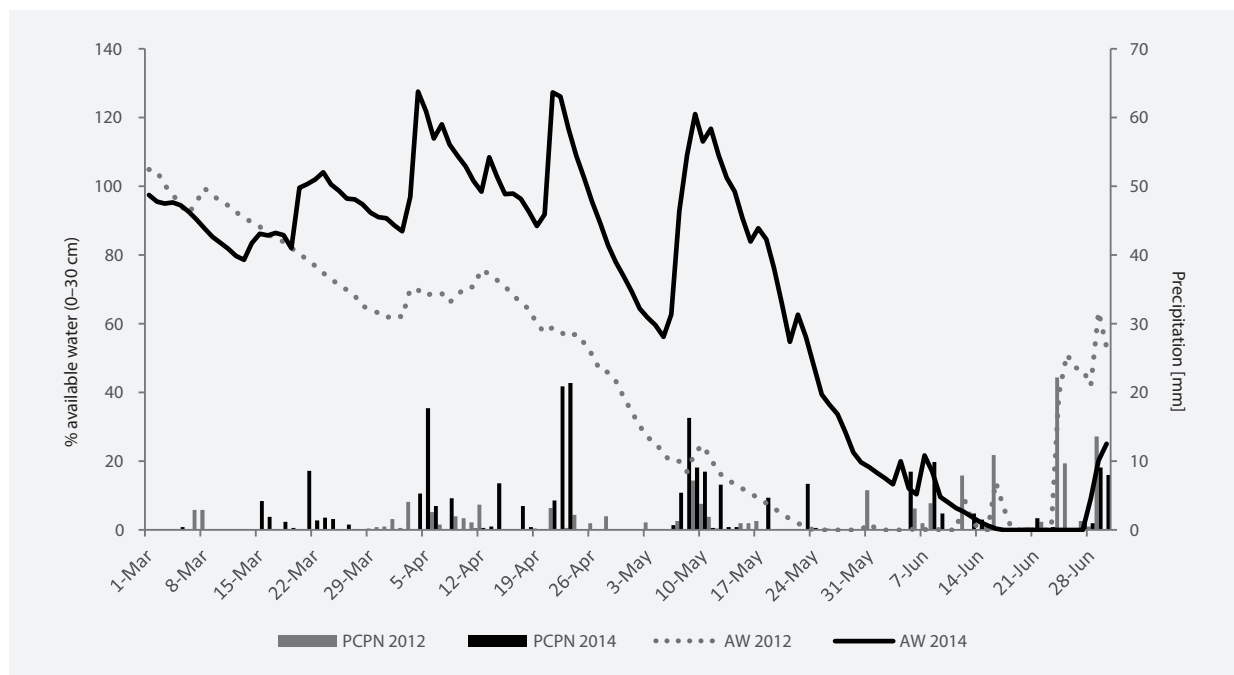


FIGURE 2
Precipitation (PCPN) and available water (AW) under winter wheat in Trenthorst/Wulmenau, Germany in 2012 and 2014 according to AMBAV model.

TABLE 3

Agricultural measures applied for soil management on the three experimental fields, each belonging to one out of three livestock-based farming systems (livestock I–III), in 2011, 2012, and 2013. CT: conventional tillage; RT: reduced tillage

Agricultural machinery used (ASABE, 2009)	Working depth (cm)	2011/2012 ^a			2012						2013					
		Livestock I	Livestock II	Livestock III	Livestock I		Livestock II		Livestock III		Livestock I		Livestock II		Livestock III	
					CT	RT	CT	RT	CT	RT	CT	RT	CT	RT	CT	RT
Chisel plough for stubble cultivation	10–15	04 Oct	23 Sep	03 Oct	19 Sep	19 Sep	09 Sep	09 Sep	05 Sep	05 Sep	12 Aug	12 Aug	(2x) 08 Aug	(2x) 08 Aug	11 Aug	11 Aug
Two-way mouldboard plough (5-furrow)	25–30	19 Oct	20 Oct	20 Oct												
Two-way mouldboard plough (5-furrow) with packer	25–30				20 Sep		10 Sep		08 Sep				13 Aug		14 Aug	
Two-way mouldboard plough (4-furrow)	25–30										18 Aug					
Chisel plough	10–15							(2x) 17 Sep		(2x) 17 Sep	15 Aug	15 Aug	14 Aug	14 Aug	15 Aug	15 Aug
Spring teeth harrow	10–15	25 Mar	22 Mar				18 Sep		(2x) 18 Sep							
Rotary harrow	10				20 Oct		(2x) 19 Sep		18 Sep						16 Aug	16 Aug
Seed drill + front-mounted disc harrow	5–10	26 Mar	24 Mar	25 Mar	21 Oct	21 Oct	19 Sep	19 Sep	19 Sep	19 Sep	29 Aug	29 Aug	21 Aug	21 Aug	18 Aug	18 Aug
Land roller		25 Mar	22 Mar													

a) Cultivation of the spring-grown crops field bean/oat, field pea/spring barley, and field bean, respectively.

(before introducing the different tillage systems) and again after two years on 19 May 2014 to assess the influence of tillage on collembolan communities. In 2012, the fields were planted with spring grown grain-legume cereal mixtures or pure grain-legumes (L I: field bean/oat; L II: field pea/spring barley; L III: field bean). In 2014, all fields were planted with winter grown clover-grass.

Samples taken in 2012 from the half-field subsequently managed with CT on the field of the L I rotation have also been part of the dataset when comparing the crop rotations L I and SL. Since annual effects could not be excluded, these were also examined.

2.3 Sampling and identification of collembolans

According to our study design, at each LTM-point two soil samples (subsamples) were collected with an auger (effective diameter 4 cm, depth 10 cm) resulting in eight samples per field half/field (Figure 1). This soil sampling resulted in 96 samples for the comparison of crop rotations (L I versus SL) in 2012. It resulted in 48 samples in both 2012 and 2014 for the comparison of tillage regimes (CT versus RT). The soil mesofauna was extracted from the whole samples using a MacFadyen high-gradient extractor (MacFadyen, 1961). After collection in monoethylenglycol, the extract was transferred to 96% ethanol for storage. Since a first inspection of

the samples from May 2012 showed that many collembolan individuals could be extracted from the individual samples, two out of eight samples per field-half/field were randomly selected to reduce the amount of work to a manageable level. Attention was paid to always select samples from two different LTM-points. From these two samples collembolan individuals were sorted out from the extract, counted and stored separately in ethanol. The individuals were then mounted on glass microscope slides and identified at the species level (max. magnification 400x) according to Hopkin (2007). If necessary, additionally identification keys by Gisin (1960), Bretfeld (1999), Potapov (2001), Thibaud et al. (2004), Dunger and Schlitt (2011), or Jordana (2012) were used. The nomenclature used followed the system proposed by Hopkin (2007).

Heterosminthurus bilineatus Group, *Protaphorura armata* Group, *Sminthurinus aureus* Group, and *Sminthurus viridis* Group were identified according to Hopkin (2007) as complexes of species. Furthermore, when discussing the genera *Desoria* and *Isotomurus*, Hopkin (2007) mentions difficulties in separating some species in these genera. Therefore, he

summarises them into species groups *Desoria tigrina* Group and *Isotomurus palustris* Group, which we adopted in the identification process.

2.4 Life-form traits of collembolans

We used the method proposed by Martins da Silva et al. (2016) to classify collembolan species according to their adaptation to living within the soil by calculating an eco-morphological index (EMI). This enabled us to calculate a weighted mean EMI value for each collembolan sample. This is a so-called mean trait value (mT) (Vandewalle et al., 2010).

In addition to using the EMI mT-values for describing collembolan communities, we aimed to visually compare the composition of life-forms from different collembolan communities using ternary diagrams (c.f. 2.5.3). Thus, we used publications by Stierhof (2003), Chauvat et al. (2007), Sticht et al. (2008), and Salamon et al. (2011) to assign the calculated EMI values to one of the three life-forms atmobiont, hemiedaphic, or euedaphic (Table 4). We assume that species with the same EMI score belong to the same life-form

TABLE 4 (PART 1)

Life-forms (LF) of collembolan species as derived from eco-morphological index (EMI) and publications of Stierhof (2003), Chauvat et al. (2007), Sticht et al. (2008), and Salamon et al. (2011). EMI (eco-morphological index) scores according to Martins da Silva et al. (2016). at: atmobiont; ep: epedaphic; he: hemiedaphic; eu: euedaphic. NA: No data available.

	Abbreviation	Frequency (%) ^a	Ocelli	Antenna	Furca	Scales/hairs	Pigmentation	EMI according to Martins da Silva et al. (2016)	Life-form according to Chauvat et al. (2007)	Life-form according to Sticht et al. (2008)	Life-form according to Stierhof (2003)	Life-form according to Salamon et al. (2011)	Derived Life-form
<i>Isotomurus palustris</i> Gr.	Isot.palu	56	0	2	0	0	0	0.1	ep				at
<i>Tomocerus minor</i> (Lubbock, 1862)	Tomo.mino	2	0	0	0	0	2	0.1			he		at
<i>Heteromurus nitidus</i> (Templeton, 1836)	Hete.niti	6	0	2	0	0	2	0.2		he	eu	he	at
<i>Lepidocyrtus cyaneus</i> (Tullberg, 1871)	Lepi.cyan	4	0	2	0	0	2	0.2	ep	at	he	ep	at
<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)	Lepi.lanu	42	0	2	0	0	2	0.2	ep	at	he	ep	at
<i>Lepidocyrtus lignorum</i> (Fabricius, 1775)	Lepi.lign	2	0	2	0	0	2	0.2			he		at
<i>Heterosminthurus bilineatus</i> Gr.	Hete.bili	2	0	2	0	4	0	0.3		at			he
<i>Lipothrix lubbocki</i> (Tullberg, 1872)	Lipo.lubb	2	0	2	0	4	0	0.3			he		he
<i>Pseudosinella alba</i> (Packard, 1873)	Pseu.alba	17	0	4	0	0	4	0.4	he		eu	he	he
<i>Pseudosinella decipiens</i> (Denis, 1924)	Pseu.deci	2	0	4	0	0	4	0.4					he
<i>Pseudosinella denisi</i> Gisin, 1954	Pseu.deni	2	0	4	0	0	4	0.4					he
<i>Sminthurides malmgreni</i> (Tullberg, 1876)	Smin.malm	2	0	4	0	4	0	0.4					he
<i>Sminthurides parvulus</i> (Krausbauer, 1898)	Smin.parv	2	0	4	0	4	0	0.4			he		he
<i>Cryptopygus thermophilus</i> (Axelson, 1900)	Cryp.ther	4	0	4	0	4	2	0.5		he	he	he	he
<i>Desoria tigrina</i> Gr.	Deso.tigr	2	0	4	0	4	2	0.5					he
<i>Deutosminthurus pallipes</i> (Bourlet, 1843)	Deut.pall	27	0	4	0	4	2	0.5		at		ep	he
<i>Deutosminthurus sulphureus</i> (Koch, 1840)	Deut.sulp	2	0	4	0	4	2	0.5					he
<i>Isotoma viridis</i> Bourlet, 1839	Isot.viri	69	0	4	0	4	2	0.5	ep	he	he	ep	he
<i>Parisotoma notabilis</i> (Schäffer, 1896)	Pari.nota	56	0	4	0	4	2	0.5	he	he		he	he
<i>Sminthurinus aureus</i> Gr.	Smin.aure	52	0	4	0	4	2	0.5	he	he	he	ep	he
<i>Sminthurinus niger</i> (Lubbock, 1862)	Smin.nige	2	0	4	0	4	2	0.5			he	ep	he

TABLE 4 (PART 2)

Life-forms (LF) of collembolan species as derived from eco-morphological index (EMI) and publications of Stierhof (2003), Chauvat et al. (2007), Sticht et al. (2008), and Salamon et al. (2011). EMI (eco-morphological index) scores according to Martins da Silva et al. (2016). at: atmobiont; ep: epedaphic; he: hemiedaphic; eu: euedaphic. NA: No data available. (Table 4, part 1, see previous page)

	Abbreviation	Frequency (%) ^a	Ocelli	Antenna	Furca	Scales/hairs	Pigmentation	EMI according to Martins da Silva et al. (2016)	Life-form according to Chauvat et al. (2007)	Life-form according to Sticht et al. (2008)	Life-form according to Stierhof (2003)	Life-form according to Salamon et al. (2011)	Derived Life-form
<i>Sminthurus viridis</i> Gr.	Smin.viri	12	0	4	0	4	2	0.5					he
<i>Sphaeridia pumilis</i> (Krausbauer, 1898)	Spha.pumi	21	0	4	0	4	2	0.5	he	he	he	he	he
<i>Stenacidia violacea</i> (Reuter, 1881)	Sten.viol	8	0	4	0	4	2	0.5					he
<i>Ballistura schoetti</i> (Dalla Torre, 1895)	Ball.scho	2	0	4	2	4	2	0.6					he
<i>Cryptopygus bipunctatus</i> (Axelson, 1903)	Cryp.bipu	4	0	4	0	4	4	0.6		he		he	he
<i>Parisotoma ekmani</i> (Fjellberg, 1977)	Pari.ekma	4	0	4	0	4	4	0.6					he
<i>Proisotoma minuta</i> (Tullberg, 1871)	Proi.minu	48	0	4	2	4	2	0.6		he	he		he
<i>Proisotoma tenella</i> (Reuter, 1895)	Proi.tene	2	0	4	2	4	2	0.6					he
<i>Folsomides parvulus</i> (Stach, 1922)	Fols.parv	4	0	4	2	4	4	0.7			eu	he	he
<i>Proisotoma minima</i> (Absolon, 1901)	Proi.mini	2	0	4	2	4	4	0.7			he		he
<i>Xenylla boermeri</i> Axelson, 1905	Xeny.boer	2	0	4	4	4	2	0.7					he
<i>Cryptopygus garretti</i> (Bagnall, 1939)	Cryp.garr	4	4	4	0	4	4	0.8					eu
<i>Cyphoderus albinus</i> Nicolet, 1842	Cyph.albi	10	4	4	0	4	4	0.8	he		eu		eu
<i>Isotomiella minor</i> (Schäffer, 1896)	Isot.mino	33	4	4	0	4	4	0.8	eu	eu	eu		eu
<i>Magalothorax minimus</i> Willem, 1900	Mega.mini	2	4	4	0	4	4	0.8	eu	eu	eu		eu
<i>Oncopodura crassicornis</i> Shoebottom, 1911	Onco.cras	4	4	4	0	4	4	0.8			eu		eu
<i>Folsomia candida</i> Willem, 1902	Fols.cand	4	4	4	2	4	4	0.9		he	eu		eu
<i>Folsomia spinosa</i> Kseneman, 1936	Fols.spin	2	4	4	2	4	4	0.9		he	eu		eu
<i>Isotomodes productus</i> (Axelson, 1906)	Isot.prod	10	4	4	2	4	4	0.9		eu	eu	eu	eu
<i>Mesaphorura</i> sp.	Mesa.spec	21	4	4	4	4	4	1					eu
<i>Neotullbergia crassiscuspis</i> (Gisin, 1944)	Neot.cras	2	4	4	4	4	4	1		eu	eu		eu
<i>Paratullbergia callipygos</i> (Börner, 1902)	Para.call	2	4	4	4	4	4	1	eu	eu	eu		eu
<i>Protaphorura armata</i> Gr.	Prot.arma	27	4	4	4	4	4	1	eu		eu	eu	eu
<i>Stenaphorura denisi</i> Bagnall, 1935	Sten.deni	8	4	4	4	4	4	1	eu	eu	eu	eu	eu
<i>Supraphorura furcifera</i> (Börner, 1901)	Supr.furc	2	4	4	4	4	4	1					eu
<i>Willemia anophthalma</i> (Börner, 1901)	Will.anop	6	4	4	4	4	4	1	eu	eu	eu	eu	eu

^aFrequency in % from a total of 48 samples.

type. The use of 0.7 as upper threshold for the hemiedaphic type is supported by studies of Dittmer and Schrader (2000), Salamon et al. (2004), and Querner (2008). Additionally, this threshold separates species with and without ocelli. Studies by Caravaca and Ruess (2014), D'Annibale et al. (2015), Dombos et al. (2017), Gillet and Ponge (2004), Leinaas and Bleken (1983), Lindberg and Bengtsson (2005), Ponge (2000), and Sterzynska and Kuznetsova (1995) justify separation between hemiedaphic and atmobiont at 0.3. As we followed the system proposed by Gisin (1943) we combined species described as epigeic and atmobiont under the term atmobiont.

2.5 Statistics

2.5.1 Statistical models

Generalised linear mixed models (GLMMs) were used including 'crop rotation' (L1 versus SL) as fixed effect and 'field-code' (unique to each field on the experimental station) as random intercept effect for detecting differences in collembolan abundance or species richness depending on the type of crop rotation. The 'tillage regime' (CT versus RT) was used as fixed effect in GLMM when analysing the influence of tillage on collembolan abundance. 'Sampling date' (May 2012, May 2014) and the interaction of 'sampling date' and 'tillage regime' were used as additional fixed effects to check for

temporal variability within the data. The ‘crop rotation’ (LI, LII, LIII) was used as random intercept effect. The same set-up was used when modelling collembolan species richness depending on differences in the tillage regime.

Mean trait values (EMI mT-values) were evaluated using linear mixed models (LMMs). The model evaluating the influence of ‘crop rotation’ used ‘crop rotation’ (LI versus SL) as fixed effect and ‘field-code’ as random intercept effect. After applying a backward selection procedure, the model describing the influence of ‘tillage regime’ on EMI mT-values used ‘sampling date’ (May 2012, May 2014) as fixed effect and ‘crop rotation’ (LI, LII, LIII) as random intercept effect.

Statistical analyses were conducted using R3.2.2 (R Development Core Team, 2016). All GLMMs were calculated for negative-binomial distributed count data. We used the R-package glmmADMB (Skaug et al., 2015) for calculating GLMMs. For negative-binomial models the package uses the log as standard link-function. The estimation method used in glmmADMB is Laplace. Linear mixed models were calculated using the R-package lme4 (Bates et al., 2015). After setting up models LS-Means and pairwise comparisons were obtained using the R-package lsmeans (Lenth, 2016). Abundance, species richness and EMI mT-values presented in the results section are LS-means.

2.5.2 Non-metric multidimensional scaling (NMDS)

Non-metric multidimensional scaling (NMDS) and associated analyses were conducted using the R-package vegan (Oksanen et al., 2015). After conducting NMDS, differences between centroids for factor levels were analysed using permutational multivariate analysis of variance using distance matrices (R-function `vegan::adonis`). Homogeneity of multivariate spread is a prerequisite for comparing centroids and was therefore checked in advance (R-function `vegan::beta-disper`). The adjustment of p-values obtained from pairwise comparisons of centroids was conducted using Bonferroni correction. NMDS were calculated using abundance values and used Bray-Curtis as dissimilarity measure. The final NMDS analysis for the comparisons between crop rotations and tillage regimes both used three dimensions and had stress values of twelve and eleven, respectively. When displaying species in the NMDS plots they had to be weighted. Only the main species were displayed to avoid overlapping of species labels. Species weighting was done as follows: (1) calculating the share of each species in every sample; (2) calculating the share of samples in which the share of a species was greater than or equal to 3.2%; (3) weighting of species according to this share of samples. The threshold of 3.2% was chosen according to Engelmann (1978) who proposed this level for separation of main and other species of soil arthropod communities.

2.5.3 Ternary diagrams

Ternary diagrams illustrate compositions of three components and we used them to visualise the composition of collembolan life-forms. We calculated the relative share of atmobiote, hemiedaphic, and euedaphic collembolan individuals for each

sample. For creating ternary diagrams the R-package compositions was used (van den Boogaart et al., 2014). The share of each component is 100% in the corner labelled accordingly and 0% at the line opposite to that corner.

3 Results and discussion

3.1 Abundance, species richness and life-forms

Overall, 47 collembolan species and species groups were identified within the samples analysed for this study (Table 4). Based on their occurrence in the samples of this dataset seven species are rated eudominant, eight dominant, 12 subdominant and 20 as rare according to Engelmann (1978).

3.1.1 Comparison of crop rotations: livestock I versus stockless

In May 2012, after 10 years of different crop rotation management treatments, neither collembolan abundance nor species richness differed significantly between the two crop rotations livestock I (LI) and stockless (SL) (Table 5). On fields of the LI rotation, 22 species and on fields of the SL rotation 29 species were identified. While not significant, collembolan abundance, the overall number of species, and the number of species per sample were higher in the stockless rotation. These trends found in our study are in line with results of studies conducted by Kautz et al. (2006) and Pommeresche et al. (2017). Kautz et al. (2006) found a positive effect of regular application of straw and green manure on overall collembolan abundance which they attributed to improved soil physical properties and good food supply. In addition, Pommeresche et al. (2017) observed a decrease in collembolan abundance after slurry application, which was more pronounced for epigeic than for endogeic collembolan species. According to Domene et al. (2010), this negative effect of manuring can be ascribed to extractable ammonium from the slurry which is toxic for collembolans. Within our study, a higher proportion of plant residues remained on the fields of the stockless rotation while the fields of the livestock I rotation were regularly manured with slurry (cf. Table 2).

TABLE 5

Results of statistical modelling (GLMM) to reveal the influence of different crop rotations (LI vs. SL) on abundance and species richness of collembolans (n=24). Least square means (LSM) as well as lower (LCL) and upper (UCL) confidence levels are given.

Response	p	Effect level	LSM	Asymptotic LCL	Asymptotic UCL
Abundance (Individuals m ⁻²)	0.4384	LI	19,126	8,015	45,645
		SL	31,107	13,033	74,244
Species richness (Species per sample)	0.2131	LI	5	3	7
		SL	7	5	10

There was no significant difference between EMI mT-values of the two crop rotations in May 2012 (LI: 0.51 ± 0.06 ; SL: 0.55 ± 0.06 ; $p=0.6452$). When visually comparing the proportions of life-forms between LI and SL fields, a higher relative share of euedaphic individuals under LI could be revealed, while the relative share of hemiedaphic individuals was higher under SL (Figure 3). Because the 95 % CIs overlap these differences are considered as not significant. The trend towards higher relative share of euedaphic individuals in the livestock I rotation may be caused by negative effects of regular slurry application on surface dwelling collembolans (Pommeresche et al., 2017).

3.1.2 Comparison of tillage regimes: conventional versus reduced

No significant differences in collembolan abundance or species richness were observed in either 2012, before setting aside the plough, or in 2014, after two years of different tillage regimes in place when comparing conventional tillage (CT) and reduced tillage (RT) (Table 6). Furthermore, there was no significant interaction between tillage regime and year of sampling.

As in our study, Petersen (2002) did not find any difference in collembolan abundance when comparing conventional tillage with ploughing and non-inverting deep tillage in a one-year case study. Sabatini et al. (1997) support this result for the long run when studying fields constantly managed with three different tillage intensities for 15 years prior to sampling. In contrast, Miyazawa et al. (2002) revealed a positive effect of reduced tillage on collembolan abundance. The fact that we did not observe any differences between

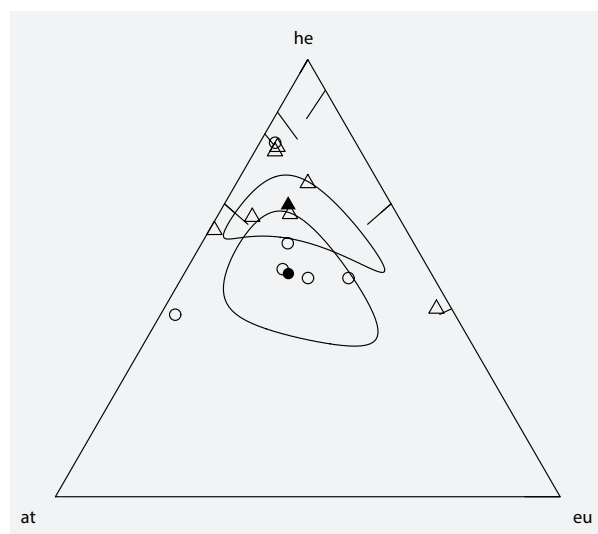


FIGURE 3 Ternary diagram representing the relative proportions of life-forms (eu: euedaphic, he: hemiedaphic, at: atmobiote) in the collembolan communities on the fields of the livestock I (LI) and stockless (SL) rotation in 2012. Data from SL marked with triangles and data from LI with circles. Solid markings represent the geometrical means. In addition 95 % CI are shown.

TABLE 6

Results of statistical modelling (GLMM) to reveal the influence of different tillage regimes (CT vs. RT) on abundance and species richness of collembolans (n=24). Least square means (LSM) as well as lower (LCL) and upper (UCL) confidence levels are given.

Response	Grouping	p	Effect Level	LSM	Asymptotic LCL	Asymptotic UCL
Abundance (Individuals m ⁻²)	2012	0.0514	CT	8,220	5,317	12,708
			RT	12,046	7,762	18,693
	2014	0.4821	CT	29,067	18,804	44,933
			RT	25,357	16,419	39,161
	CT	<0.0001	2012	8,220	5,317	12,708
			2014	29,067	18,804	44,933
	RT	0.0002	2012	12,046	7,762	18,693
			2014	25,357	16,419	39,161
Species number (Species per sample)	2012	0.8995	CT	5	3	8
			RT	5	3	8
	2014	0.8206	CT	6	4	10
			RT	6	4	9
	CT	0.2881	2012	5	3	8
			2014	6	4	10
	RT	0.476	2012	5	3	8
			2014	6	4	9

conventional and reduced tillage could be due to our use of a rather intensive form of reduced tillage with the use of chisel plough and rotary harrow. In addition, the sampling in May 2014 took place nine months after the last ploughing and the time might have been long enough for the collembolan communities to recover from this disturbance (Petersen, 2002). Furthermore, the influence of soil tillage on collembolan abundance is mediated by abiotic soil properties. When evaluating twelve datasets from nine German studies van Capelle et al. (2012) showed an overall positive effect of conventional tillage on collembolan abundance and diversity, but also highlighted that this overall effect did not hold true for all combinations of soil type and life-forms. For instance, species of all life-forms were promoted by reduced tillage and not by conventional tillage in silty soils.

In our study collembolan abundance was significantly higher in May 2014 as compared to May 2012 under both tillage regimes. We ascribe this result to higher soil moisture in 2014 and the different crops under study in 2012 (spring grown grain-legume cereal mixtures or pure grain-legumes) and in 2014 (winter grown clover-grass). Seasonal effects on collembolan communities based on differences in soil moisture rather than on differences in management were also shown by D'Annibale et al. (2017). Due to the setup of our investigating it was not possible to distinguish the effect of year and cultivated crops, but we could show that there was no effect of tillage regime on collembolan abundance or species richness in our study.

A visual comparison of the proportions of life forms under CT and RT in May 2012 (Figure 4a) and May 2014 (Figure 4b) was possible using ternary diagrams. There was no difference in the proportions of life forms in May 2012. In May 2014, the

relative share of atmobiont individuals was higher under CT than under RT whereas under RT the relative share of hemiedaphic individuals was higher (Figure 4b). The 95 % CIs only overlap slightly for the data from May 2014.

Martins da Silva et al. (2016) found an increase in euedaphic collembolans in soil habitats offering stable conditions in terms of resource availability, soil moisture, or disturbance in a Europe-wide study of different habitat types (forests, grasslands, arable land). Therefore, we hypothesise that the trend towards a higher relative share of hemiedaphic individuals after two years of reduced tillage indicates the early stages of the stabilisation of habitat conditions on the field-halves that were not ploughed.

Irrespective of the tillage regime, the EMI mT-value was significantly higher in May 2012 than in May 2014 (2012: 0.61 ± 0.04 ; 2014: 0.44 ± 0.04 ; $p < 0.01$). Higher EMI mT-values indicate a higher relative share of euedaphic individuals, which we assume is due to the dry weather conditions in 2012 decreasing the relative share of hemiedaphic and atmobiont individuals.

3.2 Collembolan communities

In the following we use autecological information on collembolan species to characterise gradients uncovered with multivariate statistical methods. This approach must take geographical differences into account. Fjellberg (1998, 2007) characterises *Protaphorura armata* and *Sminthurus viridis* as preferring rather dry or mostly dry habitats. This is contrary to the views of other authors. While Hopkin (1997) reports that *P. armata* is susceptible to drought, Bretfeld (1999) states that *S. viridis* prefers the vegetation of moister grasslands and herbaceous fields. We suppose that these different ratings of

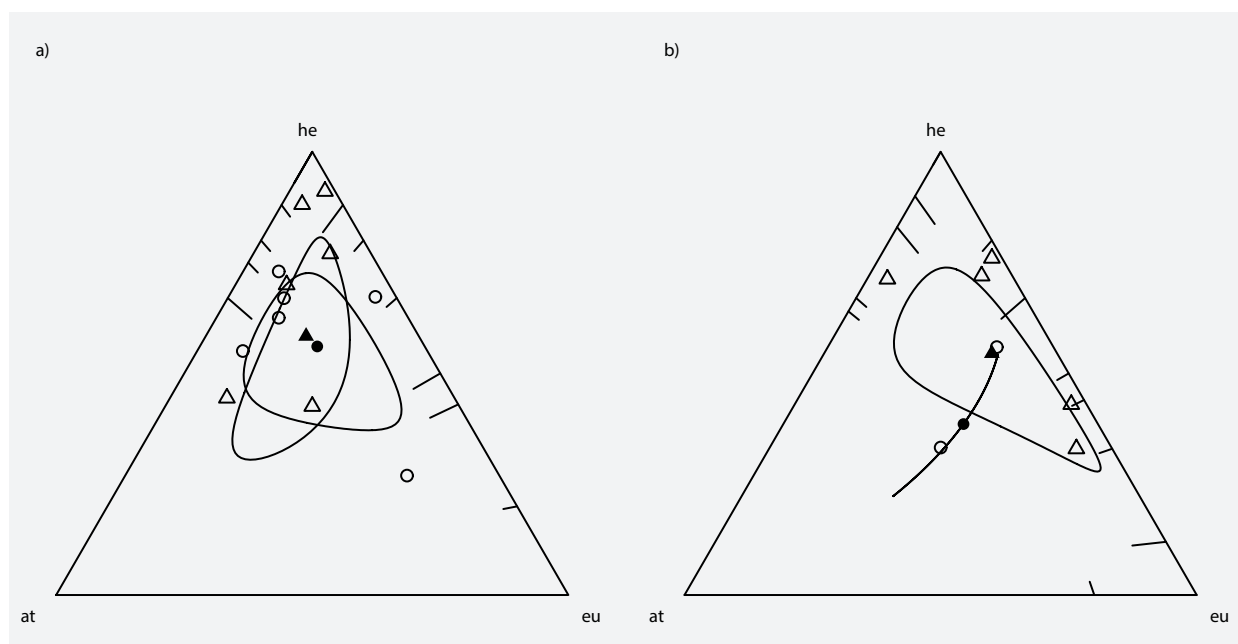


FIGURE 4

Ternary diagram representing the relative proportions of life-forms (eu: euedaphic, he: hemiedaphic, at: atmobiont) in the collembolan communities on the fields under CT and RT in May 2012 (a) and May 2014 (b). Data from RT marked with triangles and data from CT with circles. Solid markings represent the geometrical means. In addition 95 % CI are shown.

species are due to the fact that the assessments of Fjellberg (1998, 2007) are more valid for boreal and alpine regions with lower mean temperatures. Individuals of the same collembolan species are able to tolerate different humidity levels depending on the mean temperatures in their respective habitat, with individuals living in colder habitats tolerating lower humidity (Snider and Butcher, 1972, as cited in Hopkin 1997). Therefore, in the case of *P. armata* and *S. viridis* we adopted the view of Hopkin (1997) and Bretfeld (1999), respectively.

3.2.1 Comparison of crop rotations: livestock I versus stockless

In May 2012 the main gradient within the data on collembolan communities from the livestock I (LI) and the stockless (SL) rotation along the first NMDS-axis is spanned by *Protaphorura armata* Group and *Sphaeridia pumilis* and the gradient along the second axis was spanned by *Heterosminthurus bilineatus* Group and *Pseudosinella decipiens* on the one end and *Willemia anophthalma* on the other end of the axis (Figure 5a).

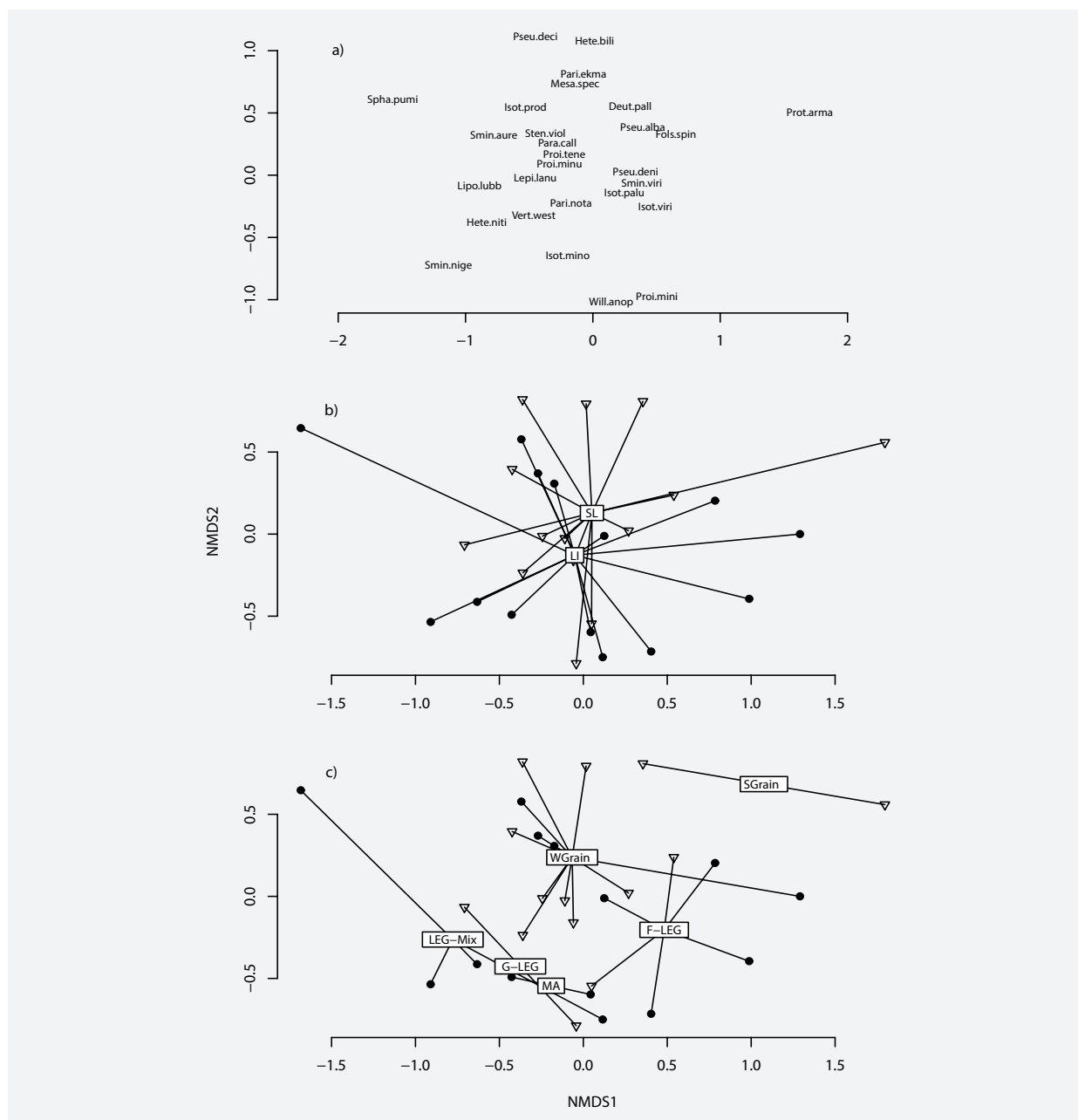


FIGURE 5
 NMDS for the collembolan data from May 2012 for the two crop rotations livestock I (LI) and stockless (SL).
 a) Ordination showing main species within the dataset (abbreviations according to Table 4).
 b) Sampling points grouped according to farming systems (SL marked with triangles and LI with circles).
 c) Sampling points grouped according to crop classes (SGrain: spring grown grain; WGrain: winter grown grain; F-LEG: fodder legumes (clover-grass mixture); G-LEG: grain legumes; LEG-Mix: mixtures of grain legumes and grains; MA: maize).

No significant difference between the centroids for the two crop rotations (LI versus SL) were identified ($p=0.105$). It is clear that there is no difference along the first axis and only little difference along the second axis (Figure 5b). When using crop-classes rather than crop rotations as grouping variables some differentiation is possible (Figure 5c). Collembolan communities differ between autumn-sown and spring-sown crops. However, none of the centroids differ significantly (Table 7).

The species spanning axis 1 can be differentiated according to their life-forms. *P. armata* is an euedaphic species, a “true soil-dweller” (Bauer and Christian, 1993), with only poor drought resistance (Hopkin, 1997). On the other hand, *S. pumilis* lives in the litter layer of soils of different humidity levels (Bretfeld, 1999; Ponge, 2000) and is a mobile epigeic species (Salamon et al., 2004). As the centroids of the livestock I and stockless rotation were not separated along this axis, both crop rotations host collembolan communities consisting of a balanced mixture of species of different life-forms after ten consistent years of different organic farming practices.

The second axis could follow a gradient of soil acidity. *P. decipiens* is characterised as not occurring under acid conditions (Ponge, 1993), while *W. anophthalma* prefers acidic habitats like peat, mor, or moder (Chauvat and Ponge, 2002; Salmon et al., 2014). Therefore, we hypothesise that the data on collembolan communities indicate more acidic conditions under the livestock I rotation than under the stockless rotation.

TABLE 7

Results of pairwise comparison of centroids from NMDS from the collembolan dataset in LI and SL in May 2012.

	adjusted p
F-LEG–G-LEG	1
F-LEG–LEG–Mix	0.9
F-LEG–MA	NA
F-LEG–SGrain	0.675
F-LEG–WGrain	0.345
G-LEG–LEG–Mix	NA
G-LEG–MA	NA
G-LEG–SGrain	NA
G-LEG–WGrain	1
G-LEG–Mix–MA	NA
LEG–Mix–SGrain	NA
LEG–Mix–WGrain	1
MA–SGrain	NA
MA–WGrain	NA
SGrain–WGrain	0.285

SGrain: spring grown grain; WGrain: winter grown grain;
 F-LEG: fodder legumes (clover-grass mixture); G-LEG: grain legumes;
 LEG–Mix: mixtures of grain legumes and grains; MA: maize.
 NA: Comparison of centroids were not possible as homogeneity of multivariate spread could not be achieved.

The differentiation between collembolan communities of different crop classes was more pronounced. Differences became apparent between autumn-sown and spring-sown crops along axis 1. As sampling took place in May, the time elapsed since tillage and sowing differed markedly between these two groups. Different crops were in different development stages causing different degrees of soil coverage. As Salmon et al. (2014) found convergence of collembolan species traits for epigeic species and those living in open habitats, the gradient along the first axis could reflect differences in habitat openness. Along the second axis, legumes and maize can be differentiated from cereals. Here the collembolan communities might uncover lower pH values in the rhizosphere of legumes and maize (Kamh et al., 2002; Maltais-Landry, 2015). Kamh et al. (2002) found enhanced release of protons from *Zea mays* under P-deficient conditions. To what extent proton release of young maize plants to dissolve phosphorus influenced soil pH was not within the scope of our study, but cannot be ruled out as a mechanism influencing habitat conditions for soil fauna on the study site (Ohm et al., 2015). Therefore, the higher relative share of legumes and maize in the livestock I rotation (cf. Table 1) could have influenced the differentiation of the livestock I and stockless rotation along the second NMDS-axis.

3.2.2 Comparison of tillage regimes: conventional versus reduced

The first axis of an NMDS on the collembolan data from fields under conventional (CT) and reduced (RT) tillage is spanned by *Sminthurides malmgreni*, *Cyphoderus albinus* and *Pseudosinella alba* on the one end and *Deuterosminthurus pallipes* and *Neotullbergia crassiscuspis* on the other end of the axis (Figure 6a). NMDS-axis 2 is spanned by *Sminthurides parvulus*, *P. armata* Group, *Supraphorura furcifera* and *Isotomurus palustris* Group on the one end and *P. alba*, *Cryptopygus thermophilus* and *Sminthurinus niger* on the other end of the axis.

Species at both ends of the first NMDS-axis are xerothermophil and prefer dry and open habitats (*C. albinus* (Bockemühl, 1956, as cited in Dekoninck et al., 2007), *P. alba* (Filser, 1995), *D. pallipes* (Bretfeld, 1999; Fjellberg, 2007; Querner, 2004), *N. crassiscuspis* (Stierhof, 2003)). Along the second axis, a humidity gradient seems to be spanned. *S. parvulus*, *P. armata*, *S. furcifera*, and *I. palustris* prefer wet or damp habitats (Bretfeld, 1999; Fjellberg, 1998, 2007; Hopkin, 1997, 2007) whereas *P. alba* and *C. thermophilus* are adapted to dry habitat conditions (Detsis, 2009; Filser, 1995; Kautz et al., 2006; Potapov, 2001).

There was no difference between centroids of CT and RT in May 2012 and in May 2014 (figure not shown). The lack of differences between conventional and reduced tillage in 2014, after two years of different management treatments, could be due to the intensive form of reduced tillage investigated in this study (cf. 3.1.2) or due to sampling of collembolans taking place nine months after the last soil tillage, so that collembolan communities may have aligned during this time. Although the centroids differed between May 2012 and May 2014 (Figure 6b), no test for significance of this difference was possible as the condition of homogeneity of multivariate

spread was not satisfied. Significant differences between spring grain crops (grain-legume/cereal mixtures; LEG-Mix) and fodder legumes (red clover-grass; F-LEG) ($p=0.003$) and between grain legumes (G-LEG) and fodder legumes (F-LEG) ($p=0.003$) could be shown (Figure 6c).

In May 2012, all fields were cultivated with grain legumes or with grain-legume/cereal mixtures, respectively. In May

2014, all fields were cultivated identically with fodder legumes. Therefore, effect of year and crop class cannot be separated in our analyses (cf. 3.1.2). However, we could show that there were no differences between collembolan communities based on tillage regimes and furthermore hypothesise that differences between data from May 2012 and May 2014 are related to differences in soil moisture.

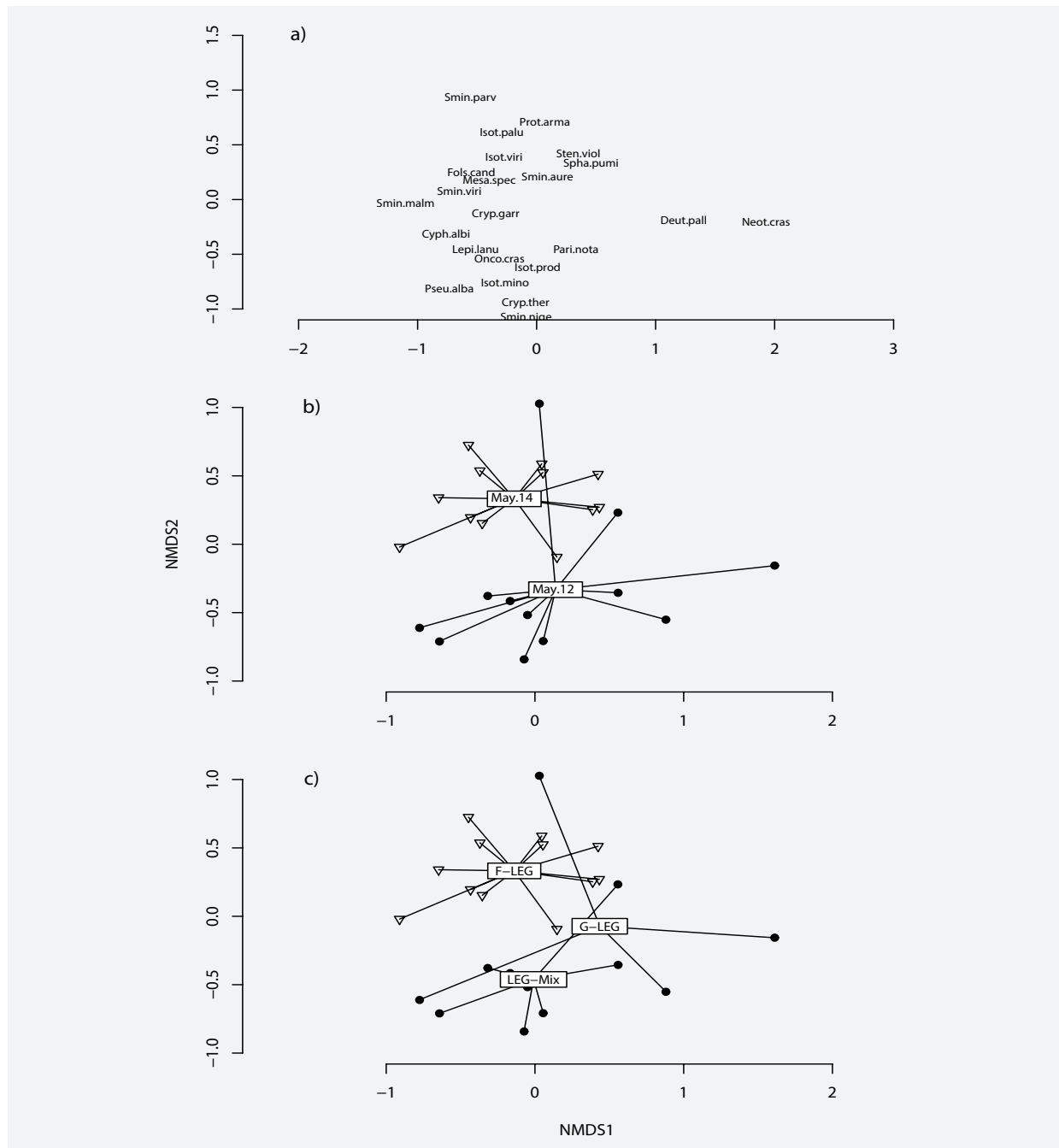


FIGURE 6
 NMDS for the collembolan data from May 2012 and May 2014 under the different management systems CT (conventional tillage) and RT (reduced tillage).
 a) Ordination showing main species within the dataset (abbreviations according to Table 4).
 b) Sampling points grouped according to sampling month (May 2012 marked with triangles and May 2014 with circles).
 c) Sampling points grouped according to crop classes (F-LEG: fodder legumes (clover-grass mixture); G-LEG: grain legumes; LEG-Mix: mixtures of grain legumes and grains).

While in 2012 spring grown crops were cultivated the grass-clover-mixture present on all fields in 2014 was a winter-grown crop. Thus, higher soil cover of the vegetation in May 2014 may have led to higher soil moisture. Alvarez et al. (2001) also discussed a positive effect of higher soil moisture due to higher weed densities as possibly influencing collembolan communities. Furthermore, data from the German Weather Service (DWD) on soil moisture revealed overall higher water content in the soil in 2014 (Figure 2).

4 Conclusion

Neither different crop rotations kept over ten years nor shorter-term changes in tillage regimes significantly influenced collembolan abundance, species richness, EMI mT-values, or collembolan species composition at this experimental station. We found that collembolan abundance and species composition reacted to intermingled effects of different crops cultivated with interannual variability. However, shifts in the relative share of the different collembolan life-forms showed some non-significant reactions to management differences. The relative share of euedaphic individuals is of particular interest, as some previous studies show that their proportion can be used as an indicator for stable soil habitat conditions. For different crop rotations, we found some first evidence that soil habitats in organic farming systems with regular manuring and a high share of green fodder crops (here clover-grass mixtures) tend to be more stable than those in systems without high input of manure and a low share of green-fodder crops.

The results of this study are of interest not just for the further development of organic arable farming systems. As techniques such as increasing crop rotation diversity and reducing tillage intensity are discussed also for non-organic farming systems, under the keywords agroecology (Tomlinson, 2013) or ecological intensification (Kleijn et al., 2019), their evaluation is of broader interest for any farming system aiming to implement sustainable management regimes.

Acknowledgements

We thank Daniel Baumgart, Regina Grünig, Magdalena Langer, Rainer Legrand and Meike Reimann for active support in the preparation of collembolan samples. In addition, we would like to thank two anonymous reviewers for valuable comments on the manuscript of this paper.

REFERENCES

- Alvarez T, Frampton GK, Goulson D (2001) Epigeic Collembola in winter wheat under organic, integrated and conventional farm management regimes. *Agric Ecosyst Environ* 83(1–2):95–110, doi:10.1016/S0167-8809(00)00195-X
- Andrén O, Lagerlöf J (1983) Soil Fauna (Microarthropods, Enchytraeids, Nematodes) in Swedish agricultural cropping systems. *Acta Agric Scand* 33(1):33–52, doi:10.1080/000–5128309435350
- ASABE (2009) ASAE S414.2: Terminology and definitions for agricultural tillage implements [online]. St. Joseph, Michigan: American Society of Agricultural and Biological Engineers. Retrieved from <https://elibrary.asabe.org/abstract.asp?aid=44205&t=2> [at 23 Dec 2020]
- ASAE (2005) ASAE EP291.3: Terminology and definitions for soil tillage and soil-tool relationships [online]. St. Joseph, Michigan: American Society of Agricultural Engineers. Retrieved from <https://prod.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs144p2_053410.pdf> [at 23 Dec 2020]
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48, doi:10.18637/jss.v067.i01
- Bauer R, Christian E (1993) Adaptations of three springtail species to granite boulder habitats (Collembola). *Pedobiologia* 37:280–290
- Blume HP, Brümmer GW, Horn R, Kandeler E, Kögel-Knabner I, Kretschmar R, Stahr K, Wilke BM (2010) Scheffer/Schachtschabel. *Lehrbuch der Bodenkunde*. 16th edition. Heidelberg: Spektrum Akademischer Verlag, 569 p
- Brennan A, Fortune T, Bolger T (2006) Collembola abundances and assemblage structures in conventionally tilled and conservation tillage arable systems. *Pedobiologia* 50(2):135–145, doi:10.1016/j.pedobi.2005.09.004
- Bretfeld G (ed) (1999) *Symphyleona*. Görlitz: Staatliches Museum für Naturkunde Görlitz, 320 p, Synopses on Palaearctic Collembola 2
- Caravaca F, Ruesch L (2014) Arbuscular mycorrhizal fungi and their associated microbial community modulated by Collembola grazers in host plant free substrate. *Soil Biol Biochem* 69:25–33, doi:10.1016/j.soilbio.2013.10.032
- Chauvat M, Ponge JF (2002) Colonization of heavy metal-polluted soils by collembola: preliminary experiments in compartmented boxes. *Appl Soil Ecol* 21(2):91–106, doi:10.1016/S0929-1393(02)00087-2
- Chauvat M, Wolters V, Dauber J (2007) Response of collembolan communities to land-use change and grassland succession. *Ecography* 30(2):183–192, doi:10.1111/j.0906-7590.2007.04888.x
- D’Annibale A, Larsen T, Sechi V, Cortet J, Strandberg B, Vincze É, Filser J, Audisio PA, Krogh PH (2015) Influence of elevated CO₂ and GM barley on a soil mesofauna community in a mesocosm test system. *Soil Biol Biochem* 84:127–136, doi:10.1016/j.soilbio.2015.02.009
- D’Annibale A, Sechi V, Larsen T, Christensen S, Krogh PH, Eriksen J (2017) Does introduction of clover in an agricultural grassland affect the food base and functional diversity of Collembola? *Soil Biol Biochem* 112:165–176, doi:10.1016/j.soilbio.2017.05.010
- Dekoninck W, Lock K, Janssens F (2007) Acceptance of two native myrmecophilous species, *Platyarthus hoffmannseggii* (Isopoda: Oniscidea) and *Cyphoderus albinus* (Collembola: Cyphoderidae) by the introduced invasive garden ant *Lasius neglectus* (Hymenoptera: Formicidae) in Belgium. *Eur J Entomol* 104(1):159–161, doi:10.14411/eje.2007.023
- Detsis V (2009) Relationships of some environmental variables to the aggregation patterns of soil microarthropod populations in forests. *Eur J Soil Biol* 45(5–6):409–416, doi:10.1016/j.ejsobi.2009.06.007
- Dittmer S, Schrader S (2000) Longterm effects of soil compaction and tillage on Collembola and straw decomposition in arable soil. *Pedobiologia* 44(3–4):527–538, doi:10.1078/S0031-4056(04)70069-4
- Dombos M, Kosztolányi A, Szilávecz K, Gedeon C, Flórián N, Groó Z, Dudás P, Bánszegi O (2017) EDAPHOLOG monitoring system: automatic, real-time detection of soil microarthropods. *Methods Ecol Evol* 8(3):313–321, doi:10.1111/2041-210X.12662
- Domene X, Colón J, Uras MV, Izquierdo R, Àvila A, Alcañiz JM (2010) Role of soil properties in sewage sludge toxicity to soil collembolans. *Soil Biol Biochem* 42(11):1982–1990, doi:10.1016/j.soilbio.2010.07.019
- Dunger W, Schlitt B (2011) *Tullbergiidae*. Görlitz: Staatliches Museum für Naturkunde Görlitz, 168 p, Synopses on Palaearctic Collembola 6/1
- Eisenhauer N (2016) Plant diversity effects on soil microorganisms: Spatial and temporal heterogeneity of plant inputs increase soil biodiversity. *Pedobiologia* 59(4):175–177, doi:10.1016/j.pedobi.2016.04.004
- Engelmann H-D (1978) Zur Dominanzklassifizierung von Bodenarthropoden. *Pedobiologia* 18:378–380
- Filser J (1995) The effect of green manure on the distribution of collembola in a permanent row crop. *Biol Fertil Soils* 19(4):303–308, doi:10.1007/BF00336099
- Fjellberg A (1998) The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha. Leiden, Boston, Köln: Brill, 184 p, Fauna Entomologica Scandinavica
- Fjellberg A (2007) The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphyleona. Leiden, Boston: Brill, 266 p, Fauna Entomologica Scandinavica 42, doi:10.1163/9789004157705.i-265

- Gillet S, Ponge JF (2004) Are acid-tolerant Collembola able to colonise metal-polluted soil? *Appl Soil Ecol* 26(3):219–231, doi:10.1016/j.apsoil.2004.01.001
- Gisin H (1943) Ökologie und Lebensgemeinschaften der Collembolen im schweizerischen Exkursionsgebiet Basels. *Rev Suisse Zool* 50:131–224
- Gisin H (1960) Collembolenfauna Europas. Geneve: Museum d'Histoire Naturelle
- Greenslade P (2007) The potential of Collembola to act as indicators of landscape stress in Australia. *Aust J Exp Agric* 47(4):424–434, doi:10.1071/EA05264
- Haneklaus S, Paulsen H, Schröder D, Leopold U, Schnug E (1998) Self-surveying: a strategy for efficient mapping of the spatial variability of time constant soil parameters. *Commun Soil Sci Plant Anal* 29(11–14):1593–1601; doi:10.1080/00103629809370052
- Hopkin SP (1997) *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press, 344 p
- Hopkin SP (2007) *A Key to the Collembola (Springtails) of Britain and Ireland*. Shrewsbury: Preston Montford, Field Studies Council, AIDGAP
- Jagers Op Akkerhuis G, De Ley F, Zwetsloot H, Ponge JF, Brussaard L (1988) Soil microarthropods (Acari and Collembola) in two crop rotations on a heavy marine clay soil. *Revue d'Ecologie et de Biologie du Sol* 25(2):175–202
- Jeffery S, Gardi C, Jones A, Montanarella L, Marmo L, Miko L, Ritz K, Peres G, Römbke J, van der Putten WH (eds) (2010) *European atlas of soil biodiversity*. Luxembourg: European Commission, Publications Office of the European Union, 128 p, doi:10.2788/94222
- Jordana R (2012) *Capbryinae & Entomobryini*. Görlitz: Staatliches Museum für Naturkunde Görlitz, 390 p, Synopses on Palaeartic Collembola 7/1
- Kamh M, Abdou M, Chude V, Wiesler F, Horst WJ (2002) Mobilization of phosphorus contributes to positive rotational effects of leguminous cover crops on maize grown on soils from northern Nigeria. *J Plant Nutr Soil Sci* 165(5):566–572, doi:10.1002/1522-2624(200210)165:5<566::AID-JPLN566>3.0.CO;2-O
- Kanal A (2004) Effects of fertilisation and edaphic properties on soil-associated Collembola in crop rotation. *Agron Res* 2(2):153–168
- Kautz T, López-Fando C, Ellmer F (2006) Abundance and biodiversity of soil microarthropods as influenced by different types of organic manure in a long-term field experiment in Central Spain. *Appl Soil Ecol* 33(3):278–285, doi:10.1016/j.apsoil.2005.10.003
- Kleijn D, Bommarco R, Fijen TPM, Garibaldi LA, Potts SG, van der Putten WH (2019) Ecological intensification: Bridging the gap between science and practice. *Trends Ecol Evol* 34(2):154–166, doi:10.1016/j.tree.2018.11.002
- Leinaas HP, Bleken E (1983) Egg diapause and demographic strategy in *Lepidocyrtus lignorum* Fabricius (Collembola; Entomobryidae). *Oecologia* 58(2):194–199, doi:10.1007/BF00399216
- Lenth RV (2016) Least-squares means: The R package lsmmeans. *J Stat Softw* 69(1):1–33, doi:10.18637/jss.v069.i01
- Lindberg N, Bengtsson J (2005) Population responses of oribatid mites and collembolans after drought. *Appl Soil Ecol* 28(2):163–174, doi:10.1016/j.apsoil.2004.07.003
- Löpmeier F (1994) The calculation of soil moisture and evapotranspiration with agrometeorological models (in German). *Z Bewässerungswirtschaft* 29(2):157–167
- MacFadyen A (1961) Improved funnel-type extractors for soil arthropods. *J Anim Ecol* 30(1):171–184, doi:10.2307/2120
- Mäder P, Berner A (2012) Development of reduced tillage systems in organic farming in Europe. *Renew Agric Food Syst* 27(51):7–11; doi:10.1017/S1742170511000470
- Maltais-Landry G (2015) Legumes have a greater effect on rhizosphere properties (pH, organic acids and enzyme activity) but a smaller impact on soil P compared to other cover crops. *Plant Soil* 394:139–154, doi:10.1007/s11104-015-2518-1
- Martins da Silva P, Carvalho F, Dirilgen T, Stone D, Creamer R, Bolger T, Sousa JP (2016) Traits of collembolan life-form indicate land use types and soil properties across an European transect. *Appl Soil Ecol* 97:69–77, doi:10.1016/j.apsoil.2015.07.018
- Miyazawa K, Tsuji H, Yamagata M, Nakano H, Nakamoto T (2002) The effects of cropping systems and fallow managements on microarthropod populations. *Plant Prod Sci* 5(3):257–265; doi:10.1626/pp.s.5.257
- Moos JH, Schrader S, Paulsen HM, Rahmann G (2016) Occasional reduced tillage in organic farming can promote earthworm performance and resource efficiency. *Appl Soil Ecol* 103:22–30, doi:10.1016/j.apsoil.2016.01.017
- Ohm M, Schüler M, Fyströ G, Paulsen HM (2015) Redistribution of soil phosphorus from grassland to cropland in an organic dairy farm. *Landbauforsch Appl Agric Forestry Res* 65(3/4):193–203; doi:10.3220/LBF1452867403000
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H et al. (2015) *Vegan: Community Ecology Package*. R package version 2.3-0
- Orgiazzi A, Panagos P, Yigini Y, Dunbar MB, Gardi C, Montanarella L, Ballabio C (2016) A knowledge-based approach to estimating the magnitude and spatial patterns of potential threats to soil biodiversity. *Sci Total Environ* 545–546:11–20, doi:10.1016/j.scitotenv.2015.12.092
- Peigné J, Ball BC, Roger-Estrade J, David C (2007) Is conservation tillage suitable for organic farming? A review. *Soil Use Manag* 23(2):129–144, doi:10.1111/j.1475-2743.2006.00082.x
- Petersen H (2002) Effects of non-inverting deep tillage vs. conventional ploughing on collembolan populations in an organic wheat field. *Eur J Soil Biol* 38(2):177–180, doi:10.1016/S1164-5563(02)01145-7
- Platen R, Glemnitz M (2016) Does digestate from biogas production benefit to the numbers of springtails (Insecta: Collembola) and mites (Arachnida: Acari)? *Ind Crop Prod* 85:74–83, doi:10.1016/j.indcrop.2016.02.041
- Pommeresche R, Løes AK, Torp T (2017) Effects of animal manure application on springtails (*Collembola*) in perennial ley. *Appl. Soil Ecol.* 110:137–145, doi:10.1016/j.apsoil.2016.10.004
- Ponge JF (1993) Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems [online]. *Pedobiologia* 37(4):223–244
- Ponge JF (2000) Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. *Biol Fertil Soils* 32(6):508–522, doi:10.1007/s003740000285
- Potapov M (ed) (2001) *Isotomidae*. Görlitz: Staatliches Museum für Naturkunde Görlitz, 607 p, Synopses on Palaeartic Collembola 3
- Querner P (2004) Epigäische Springschwänze (Collembola) von Trockenrasenstandorten in Wien, Niederösterreich und Burgenland [Epigeic springtails (Collembola) of dry grassland sites in Vienna, Lower Austria and Burgenland]. *Beitr Entomofaunist* 5:17–26
- Querner P (2008) *Collembola in landscape ecology*. 83 p, Vienna: Universität für Bodenkultur (BOKU), PhD Thesis
- R Development Core Team (2016) *R: a language and environment for statistical computing* [online]. Vienna: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/> [at 23 Dec 2020]
- Sabais ACW, Scheu S, Eisenhauer N (2011) Plant species richness drives the density and diversity of Collembola in temperate grassland. *Acta Oecologica* 37(3):195–202, doi:10.1016/j.actao.2011.02.002
- Sabatini MA, Rebecchi L, Cappi C, Bertolani R, Fratello B (1997) Long-term effects of three different continuous tillage practices on Collembola populations. *Pedobiologia* 41:185–193
- Salamon J-A, Schaefer M, Alpehi J, Schmid B, Scheu S (2004) Effects of plant diversity on Collembola in an experimental grassland ecosystem. *Oikos* 106(1):51–60, doi:10.1111/j.0030-1299.2004.12905.x
- Salamon JA, Wissuwa J, Moder K, Frank T (2011) Effects of *Medicago sativa*, *Taraxacum officinale* and *Bromus sterilis* on the density and diversity of Collembola in grassy arable fallows of different ages. *Pedobiologia* 54(2):63–70, doi:10.1016/j.pedobi.2010.08.007
- Salmon S, Ponge JF, Gachet S, Deharveng L, Lefebvre N, Delabrosse F (2014) Linking species, traits and habitat characteristics of Collembola at European scale. *Soil Biol Biochem* 75:73–85, doi:10.1016/j.soilbio.2014.04.002
- Schachtschabel P (1954) Das pflanzenverfügbare Magnesium des Boden und seine Bestimmung. *Z Pflanzenernaehr Dueng Bodenkd* 67(1):9–23, doi:10.1002/jpln.19540670103
- Schüller H (1969) Die CAL-Methode, eine neue Methode zur Bestimmung des pflanzenverfügbaren Phosphates in Böden. *J Plant Nutr Soil Sci* 123(1):48–63, doi:10.1002/jpln.19691230106
- Skaug H, Fournier D, Bolker B, Magnusson A, Nielsen A (2015) *Generalized linear mixed models using 'AD Model Builder'*. R package version 0.8.1
- Sterzynska M, Kuznetsova NA (1995) The faunal complex of Collembola in lowland subcontinental pine forests (Peucedano-Pinetum) of Poland,

- Byelorussia, Lithuania and Russia. *Fragm Faun* 38(4):145–153, doi:10.3161/00159301FF1995.38.4.145
- Sticht C, Schrader S, Gieseemann A, Weigel HJ (2008) Atmospheric CO₂ enrichment induces life strategy- and species-specific responses of collembolans in the rhizosphere of sugar beet and winter wheat. *Soil Biol Biochem* 40(6):1432–1445, doi:10.1016/j.soilbio.2007.12.022
- Stierhof T (2003) Collembolengemeinschaften in baden-württembergischen Waldböden. Ergänzungsband zur Dissertation. Gießen: Institut für Allgemeine und Spezielle Zoologie, Bereich Tierökologie. Justus-Liebig-Universität Gießen, 375 p
- Thibaud JM, Schulz HJ, Da Gama Assalino MM (2004) Hypogastruridae. Görlitz: Staatliches Museum für Naturkunde Görlitz, 607 p, Synopses on Palearctic Collembola 4
- Tomlinson I (2013) Doubling food production to feed the 9 billion: A critical perspective on a key discourse of food security in the UK. *J Rural Stud* 29: 81–90, doi:10.1016/j.jrurstud.2011.09.001
- van Capelle C, Schrader S, Brunotte J (2012) Tillage-induced changes in the functional diversity of soil biota: A review with a focus on German data. *Eur J Soil Biol* 50:165–181, doi:10.1016/j.ejsobi.2012.02.005
- van den Boogaart KG, Tolosana R, Bren M (2014) Compositions: Compositional Data Analysis. R package version 1.40-1. Vienna: Stat Comput
- Vandewalle M, Bello F, Berg MP, Bolger T, Dolédec S, Dubs F, Feld CK, Harrington R, Harrison PA, Lavorel S, et al. (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodivers Conserv* 19(10):2921–2947, doi:10.1007/s10531-010-9798-9

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