Dynamics of Collembola ecomorphological groups within a no-till arable system

by Natalio, A.I.M., Back, M.A., Richards, A. and Jeffery, S.

Natalio, A.I.M., Back, M.A., Richards, A. and Jeffery, S. (2024) 'Dynamics of Collembola ecomorphological groups within a no-till arable system'. *Agricultural and Forest Entomology*.

23 November 2024

Received: 5 February 2024 | Accepted: 7 November 2024

DOI: 10.1111/afe.12666

ORIGINAL ARTICLE

Agricultural and Forest Entomology

Dynamics of Collembola ecomorphological groups within a no-till arable system

Ana I. M. Natalio[1] | **Matthew A. Back**[1] | **Andrew Richards**[2] | **Simon Jeffery**[1]

[1]Centre for Crop and Environmental Science, Agriculture and Environment Department, Harper Adams University, Newport, UK

[2]Agrii Andoversford, Cheltenham, UK

Correspondence
Ana I. M. Natalio, Centre for Crop and Environmental Science, Agriculture and Environment Department, Harper Adams University, Newport TF10 8N, UK.
Email: ana.natalio@harper-adams.ac.uk

Funding information
HORIZON EUROPE Framework Programme

Abstract

1. Collembolan ecomorphological groups (i.e., epiedaphic, hemiedaphic and euedaphic) have been proposed as bioindicators of soil health with potential to be applied in agricultural systems. While some studies have investigated disturbance gradients, there is a lack of monitoring studies showing trends over time evaluating changes in management posited to improve soil health.
2. We investigated the status of a soil in an arable rotation following conversion to no-till. The response in abundance of Collembola ecomorphological groups, along with soil physicochemical properties, was monitored over 2 years, in two field experiments established on different soil types within the same field. The treatments were standard practice and green manure (GM) in both Experiments 1 and 2, and farmyard manure (FYM) in Experiment-1 only.
3. Significant responses to treatments were mostly observed with euedaphic Collembola during the first year, but treatment effects were no longer evident in the second year. A decline in epiedaphic abundance was recorded in Year-2 in the GM treatment. A negative association was observed with total soil nitrogen and pH, while a positive association was observed between gravimetric water content and euedaphic Collembola abundance.
4. This study demonstrated that euedaphic Collembola quickly responded to changes in management practice, but the impact of treatments was transient. The abundance of Collembola ecomorphological groups discriminated between short-term impacts but were an ineffective bioindicator of treatment effects over a two-year period suggesting that they may be best applied for monitoring short-term effects in response to intermittent inputs.

KEYWORDS
abiotic stress, arthropods, mesofauna, particle size, soil enrichment, soil quality

INTRODUCTION

Shifts in land use have been linked to soil biodiversity loss and consequent impacts on ecosystem functions and services (FAO et al., 2020; IPBES, 2019; UNEP, 2022). Land use impacts both the biological and chemical aspects of soil, and organisms populate sites conducive to their development and success (Giller, 1996). Because of this, soil bioindicators have been recommended for monitoring studies attempting to determine the health status of a soil (Bispo et al., 2009; Huber et al., 2008). Recently the motion on Soil Protection was

---

approved by the European Parliament (EP, 2021), which includes the protection of natural resources, including soil fauna and flora, to limit or prevent soil pollution and degradation; it is evident that soils and the life they harbour have been placed on the global agenda.

The suggestion of using Collembola as bioindicators of soil health arises from their abundant and ubiquitous nature, and their response to land use change (Gisin, 1943; Hopkin, 1997; Janssens, 2017; Ponge et al., 2003; Vanderwalle et al., 2010). Their varied diet can consist of algae, nematodes, bacteria and fungi (Chahartaghi et al., 2005; Potapov et al., 2016; Ruess et al., 2007; Rusek, 1998). Thus, they contribute to soil decomposition and nutrient cycling processes while stimulating microbial activity (ABear et al., 2014; Baudry & Merriam, 1987; Crowther et al., 2012; Moore & de Ruiter, 1991; Ponge, 2015; Vanderwalle et al., 2010). Ecomorphological groups are adaptations that permit Collembola to inhabit a variety of habitats including litter layers and soil strata. Grouping Collembola using ecomorphological traits is practical and can be implemented widely as the technical knowledge required to conduct such type of analysis can be quickly taught (FAO et al., 2020). It involves the categorisation into three groups providing insights into habitat adaptations and response to nutrient availability and changes in habitable space (Jørgensen et al., 2005; Potapov et al., 2016; Song et al., 2016). Collembola that live on the surface of soil, within the litter layer, are categorised as epiedaphic. These are relatively large individuals with long antennae and legs, which are pigmentated and have a well-developed furca. Hemiedaphic Collembola can cross between the surface and topsoil and are smaller with shorter limbs and furca. In contrast, euedaphic Collembola are true soil-dwellers and are unpigmented with shorter appendages (Filho et al., 2016; Hopkin, 1997, 2014; Malcicka et al., 2017; Ponge, 1993; Salmon et al., 2014; Vanderwalle et al., 2010).

Collembola play both a direct and indirect role in the comminution of organic material, either through predation of microorganisms or by the physico-chemical transformation of the material itself (Lavelle et al., 1997). They rely on ecosystem engineers, such as earthworms and roots, for the bulk distribution of organic matter and pore spaces. As such, Collembola are sensitive to changes in soil structure, texture and compaction with an impact on their abundance (Larsen et al., 2004; Lavelle et al., 1997). No-till promotes good soil structure by improving porosity, which subsequently improves habitable space, and by also preventing soil erosion and helping with moisture retention (Dicks et al., 2019; Halley, 1982). It is recommended in combination with other practices such as adding manures/composts and/or sowing a diversity of crops as part of sustainable soil management plans (Halley, 1982). Temporal variation was compared under three different inputs to determine the effects of a leguminous cover crop, animal manure and synthetic fertiliser. Initially, the cover crop harboured greater abundance of Collembola than the animal manure treatment, but the latter saw a greater increase in Collembola abundance past 1 month post application. Whereas the fertiliser treatment resulted in increasing numbers too but to a significantly lower level than the manure treatment (Karlen et al., 1997). Moreover, a study looking at stocking density of sheep, which can cause compaction, reported that grazing pressure led to an increase in the abundance of Collembola, likely a result of substrate enrichment by the animal's manure (Dombos, 2001). Abiotic factors such as precipitation may also affect collembolan species differently and species-specific factors that influence their ecology are not always known. Thus, implementing a life-form approach in soil health monitoring may provide transferable information on the impacts of management practices in agricultural systems which could otherwise be missed (Betsch & Vannier, 1977; Coyle et al., 2017; González-Macé & Scheu, 2018; Ireson, 1990; Rusek, 1989; Testerink, 1981, 1983).

This study applied diachronic analysis of Collembola ecomorphological groups over a two-year period with the aim of testing treatment effects on soil health by quantifying Collembola as the bioindicator. To do so, two field experiments were established in Year-1 using soil amendments at the rates commonly applied in the United Kingdom to improve soil health: farmyard manure (FYM) and green manure (GM). These were compared to the standard practice (SP) treatment receiving N-fertiliser. In Year-1, the cover crop mix of *Raphanus sativus* and *Vicia* sp. was direct drilled to act as green manure in Year-2. FYM was spread in Year-1 only, and N-fertiliser was applied in the SP plots in Year-1 and then on all plots in Year-2. It was hypothesised that:

1. FYM will lead to increased abundance of all three ecomorphological groups (i.e., epiedaphic, hemiedaphic and euedaphic) in the first year.
2. GM will lead to increased abundance of all three ecomorphological groups (due to greater litter content).
3. Detectable treatment effects will vary due to intermittent inputs.

MATERIALS AND METHODS

Experimental design

Two field experiments were established in 2017 at Norbury Park, Staffordshire, UK (Lat 52.805799, Lon -2.297185) in a completely randomised design. Experiment-1 consisted of three treatments that were replicated six times (18 plots of 200 × 6 m each): farmer's standard practice (SP; received 150 kg ha^{-1} N-fertiliser, Nitram 34.5% N); farmyard manure (FYM; received 14 t/plot of farmyard manure, 40 t ha^{-1}, and 125 kg ha^{-1} of N-fertiliser—i.e., standardised for N input against SP); green manure (cover crops) (GM) direct drilled with 50/50 (w/w) fodder radish (*Raphanus sativus*) and vetch (*Vicia* sp.) at 29 kg ha^{-1}. Experiment-2 was placed on a slope where there was an intrusion of sandier soil into the same field and consisted of two treatments, SP and GM. Treatments were replicated eight times in the GM treatment and nine in SP (17 plots of 24 × 6 m each). Spring wheat, *Triticum aestivum* L. *var.* Mulika (with Beret Gold seed dressing), was direct drilled in May 2017 of Year-1 at 150 kg ha^{-1} on all plots except the GM plots. In Year-2's crop season, winter oats, *Avena sativa var.* Mascani (with Beret Gold seed dressing), was direct drilled at the rate of 160 kg ha^{-1} in October 2017 across all plots of Experiment-1 and 2 (Figure 1). A detailed experimental design is available in Natalio et al. (2024). Historic station data in Table 1 shows the mean values of meteorological data from the two experimental years. In 2018, the United Kingdom was hit by the 'Beast from the East', an interaction

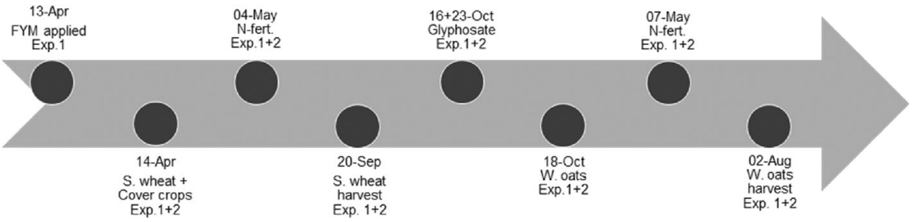

FIGURE 1 Timeline of experimental inputs and harvest periods for both Experiments 1 and 2 (in Natalio et al., 2024).

TABLE 1 Climatic conditions registered by Shawburys weather station, United Kingdom (Lat 52.794, Lon -2.663).

Year	Months	Tmax (°C)	Tmin (°C)	af (days)	Rain (mm)	Sun (h)
2016/7	10–4	⇩ 11	3	7	44	85
2017/8	10–4	10	3	⬆ 8	⬆ 61	⇩ 71
2017	5–9	19	10	0	63	147
2018	5–9	⬆ 21	10	0	⇩ 47	⬆ 199

Note: The historic data for the years 2016–2018 consists of: mean daily maximum temperature (Tmax, °C); mean daily minimum temperature (Tmin, °C); days of air frost (af, days); total rainfall (rain, mm); total sunshine duration (sun, h). Months have been grouped to cover periods between sampling campaigns (October–April, 10–4; May–September, 5–9). Arrows represent increases or decreases comparisons between the same periods (Met Office, 2021).

between storm Emma and the anticyclone Hartmut bringing unusually low temperatures, heavy snowfall and strong winds. Heatwaves followed that year during the spring and summer months (Met Office, 2018; Mieszkowska, 2019).

Collembola extraction and processing

Samples were collected twice in each crop season, in May and October 2017–2018 in Experiment-1, and once in each crop season November 2017–2018 in Experiment-2. Soil cores were collected using an auger (10 cm depth * 4 cm diameter), kept in press-grip bags in the shade inside cool boxes until extraction. A total of 14 cores per plot were collected from random locations within plots in Experiment-1, and 5 cores per plot in Experiment-2. Collembola were extracted from fresh soil within 24 h of sampling using Tullgren funnels for heat extraction for 2 weeks (Hopkin, 2014). A collection tube filled with 70% industrial methylated spirit was used to collect specimens. Categorisation to one ecomorphological group based on their morphology was done using a dissecting microscope (100× magnification, Table 2) (Hopkin, 2014). In Experiment-1, a total of 22, 361, 3700 and 3019 individuals were categorised in May–October 2017 and 2018, respectively. In Experiment-2, a total of 305 and 708 individuals were categorised in November 2017 and 2018, respectively.

TABLE 2 Morphological characteristics used to discriminate between Collembola ecomorphological groups.

Characteristics	Criteria	Score
Ocelli	Present	0
	Absent	4
Antenna length	> Body	0
	> 1/2 Body	2
	< 1/2 Body	4
Furca	Fully developed	0
	Reduced	2
	Absent	4
Hairs/Scales	Present	0
	Absent	4
Pigmentation	Present with patterns	0
	Present	2
	Absent	4

Note: Interpretation: Epiedaphic 0 >score <8; hemiedaphic 7 >score <14; euedaphic 12 > score < 21. (Adapted from Filho et al., 2016; Vanderwalle et al., 2010).

Statistical analysis

All statistical analyses were conducted in RStudio (R version 4.0.5 (2021-03-31)—'Shake and Throw'). The packages used were: 'lme4' (Bates et al., 2015), 'ggplot2' (Wickham, 2016), 'gridExtra' (Auguie & Antonov, 2017), 'NCmisc' (Cooper, 2018), 'plyr' (Wickham, 2016), 'rcompanion' (Mangiafico, 2021).

Generalised linear models were computed using Quasi-Poisson regression to account for over- or under-dispersion. The three different ecomorphological groups (epiedaphic, hemiedaphic and euedaphic) were added to the model individually as the response categorical variable, with the treatments as the fixed-effect categorical variable, and gravimetric water content (%GWC), percentage total nitrogen in soil (%tN) and soil pH as the continuous random covariates

(Table 4). The interaction between treatment categorical variables was added to the reduced model with the significant continuous variables %GWC or pH. Differences between treatments were tested per sampling period for each experiment, that is, Experiment-1 included May and October 2017–2018, and Experiment-2 included November 2017–2018. A further model included soil texture (percentage sand, silt or clay) as continuous variables instead of the variables %GWC, %tN or pH (Tables 3 and 4).

Principal component analysis (PCA) was used to explore relationships between Collembola ecomorphological groups, soil texture (%sand, %silt and %clay) and soil properties (%GWC, pH and %tN) in both Experiments 1 and 2. The function 'prcomp' available in the default R-package 'stats' was used to perform the PCAs, where 'the calculation is done by a singular value decomposition of the (centred to means = 0, and scaled to standard deviation = 1) data matrix' (R Core Team, 2019). The eigenvalues in each ordination were averaged by treatments and sampling period for both experiments and respective standard errors of the mean (SE) calculated. Subsequently, the mean values and SEs were plotted on the PCA ordinations.

TABLE 3 Percentage textural classes in each experiment.

Textural class	Experiment-1 (%)	Experiment-2 (%)
Loamy sand	2.4	73.5
Sandy loam	48.4	26.5
Sandy clay loam	45.2	0.0
Clay loam	4.0	0.0

Note: The soil was classified using diameter limits as per the WRB classification system (IUSS Working Group WRB, 2015): sand 2.00–0.063 mm; silt 0.063–0.002 mm; clay <0.002 mm.

RESULTS

Generalised linear models

Experiment-1

The abundance of euedaphic Collembola in May 2017 was significantly greater in the FYM and SP treatments ($p < 0.001$) than the GM (Figure 2c). Higher %GWC in the SP treatment led to higher numbers of euedaphic Collembola than in the FYM treatment ($p = 0.02$). Similarly, when pH was included as a treatment interaction, the abundance of euedaphic Collembola was shown to decline more in FYM than SP ($p < 0.001$), and the same was observed with the GM treatment in comparison with FYM ($p < 0.001$).

In October 2017, the abundance of euedaphic Collembola was significantly greater in the FYM treatment than GM ($p = 0.03$) (Figure 2). The interaction between GM treatment and pH (Table 3) showed an inverse relationship whereby euedaphic abundance declined in GM in comparison with FYM when pH increased ($p = 0.02$).

The soil's %tN content had a significant impact on community structure in May 2018, particularly in the GM treatment where the abundances of epiedaphic ($p = 0.02$) and euedaphic Collembola

TABLE 4 Soil properties applied in GLM models for both Experiments 1 and 2, sampled over a period of 2 years.

		GWC (%)	pH	Total-*N* (%tN)
	Treatment	Mean ± SD	Mean ± SD	Mean ± SD
Experiment-1	SP-M17	13 (± 1.1)	7.0 (± 0.1)	0.217 (± 0.02)
	FYM-M17	14 (± 0.6)	6.8 (± 0.1)	0.182 (± 0.02)
	GM-M17	13 (± 2.1)	6.7 (± 0.2)	0.185 (± 0.04)
	SP-O17	18 (± 2.2)	6.6 (± 0.2)	0.222 (± 0.05)
	FYM-O17	18 (± 1.8)	6.6 (± 0.1)	0.200 (± 0.03)
	GM-O17	17 (± 2.1)	6.8 (± 0.4)	0.212 (± 0.04)
	SP-M18	17 (± 1.8)	6.8 (± 0.3)	0.202 (± 0.04)
	FYM-M18	18 (± 1.2)	6.8 (± 0.3)	0.213 (± 0.04)
	GM-M18	16 (± 3.3)	6.9 (± 0.2)	0.185 (± 0.02)
	SP-O18	13 (± 2.5)	6.6 (± 0.4)	0.202 (± 0.04)
	FYM-O18	13 (± 1.3)	6.6 (± 0.2)	0.212 (± 0.04)
	GM-O18	12 (± 1.7)	6.7 (± 0.3)	0.185 (± 0.02)
Exp-2	SP-N17	15 (± 0.8)	6.2 (± 0.2)	0.152 (± 0.02)
	GM-N17	15 (± 0.8)	6.2 (± 0.3)	0.143 (± 0.03)
	SP-N18	12 (± 0.9)	6.2 (± 0.3)	0.148 (± 0.03)
	GM-N18	13 (± 1.1)	6.4 (± 0.4)	0.150 (± 0.02)

Note: Percentage GWC and tN mean values are shown for each treatment, and respective standard deviation of the mean (±SD). Experiment-1 treatments: standard practice (SP); green manure (GM); farmyard manure (FYM); $n = 6$. Experiment-2 treatments: SP, $n = 9$; green manure (GM), $n = 8$. Sampling times: May and October 2017–2018 (M17, O17, M18 and O18); November 2017–2018 (N17 and N18).

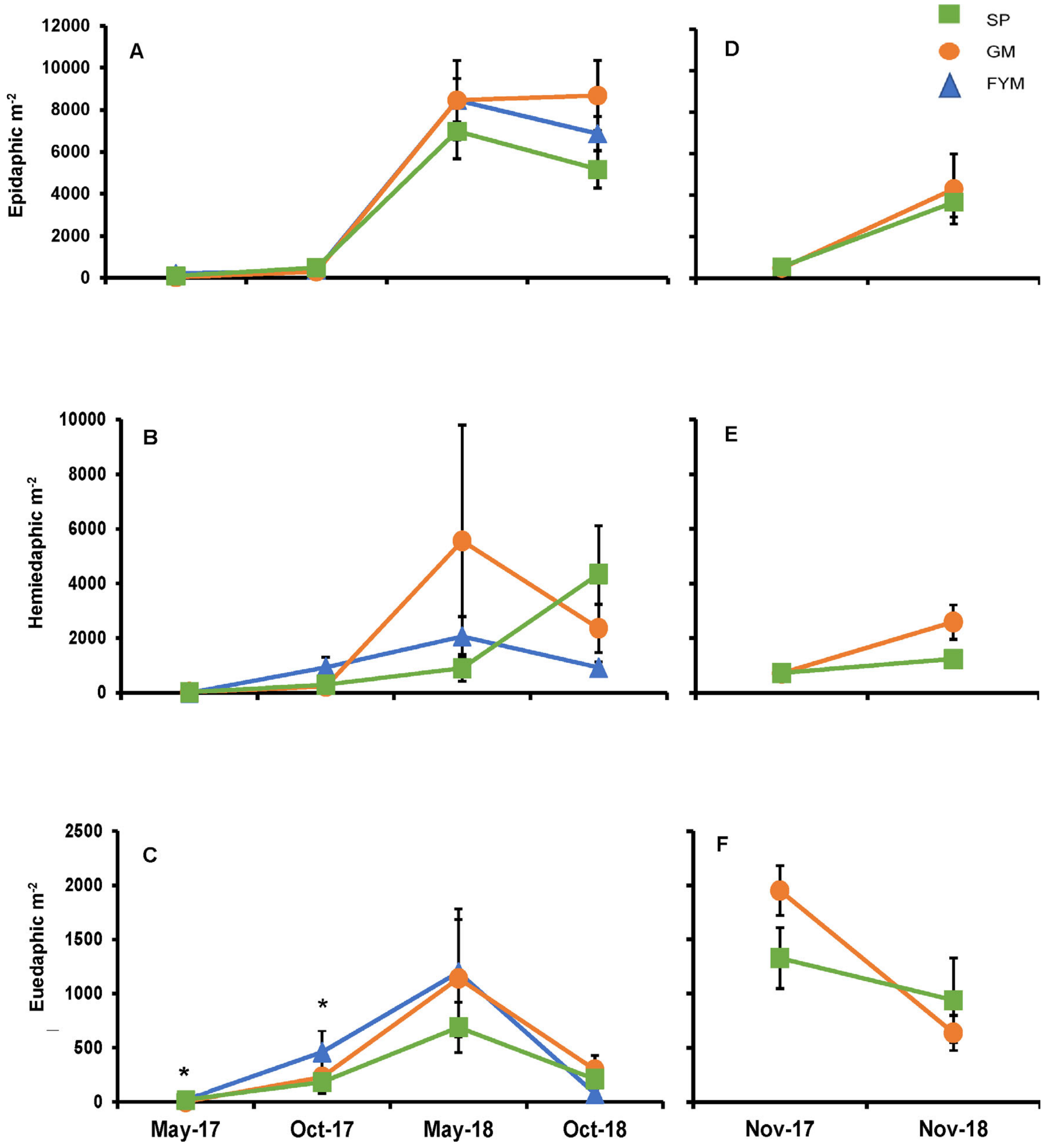

FIGURE 2 Mean abundance of Collembola ecomorphological groups, that is, epiedaphic, hemiedaphic, euedaphic, observed over a two-year period. Treatments: Experiment-1 (A, B and C) treatments are: standard practice (SP); green manure (GM); farmyard manure (FYM); $n = 6$, ± SE. Experiment-2 (D, E and F) treatments: standard practice (SP), $n = 9$; green manure (GM), $n = 8$; ± SE. (note the differences in scale of the Y axis).

($p = 0.04$) decreased in comparison with FYM when %tN increased. Euedaphic Collembola interacted positively with soil moisture (% GWC) in GM in relation to FYM ($p = 0.04$). The abundance of hemiedaphic Collembola showed a significant interaction effect between treatment and pH ($p = 0.04$).

Experiment-2

In November 2017, a greater concentration of total soil nitrogen (% tN) in the GM treatment was observed along with greater abundance of epidaphic Collembola ($p = 0.007$) in comparison with SP, while the opposite was seen with the euedaphic Collembola ($p = 0.006$). The % GWC of the soil had a significant impact on the abundance of epidaphic Collembola ($p = 0.04$).

Principal component analysis

No relationships were observed between hemiedaphic and epiedaphic Collembola and soil properties (%sand, %tN, %GWC and pH; Tables 3 and 4; Figures 2–6). Discrimination was observed between

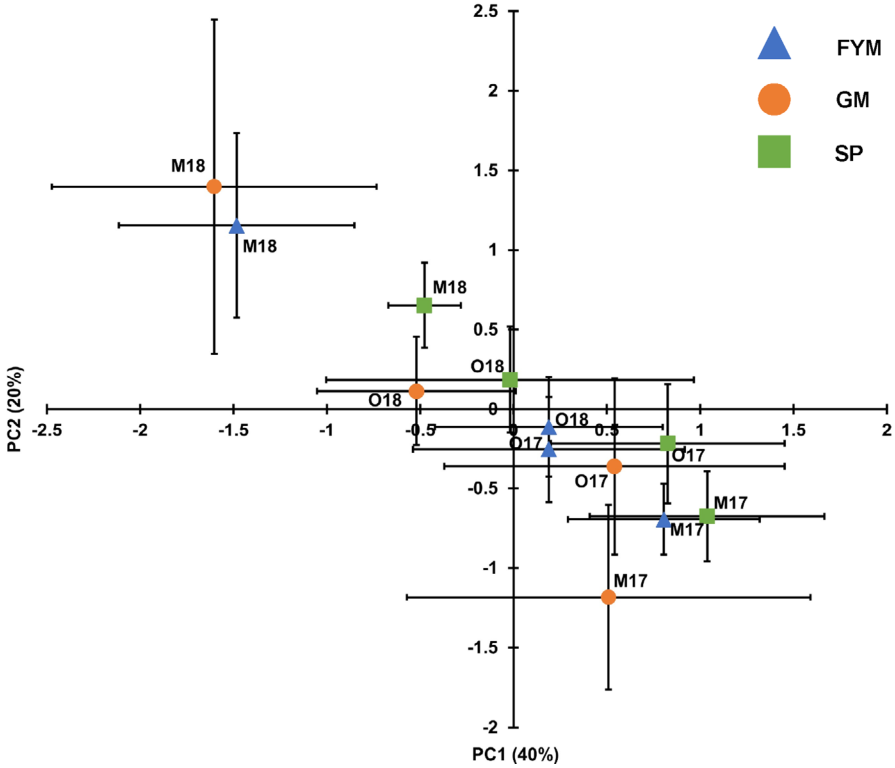

FIGURE 3 Relationships between Collembola ecomorphological groups (epiedaphic, hemiedaphic and euedaphic) and soil properties (pH, %GWC, %tN and %soil particles) of Experiment-1 were visualised using principal component analysis (PCA). Distribution of the principal component mean scores for each treatment (standard practice = SP, green manure = GM, farmyard manure = FYM) and relevant sampling periods (Exp-1 = May and October 2017–2018) following a fallow period before experiments started.

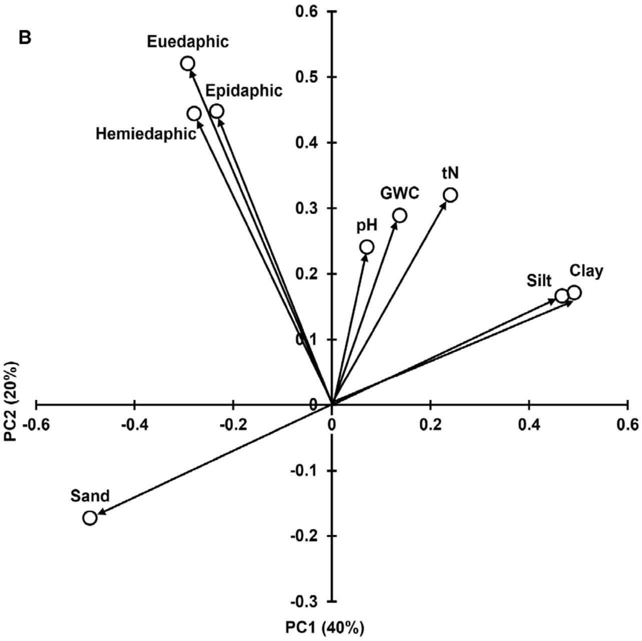

FIGURE 4 Distribution of the variables (ecomorphological groups and soil properties) of Experiment-1 on the principal component analysis (PCA) ordination plot (PC1 = 40%, PC2 = 20%).

Experiment-1 and Experiment-2 in PC1, with soil texture and the abundance of euedaphic Collembola being the main drivers for that observed discrimination. Discrimination in Experiment-1 occurred between 2017 and 2018 years in PC2 with the main loadings driving that discrimination being %tN, pH and euedaphic Collembola, hemiedaphic and epiedaphic abundances, with a lower contribution of % GWC (Figures 2–6).

DISCUSSION

Treatment responses by Collembola ecomorphological groups were detected in the first year of Experiment-1, but effects were no longer significant in the second year. However, the mean number of epiedaphic Collembola surged in Year-2 so did the euedaphic Collembola in the spring sampling of the same year. Whereas the response of hemiedaphic Collembola was varied across all treatments, in the GM treatment numbers surged to over 5000 individuals m^{-2} in comparison to 200 individuals m^{-2} in the previous autumn period. This response could relate to an increase in saprotrophic fungi in response to the available biomass for decomposition from the cover crop which was sprayed off with glyphosate. Collembola have been shown to preferentially feed on these, which decompose organic matter and so are expected to be correlated with increased substrate availability (Hunter, 2001; Jørgensen et al., 2008). Both Experiments 1 and 2 had significant interactions between treatments and pH, %GWC and %tN, consequently impacting the abundance of ecomorphological groups. The decline of euedaphic Collembola in both experiments post-2018 harvest was possibly due to the particularly extreme climatic

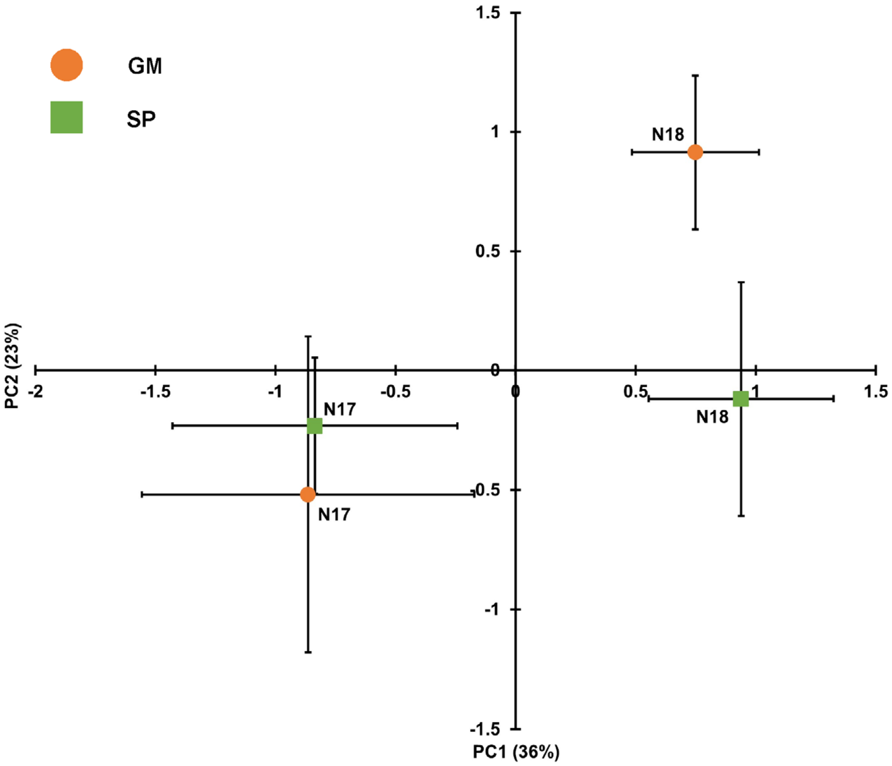

FIGURE 5 Distribution of the variables (ecomorphological groups and soil properties) of Experiment-2 on the principal component analysis (PCA) ordination plot (PC1 = 36%, PC2 = 23%).

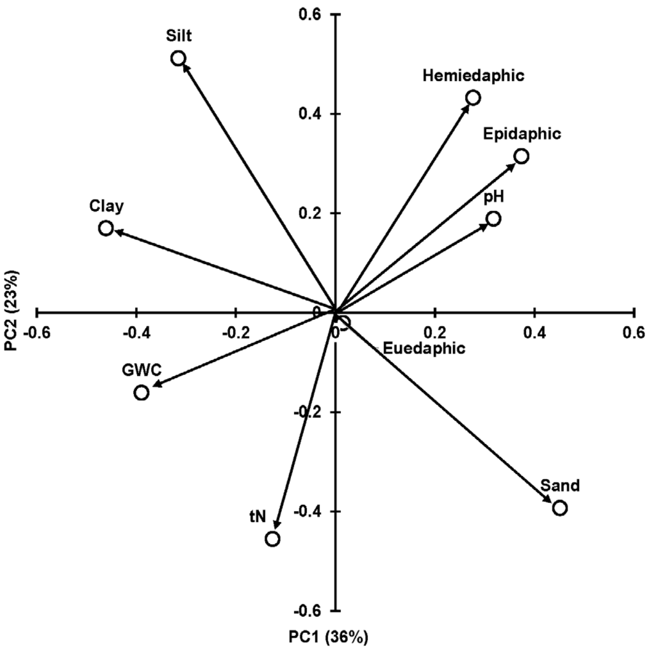

FIGURE 6 Relationships between Collembola ecomorphological groups (epidaphic, hemiedaphic and euedaphic) and soil properties (pH, %GWC, %tN and %sand) of Experiment-2 were visualised using principal component analysis (PCA). Distribution of the principal component mean scores for each treatment (standard practice = SP, green manure = GM) and relevant sampling periods (November 2017–2018) following a fallow period before experiments started.

conditions of that year, which saw the arrival of 'Beast from the East', and a series of heatwaves (Met Office, 2018; Mieszkowska, 2019). In fact, in manipulation and field studies, the abundance of euedaphic Collembola declined under drought conditions, but it was found that fungal enriched corridors connecting to more favourable habitats permitted higher dispersal and net movement, and greater survival rates (Ferrín et al., 2023; Li et al., 2021 and 2023). In Sanders et al. (2024) study, warm temperatures followed by a dry spell were especially detrimental to Collembola diversity and abundance. Weather patterns largely influence soil temperature and moisture, and these abiotic factors command food source availability subsequently changing the foraging potential of Collembola communities (Jørgensen et al., 2008; Potapov et al., 2023; Querejeta et al., 2021). Collembola species share habitats by partitioning food resources, but they feed on alternative food sources when their preferred diet is scarce due to climatic induced spatial isolation (Jørgensen et al., 2008; Potapov et al., 2016). However, a lack of significant response in general to treatment effects in Year-2 due to the added manures being largely utilised could not be ruled out. The results are in line with expectations and show that Hypotheses 1 to 3 should all be accepted. It further suggests that the use of Collembola ecomorphological groups was an effective means of identifying short-term management impacts.

Management practices like fallow, as per the establishment of experiments, are unfavourable to soil communities (Bhagawati et al., 2020; Natalio et al., 2024). Fallowed soils are exposed to greater fluctuations in temperature and precipitation than those with permanent crop cover, thus harbouring conditions which are detrimental to biota (Giller, 1996). This could help explain the reduced numbers encountered in May 2017 when the first sampling was done. However, Collembola species encountered in agricultural habitats have been found to be less sensitive to adverse conditions than those from woodlands and so able to recover faster (Betsch & Vannier, 1977; Ponge et al., 2006; Rusek, 1989). The opposite has also been reported, and species specific spatial distribution and adaptation may have a greater role in their habitat preference than what is currently known (Martins da Silva et al., 2016). For example, epiedaphic Collembola can survive extensive periods of adverse conditions in arable systems as eggs then synchronously emerge in response to rainfall (Alvarez et al., 1999). Furthermore, a long-term study found seasonal environmental effects on Collembola (Lindberg & Bengtsson, 2005), while another reported euedaphic Collembola recovered slower post disturbance (Kardol et al., 2011). Metabolic adaptations such as the emptying of the guts by epiedaphic Collembola permits its survival through drought and freezing temperatures and so overcome abiotic stress (Alvarez et al., 1999; Sanders et al., 2024). Whereas other species remain active through periods of snow cover by feeding on microbes growing on the snow itself which has been suggested to be a symbiotic relationship enabling the epiedaphic Collembola to thrive in winter (Hao et al., 2020). The similar response in Experiment-1 of epiedaphic and euedaphic Collembola, up to May 2018 and regardless of treatment, suggests that the species encountered were adapted to cope with the conditions of this study and so recover to great numbers within 1 year. The response post-spring 2018 followed similar patterns across both experiments even though the abundances of euedaphic Collembola were greater in Experiment-2 than in 1.

Soil spatial heterogeneity is influenced by many factors including texture and management practices. Sandier soils can harbour greater abundance of mesofauna, such as Collembola, as they often have more pore habitable spaces (Coleman et al., 2024; Giller, 1996). In Experiment-2, with sandier soil, higher number of euedaphic Collembola were observed than in Experiment-1. This study's fine scale spatial variation was also separated by year. A clear discrimination in samples between May 2017 and 2018 of Experiment-1, and November 2017 and 2018 of Experiment-2 was observed along Principal Component 1 and 2 (PC-1 and PC-2). The main driver for this discrimination was differences in abundances of all three morphological groups of Collembola compared to other sampling sessions in Experiment-1 (Figure 4). Strong positive loadings for %GWC, %tN and pH, %clay and %silt, and strong negative loadings were observed along PC-1 for %sand. However, these mainly contributed to variance within sampling sessions, as shown by the lack of discrimination on those vectors in Figures 3 and 4. In Experiment-2 hemiedaphic and epiedaphic Collembola mainly drove the observed discrimination in samples collected from November-2018 compared to other samples (Figure 5). Other strong loadings were observed Figure 5 but again these contributed mainly to within sample variance as shown by the lack of discrimination between samples in those vectors (Figure 6). Spatial variations in this study were slightly better predictors of Collembola distribution than treatment effects. This is in accordance with Holmstrup et al. (2013), their study compared sites with historical drought and wet treatments but failed to detect differences in Collembola community structure as determined by ecomorphological groups. Spatial variation explained better the community composition several months after treatments were established (Holmstrup et al., 2013). Emphasising that weather patterns alone may not explain variations in Collembola communities and underlying processes like soil texture combined with management contribute to responses should be included. Such as in the case of Yin et al. (2019) study showing that management practices primarily controlled the responses of ecomorphological groups. In their study cereal rotations had fewer epiedaphic and hemiedaphic Collembola than the less disturbed managed grasslands (Yin et al., 2019). Cultivation practices like no-till alone, as done in this study, can create conditions which are conducive to the rapid development of Collembola communities that crop residues or N-fertilisation cannot achieve (Coulibaly et al., 2017).

Gravimetric water content (%GWC) was an effective predictor of euedaphic abundance in the first year of both Experiments 1 and 2 in May and November 2017, respectively, but not thereafter. The abundance of euedaphic Collembola was lower in October 2018 than May 2018 in Experiment-1, after an increase from spring 2017. Similarly, their abundance declined in November 2018 in Experiment-2. The differences observed due to %GWC were possibly in response to past precipitation conditions that influenced 2017 baseline results; severe winter weather hit the United Kingdom early 2018, and was followed by an intense drought in the summer, which may have had less of an impact because the groups present had already been exposed to a particular dry winter in 2016/2017 (Met Office, 2018, 2021; Turner et al., 2021). This meant that sensitive collembolan species were already lost in either experiment or were never present. Alternatively, changes in %GWC may not have been sufficiently extreme, around the time of sampling, to trigger measurable changes in the abundance of ecomorphotypes and thus show obvious seasonal variations. A study simulating future climate by manipulating conditions such as temperature and drought, also did not observe conclusive responses based on several traits to these parameters or even that communities were seen to adapt to a changing climate (Bonfanti et al., 2022).

The application of FYM led to increased numbers of euedaphic Collembola in May 2017, but the same increase in abundance was not observed for the other ecomorphological groups. The addition of a favourable nutrient source facilitates the rapid proliferation of fungi and microbes, thus inducing Collembola to aggregate (Hunter, 2001). However, the distribution of ecomorphological groups was also affected by soil pH, which can be modified by FYM, in both the May and October 2017 sampling periods. Soil pH has previously been reported as being negatively correlated with Collembola community traits and species richness (de Boer et al., 2010; Martins da Silva et al., 2016). In the study by Martins da Silva et al. (2016), changes in soil pH, particularly increased acidity, were observed to significantly impact euedaphic communities, which was also associated with a decline in species richness in arable sites but not forest soils. This could be attributed to species distribution and their habitat specific adaptations as reported by another study, where a drop in substrate pH caused physiological changes in *Folsomia candida* triggering upregulation of gene expression responsible for cellular processes (de Boer et al., 2010).

Interactions between inputs, such as manures and N-fertilisers, and pH and land use have been shown to affect the abundance of Collembola with response being morphotype dependent (Martins da Silva et al., 2016; Pommeresche et al., 2017; Song et al., 2016). Bursts of nitrogen fertiliser can lead to a decrease in the numbers of Collembola, with the euedaphic and hemiedaphic Collembola being more susceptible (Song et al., 2016). Conversely, epiedaphic Collembola have been reported to be more susceptible to the spreading of slurry, that is, liquid manure, and showing slower recovery than euedaphic Collembola (Pommeresche et al., 2017). In this study, the incorporation of FYM was seen to benefit the euedaphic Collembola with their population increasing more rapidly here too than the other two morphotypes. Greater fluctuations in the abundance of hemiedaphic and euedaphic Collembola were observed throughout the two-year monitoring under these experimental conditions. The switch to N-fertiliser across both experiments in Year-2 appeared to have an impact on hemiedaphic abundance in Experiment-1 and on the euedaphic Collembola in Experiment-2. These responses were likely to have been a larger perturbation in the GM treatment in comparison with SP and FYM treatments because it had not received any N-inputs in the form of N-fertiliser and/or FYM in Year-1.

CONCLUSION

FYM application was conducive to increasing abundance of euedaphic Collembola, but the hemiedaphic and epidaphic Collembola were not as sensitive. Results suggest that N-fertiliser applied after the cover crop reduces the numbers of epiedaphics and euedaphic Collembola, most likely due to the short-term changes in soil properties. The conversion to no-till, the sowing of crops and nutritional enrichment were sufficient to increase the abundance of all ecomorphological groups in the short-term, but significant treatment effects were not observed after 2 years, and spatial heterogeneity impacted Collembola community composition more. These results suggest that the use of Collembola ecomorphological groups were not an effective bioindicator of management practices under the conditions of this study, and may only be useful in short-term investigations of <1 year or under continuous repeated treatment inputs. Therefore, this may limit conclusions that could be inferred about soil health in an arable system which aid long-term agronomic decisions because in-farm decision-making, in the United Kingdom, often does not incorporate manures or cover crops on a yearly basis. Furthermore, it is necessary to consider soil heterogeneity in monitoring studies as its influence can exceed that of responses to management practices, which may lead to misinterpretation of results if excluded. In fact, this study demonstrated that Collembola respond to localised favourable conditions which were often decoupled from the experimental design. Furthermore, with the expectation of an increase in the frequency of extreme climatic conditions due to anthropogenic induced climate change, it is critical to report unusual events to aid our understanding on how Collembola might react to these extremes under non-manipulated field conditions.

AUTHOR CONTRIBUTIONS

Ana I. M. Natalio: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing – original draft; writing – review and editing. **Matthew A. Back:** Conceptualization; funding acquisition; supervision; validation; writing – review and editing. **Andrew Richards:** Funding acquisition; supervision; writing – review and editing. **Simon Jeffery:** Conceptualization; funding acquisition; project administration; supervision; validation; writing - reviewing and editing.

ACKNOWLEDGEMENTS

This work was part of the AgroCycle EU project which received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 690142. The authors would like to thank the owner of Norbury Park Estate, Professor Jo Bradwell, for making the experimental site available, Mr. Simon Allen for his agronomy work, Mr. John Braithwaite for sharing the history of the farm and the many enjoyable farm walks, Weaving Machinery for the lending of the drill, Mr. Kevin Jones for his demonstration work on analytical techniques, CERC for their machinery work during crop management field trials and last but not least Dr. Ed Harris for the code discussions.

CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

Data will be submitted to an EU approved repository.

ORCID

Ana I. M. Natalio https://orcid.org/0000-0003-3175-9047

REFERENCES

ABear, A.D., Jones, T.H., Kandeler, E. & Boddy, L. (2014) Interactive effects of temperature and soil moisture on fungal-mediated wood decomposition and extracellular enzyme activity. *Soil Biology and Biochemistry*, 70, 151–158. Available from: https://doi.org/10.1016/j.soilbio.2013.12.017

Alvarez, T., Frampton, G.K. & Goulson, D. (1999) The effects of drought upon epigeal Collembola from arable soils. *Agricultural and Forest Entomology*, 1, 243–248. Available from: https://doi.org/10.1046/j.1461-9563.1999.00032.x

Auguie, B. & Antonov, A. (2017) gridExtra: miscellaneous functions for "grid" graphics. CRAN. https://cran.r-project.org/web/packages/gridExtra/gridExtra.pdf

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software*, 67(1), 48. Available from: https://doi.org/10.18637/jss.v067.i01

Baudry, J. & Merriam, H.G. (1987) Connectivity and connectedness: functional versus structural patterns in landscapes, connectivity in landscape ecology. In: *Proceedings of the Second International Seminar of the International Association for Landscape Ecology*, Vol. 29. Muenster: Muenstersche Geographische Arbeiten, pp. 23–28.

Betsch, J.-M. & Vannier, G. (1977) Caractérisation des deux phases juvéniles d*Allacma fusca* (Collembola, Symphypleona) par leur morphologie et leur écophysiologie. *Journal of Zoological Systematics and Evolutionary Research*, 15(2), 124–141. Available from: https://doi.org/10.1111/j.1439-0469.1977.tb00534.x

Bhagawati, S., Bhattacharyya, B., Medhi, B.K., Bhattacharjee, S. & Mishra, H. (2020) Diversity and density of Collembola as influenced by soil physico-chemical properties in fallow land ecosystem of Assam, India. *Journal of Environmental Biology*, 41, 1626–1631. Available from: https://doi.org/10.22438/JEB/41/6/SI-229

Bispo, A., Cluzeau, D., Creamer, R., Dombos, M., Graefe, U., Krogh, P.H. et al. (2009) Indicators for monitoring soil biodiversity. *Integrated Environmental Assessment and Management*, 5, 717–719. Available from: https://doi.org/10.1897/IEAM-2009-064.1

Bonfanti, J., Hedde, M., Cortet, J., Krogh, P.H., Larsen, K.S. & Holmstrup, M. (2022) Communities of Collembola show functional resilience in a long-term field experiment simulating climate change. *Pedobiologia*, 90, 150789. Available from: https://doi.org/10.1016/j.pedobi.2022.150789

Chahartaghi, M., Langel, R., Scheu, S. & Ruess, L. (2005) Feeding guilds in Collembola based on nitrogen stable isotope ratios. *Soil Biology and Biochemistry*, 37(9), 1718–1725. Available from: https://doi.org/10.1016/j.soilbio.2005.02.006

Coleman, D.C., Geisen, S. & Wall, D.H. (2024) Soil fauna: occurrence, biodiversity, and roles in ecosystem function. In: Rizwan, R. & Valentino, S. (Eds.) *Soil microbiology, ecology and biochemistry*, 5th edition, Amsterdam, The Netherlands: Elsevier, pp. 131–159. Available from: https://doi.org/10.1016/B978-0-12-822941-5.00005-3

Cooper, N. (2018) NCmisc: miscellaneous functions for creating adaptive functions and scripts. CRAN. https://cran.r-project.org/package=NCmisc

Coulibaly, S.F.M., Coudrain, V., Hedde, M., Brunet, N., Mary, B., Recous, S. et al. (2017) Effect of different crop management practices on soil Collembola assemblages: a 4-year follow-up. *Applied Soil Ecology*, 119, 354–366. Available from: https://doi.org/10.1016/j.apsoil.2017.06.013

Coyle, D.R., Nagendra, U.J., Taylor, M.K., Campbell, J.H., Cunard, C.E., Joslin, A.H. et al. (2017) Soil fauna responses to natural disturbances, invasive species, and global climate change: current state of the science and a call to action. *Soil Biology & Biochemistry*, 110, 116–133. Available from: https://doi.org/10.1016/j.soilbio.2017.03.008

Crowther, T.W., Boddy, L. & Jones, T.H. (2012) Functional and ecological consequences of saprotrophic fungus-grazer interactions. *The ISME Journal*, 6, 1992–2001. Available from: https://doi.org/10.1038/ismej.2012.53

de Boer, T.E., Holmstrup, M., van Straalen, N.M. & Roelofs, D. (2010) The effect of soil pH and temperature on *Folsomia candida* transcriptional regulation. *Journal of Insect Physiology*, 56, 350–355. Available from: https://doi.org/10.1016/j.jinsphys.2009.11.004

Dicks, L.V., Rose, D.C., Ang, F., Aston, S., Birch, A.N.E., Boatman, N. et al. (2019) What agricultural practices are most likely to deliver "sustainable intensification" in the UK? *Food and Energy Security*, 8, e00148. Available from: https://doi.org/10.1002/fes3.148

Dombos, M. (2001) Collembola of loess grassland: effects of grazing and landscape on community composition. *Soil Biology and Biochemistry*, 33, 2037–2045. Available from: https://doi.org/10.1016/S0038-0717(01)00125-0

EP - European Parliament. (2021) European Parliament resolution of 28 April 2021 on soil protection, The European Parliament. Available at: https://www.europarl.europa.eu/doceo/document/TA-9-2021-0143_EN.html (Accessed: 12 May 2021)

FAO, ITPS, GSBI, SCBD and EC. (2020) State of knowledge of soil biodiversity - Status, challenges and potentialities, Report 2020. Rome. https://doi.org/10.1016/b978-0-12-348536-6.50017-4

Ferrín, M., Márquez, L., Petersen, H., Salmon, S., Ponge, J.F., Arnedo, M. et al. (2023) Trait-mediated responses to aridity and experimental drought by springtail communities across Europe. *Functional Ecology*, 37, 44–56. Available from: https://doi.org/10.1111/1365-2435.14036

Filho, L.C.I.d.O., Filho, O.K., Baretta, D., Tanaka, C.A.S. & Sousa, J.P. (2016) Collembola community structure as a tool to assess land use effects on soil quality. *Revista Brasileira de Ciência do Solo*, 40:e015043, 1–18. Available from: https://doi.org/10.1590/18069657rbcs20150432

Giller, P.S. (1996) The diversity of soil communities, the "poor mans tropical rainforest". *Biodiversity and Conservation*, 5, 135–168. Available from: https://doi.org/10.1007/BF00055827

Gisin, H. (1943) Ökologie und Lebensgemeinschaften der Collembolen im Schweizerischen Exkursionsgebiet Basels. *Revue Suisse de Zoologie*, 50(4), 131–224.

González-Macé, O. & Scheu, S. (2018) Response of collembola and acari communities to summer flooding in a grassland plant diversity experiment. *PLoS One*, 13(8), 1–18. Available from: https://doi.org/10.1371/journal.pone.0202862

Halley, R.J. (Ed.). (1982) *The agricultural notebook*, 17th edition. London: Butterworths & Co.

Hao, C., Chen, T.W., Wu, Y., Chang, L. & Wu, D. (2020) Snow microhabitats provide food resources for winter-active Collembola. *Soil Biology and Biochemistry*, 143, 107731. Available from: https://doi.org/10.1016/j.soilbio.2020.107731

Holmstrup, M., Sørensen, J.G., Schmidt, I.K., Nielsen, P.L., Mason, S., Tietema, A. et al. (2013) Soil microarthropods are only weakly impacted after 13 years of repeated drought treatment in wet and dry heathland soils. *Soil Biology and Biochemistry*, 66, 110–118. Available from: https://doi.org/10.1016/j.soilbio.2013.06.023

Hopkin, S.P. (1997) *Biology of the springtails: (Insecta: Collembola)*. Oxford: Oxford University Press.

Hopkin, S.P. (2014) *A key to the Collembola (springtails) of Britain and Ireland*. Telford, UK: FSC Publications.

Huber, S., Prokop, G., Arrouays, D., Banko, G., Bispo, A., Jones, R.J.A. et al. (Eds.). (2008) *Environmental assessment of soil for monitoring - volume I: indicators & criteria*. Luxembourg: European Commission.

Hunter, M.D. (2001) Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology*, 3, 77–84. Available from: https://doi.org/10.1046/j.1461-9563.2001.00100.x

IPBES (2019) In: Brondizio, E.S., Settele, J., Díaz, S. & Ngo, H.T. (Eds.) *Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services*. Bonn, Germany: IPBES secretariat, P. 1148. Available from: https://doi.org/10.5281/zenodo.3831673

Ireson, J.E. (1990) *Studies on lucerne flea, Sminthurus viridis (L.) (Collembola: Sminthuridae) and other Collembola in the Tasmanian culture steppe*. Tasmania: University of Tasmania.

IUSS Working Group WRB. (2015) World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106, World Soil Resources Reports No. 106. Rome.

Janssens, F. (2017) *Checklist of the Collembola*. Available at: http://www.collembola.org/ (Accessed: 27 August 2017)

Jørgensen, H.B., Hedlund, K. & Axelsen, J.A. (2008) Life-history traits of soil collembolans in relation to food quality. *Applied Soil Ecology*, 38(2), 146–151. Available from: https://doi.org/10.1016/j.apsoil.2007.10.003

Jørgensen, H.B., Johansson, T., Canbäck, B., Hedlund, K. & Tunlid, A. (2005) Selective foraging of fungi by collembolans in soil. *Biology Letters*, 1, 243–246. Available from: https://doi.org/10.1098/rsbl.2004.0286

Kardol, P., Reynolds, W.N., Norby, R.J. & Classen, A.T. (2011) Climate change effects on soil microarthropod abundance and community structure. *Applied Soil Ecology*, 47, 37–44. Available from: https://doi.org/10.1016/j.apsoil.2010.11.001

Karlen, D.L., Mausbach, M.J., Doran, J.W., Cline, R.G., Harris, R.F. & Schuman, G.E. (1997) Soil quality: a concept, definition, and framework for evaluation. *Soil Science Society of America Journal*, 61, 4–10.

Larsen, T., Schjønning, P. & Axelsen, J. (2004) The impact of soil compaction on euedaphic Collembola. *Applied Soil Ecology*, 26, 273–281. Available from: https://doi.org/10.1016/j.apsoil.2003.12.006

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P. et al. (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology*, 33(4), 159–193.

Li, D., Clements, C.F., Shan, I.L.G. & Memmott, J. (2021) Corridor quality affects net movement, size of dispersers, and population growth in experimental microcosms. *Oecologia*, 195, 547–556. Available from: https://doi.org/10.1007/s00442-020-04834-2

Li, D., Memmott, J. & Clements, C.F. (2023) Corridor quality buffers extinction under extreme droughts in experimental metapopulations. *Ecology and Evolution*, 13, e10166. Available from: https://doi.org/10.1002/ece3.10166

Lindberg, N. & Bengtsson, J. (2005) Population responses of oribatid mites and collembolans after drought. *Applied Soil Ecology*, 28, 163–174. Available from: https://doi.org/10.1016/j.apsoil.2004.07.003

Malcicka, M., Berg, M.P. & Ellers, J. (2017) Ecomorphological adaptations in Collembola in relation to feeding strategies and microhabitat. *European Journal of Soil Biology*, 78, 82–91. Available from: https://doi.org/10.1016/j.ejsobi.2016.12.004

Mangiafico, S. (2021) Rcompanion: functions to support extension education program evaluation. R Package Version 2.4.1. https://cran.r-project.org/package=rcompanion

Martins da Silva, P., Carvalho, F., Dirilgen, T., Stone, D., Creamer, R., Bolger, T. et al. (2016) Traits of collembolan life-form indicate land use types and soil properties across an European transect. *Applied Soil Ecology*, 97, 69–77. Available from: https://doi.org/10.1016/j.apsoil.2015.07.018

Met Office. (2018). February and March 2018) *Snow and low temperatures - the beast from the east*. Devon, UK: Met Office. Available from: https://www.metoffice.gov.uk/binaries/content/assets/metofficegovuk/pdf/research/library-and-archive/library/publications/historical-weather-factsheets/beastfromtheeastfebruarymarch2018.pdf

Met Office. (2021) Historic station data - Shawbury. Available at: https://www.metoffice.gov.uk/research/climate/maps-and-data/historic-station-data%0A (Accessed: 1 June 2021)

Mieszkowska, N. (2019) MarClim annual welsh intertidal climate monitoring survey 2018. In: *Natural Resources Wales evidence report No. 345*. Bangor: Natural Resources Wales. www.naturalresourceswales.gov.uk

Moore, J.C. & de Ruiter, P.C. (1991) Temporal and spatial hetrogeneity of trophic interactions within below-ground food webs. In: Crossley, D.A., Jr. et al. (Eds.) *Modern techniques in soil ecology*. New York: Elsevier Science Publication. Co, pp. 371–397.

Natalio, A.I.M., Back, M.A., Richards, A. & Jeffery, S. (2024) Field-scale heterogeneity overrides management impacts following conversion to no-till within an arable system. *Applied Soil Ecology*, 193, 105104. Available from: https://doi.org/10.1016/j.apsoil.2023.105104

Pommeresche, R., Løes, A.K. & Torp, T. (2017) Effects of animal manure application on springtails (Collembola) in perennial ley. *Applied Soil Ecology*, 110, 137–145. Available from: https://doi.org/10.1016/j.apsoil.2016.10.004

Ponge, J.-F. (1993) Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems. *Pedobiologia*, 37(4), 223–244.

Ponge, J.-F. (2015) *Bioindication and Collembola*. France: HAL, pp. 1–2 https://hal.archives-ouvertes.fr/hal-01224906

Ponge, J.-F., Dubs, F., Gillet, S., Sousa, J.P. & Lavelle, P. (2006) Decreased biodiversity in soil springtail communities: the importance of dispersal and landuse history in heterogeneous landscapes. *Soil Biology and Biochemistry*, 38, 1158–1161. Available from: https://doi.org/10.1016/j.soilbio.2005.09.004

Ponge, J.-F., Gillet, S., Dubs, F., Fédoroff, E., Haese, L., Sousa, J.P. et al. (2003) Collembolan communities as bioindicators of land use intensification. *Soil Biology and Biochemistry*. Elsevier, 35, 813–826. Available from: https://doi.org/10.1016/S0038-0717(03)00108-1

Potapov, A.A., Semenina, E.E., Korotkevich, A.Y., Kuznetsova, N.A. & Tiunov, A.V. (2016) Connecting taxonomy and ecology: trophic niches of collembolans as related to taxonomic identity and life forms. *Soil Biology and Biochemistry*, 101, 20–31. Available from: https://doi.org/10.1016/j.soilbio.2016.07.002

Potapov, A.M., Guerra, C.A., van den Hoogen, J., Babenko, A., Bellini, B.C., Berg, M.P. et al. (2023) Globally invariant metabolism but density-diversity mismatch in springtails. *Nature Communications*, 14(674), 13. Available from: https://doi.org/10.1038/s41467-023-36216-6

Querejeta, J.I., Schlaeppi, K., López-García, Á., Ondoño, S., Prieto, I., van der Heijden, M.G.A. et al. (2021) Lower relative abundance of ectomycorrhizal fungi under a warmer and drier climate is linked to enhanced soil organic matter decomposition. *New Phytologist*, 232(3), 1399–1413. Available from: https://doi.org/10.1111/nph.17661

R Core Team. (2019) *R: a language and environment for statistical computing. Version 3.6.2, including the stats package*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.r-project.org/

Ruess, L., Schütz, K., Migge-Kleian, S., Haggblom, M.M., Kandeler, E. & Scheu, S. (2007) Lipid composition of Collembola and their food resources in deciduous forest stands – implications for feeding strategies. *Soil Biology and Biochemistry*, 39, 1990–2000. Available from: https://doi.org/10.1016/j.soilbio.2007.03.002

Rusek, J. (1989) Ecology of Collembola. In: Dallai, R. (Ed.) *3rd international seminar on Apterygota*. Siena, Italy: University of Siena, pp. 271–281.

Rusek, J. (1998) Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation*, 7, 1207–1219.

Salmon, S., Ponge, J.F., Gachet, S., Deharveng, L., Lefebvre, N. & Delabrosse, F. (2014) Linking species, traits and habitat characteristics of Collembola at European scale. *Biology and Biochemistry*, 75, 73–85. Available from: https://doi.org/10.1016/j.soilbio.2014.04.002

Sanders, S.K.D., Martínez-De León, G., Formenti, L. & Thakur, M.P. (2024) How will climate change affect the feeding biology of Collembola? *Soil Biology and Biochemistry*, 188, 109244. Available from: https://doi.org/10.1016/j.soilbio.2023.109244

Song, L., Liu, J., Yan, X., Chang, L. & Wu, D. (2016) Euedaphic and hemiedaphic Collembola suffer larger damages than epedaphic species to nitrogen input. *Environmental Pollution*, 208, 413–415. Available from: https://doi.org/10.1016/j.envpol.2015.10.008

Testerink, G.J. (1981) Starvation in a field population of litter springtails (Collembola). Methods for determining food reserves in small arthropods. *Pedobiologia*, 21, 427–433.

Testerink, G.J. (1983) Metabolic adaptations to seasonal changes in humidity and temperature in litter-inhabiting Collembola. *Oikos*, 40(2), 234–240. Available from: https://doi.org/10.2307/3544587

Turner, S., Barker, L.J., Hannaford, J., Muchan, K., Parry, S. & Sefton, C. (2021) The 2018/2019 drought in the UK: a hydrological appraisal. *Weather*, 76(8), 248–253.

UNEP. (2022) The United Nations Environment Programme, Nairobi, Kenya. Available from: https://wedocs.unep.org/bitstream/handle/20.500.11822/37946/UNEP_AR2021.pdf

Vanderwalle, M., de Bello, F., Berg, M.P., Bolger, T., Doledec, S., Dubs, F. et al. (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, 19(10), 2921–2947.

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag. Available from: https://doi.org/10.1007/978-3-319-24277-4_9

Yin, R., Gruss, I., Eisenhauer, N., Kardol, P., Thakur, M. P., Schmidt, A. et al. (2019) Land use modulates the effects of climate change on density but not community composition of Collembola. *Soil Biology and Biochemistry*, 138, 107598. Available from: https://doi.org/10.1016/j.soilbio.2019.107598

How to cite this article: Natalio, A.I.M., Back, M.A., Richards, A. & Jeffery, S. (2024) Dynamics of Collembola ecomorphological groups within a no-till arable system. *Agricultural and Forest Entomology*, 1–12. Available from: https://doi.org/10.1111/afe.12666