Push-pull cropping system positively impacts diversity and abundance of springtails (Hexapoda: Collembola) as bioindicators of soil health

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Abstract

Crop cultivation positively or negatively impacts soil biodiversity and associated ecological services. The push-pull technology (PPT), a climate-smart cereal-*Desmodium* spp.-*Brachiaria* spp. Companion cropping system, is known for providing nature-based solutions for pest and soil fertility challenges and has been practiced in sub-Saharan smallholder farmer fields for more than two decades. However, the extent to which this cropping system affects soil arthropod biodiversity in general and Collembola in particular is not well known. This study assessed the long-term effects of PPT on soil physicochemical properties, abundance, and diversity of Collembola communities, and soil biological quality (QBS) as indicators of soil health. Soil was collected from five maize monoculture and five push-pull smallholder farmer fields in western Kenya. Soil physicochemical properties were analysed using Walkley-Black and Bouyoucos hygrometer method. Collembola abundance and diversity were assessed following the Berlese funnel extraction method and morphological identification. Soil health was evaluated using a Collembola-based soil biological quality (QBS-c) index. Soil physicochemical properties significantly differed between push-pull and maize monoculture fields, with push-pull soils being less acidic, and having higher quantities of nitrogen and carbon. Compared to monoculture, push-pull soils had significantly higher number and diversity of Collembola, and QBS-c index values. Significant positive correlations were observed between Collembola abundance and soil pH, nitrogen, carbon, phosphorous, and electrical conductivity. This study provides experimental evidence that crop diversification through a push-pull cropping system soil legacies positively impacts Collembola abundance and diversity, serving as bioindicator of healthy soils.

Keywords: Agroecosystem; Collembola; Mesofauna; Push-pull technology; Soil health

1. Introduction

Agricultural practices such as cropping systems and patterns significantly impact soil quality, diversity, and biological activities of soil biota [1]. Conventional agriculture practices including application of inorganic fertilizers, pesticides, tillage, and monocropping greatly impact soil communities and their functional roles in the ecosystem service provision [[2], [3], [4]]. These practices negatively impact soil aggregate structure and subsequent biological activities and, if carried out continuously on fields, drastically degrade soil properties [2]. Farming practices that improve farm productivity, reverse soil degradation, and restore multiple below- and aboveground ecosystem services are vital for establishing an economically and ecologically sustainable agriculture [5,6].

Ecological intensification using diverse intercrops for ecosystem services restoration and yield improvement is one such farming system that is gaining traction [4,5,7,8]. Intercropping, a diversification approach which involves growing multiple crop mixtures simultaneously, has been found to revitalize soil and biodiversity, restoring ecosystem services [[9], [10], [11]]. Resource-constrained smallholder growers in the third world regularly use polyculture cropping systems due to their ability to improve farm yields, decrease expensive inputs and risks and provide better economic returns [12]. Polyculture cropping systems are associated with increased organic matter from the diverse intercrops which has positive effect on the soil physicochemical and biological qualities including diversity, abundance, and biological activities of the mesofauna [13]. Improved soil properties subsequently influence plant growth, metabolism, and resistance to diseases and pests, thus increasing plant productivity [4,6,14,15]. Intercropping also minimizes synthetic inorganic inputs including pesticides and fertilizers, resulting to higher profitability and reduction of adverse effects on the ecosystems [9].

One such intercropping system is push-pull technology (PPT), an innovative agroecological cropping system where maize (*Zea mays* L.) (Poales: Poaceae) is intercropped with a perennial pest-repellent ‘push’ plant such as desmodium (*Desmodium* spp.) (Fabales: Fabaceae), and a pest-attractive plant ‘pull’ such as Napier grass (*Pennisetum purpureum* Schumach.) (Poales: Poaceae) or brachiaria grass (*Brachiaria brizantha* (Hochst. ex A. Rich.)) (Poales: Poaceae) surround the maize farms as border crop [16]. Gravid lepidopteran females are pushed or deterred from the target crop by stimuli that mask host apparency while they are simultaneously attracted (pulled) to the trap crop, leaving the target crop protected [17]. The repellence and attraction of these push and pull plants are mediated by constitutive emission of repellent and attractive volatile semiochemicals, respectively [18]. The pull plant does not support the survival of the hatching lepidopteran larvae [19]. PPT is a cost-efficient and sustainable system that utilizes locally available biodiversity to address challenges associated with insect-pests, soil fertility and degradation, which pose constraints to cereal production in Sub-Saharan Africa [16,20,21]. The technology has been widely adopted and used over the last two decades across Africa and continues to be adopted in new areas [17,22]. Where it has been adopted across the region, crop yields such as maize have increased tremendously in comparison to maize-food legume and monoculture cropping systems [[23], [24], [25]].

Additional socio-economic and ecological services have been accrued where this technology is practiced including control of parasitic *Striga* weeds through induction of suicidal germination by the root exudates of the *Desmodium* intercrop [26]. Additional income is generated from increased milk production and the sale of excess companion plants as high value animal fodder [27]. Furthermore, soil degradation is prevented by the intercrop (*Desmodium* spp.) through cover cropping and moisture retention as well as nitrogen fixation, phosphorus solubilization and soil organic matter incorporation [28]. As a result of improved soil properties, the cropping system has manifested positive plant-soil feedbacks increasing crop plant's resistance to insect herbivores [15] and reduction of mycotoxin causing *Aspergillus* fungi in both soil and maize plants in push-pull farms [29,30]. In addition, Midega and Khan [31] demonstrated enhanced biodiversity and abundance of above-ground insect predators through push-pull companion cropping as a habitat management system. While the aboveground multitrophic interactions of PPT and the underlying mechanisms have been well studied over the last two decades, there is a notable gap in our understanding of belowground multitrophic interactions. This gap particularly pertains to the impact and interactions with soil biota.

The diversity and abundance of soil-dwelling arthropods and their ecological roles are known to be influenced by changes in soil environments. Collembola are among the most abundant and widespread mesofauna and impact ecosystem functioning through their diversity and abundance [2,32,33]. They are ecologically specialized microarthropod groups often recommended as bioindicators of management-induced changes in soil quality and health [34,35]. Collembola play critical ecological roles in nutrient recycling through the dispersal and regulation of decomposer microbial communities [34,36,37], and regulation of fungal diseases through the consumption of fungal plant pathogens [38]. They also promote nutrient uptake and plant root architecture of some plants by regulating the dispersal and activity of mycorrhizal fungi in the soil [39,40].

Collembola are known to be impacted by plant diversity and composition [37,41]. Previous studies have shown that mixtures of wheat varieties [42], introduction of legumes in agricultural grasslands [43], mulching [44] and crop rotation [2] increase Collembola species diversity and abundance in agroecosystems. Push pull technology which involves minimum tillage without synthetic insecticides and fertilizer application could positively affect diversity and abundance of soil mesofauna as opposed to conventional monoculture systems [45]. However, the effects of push-pull cropping system on relative abundance and diversity of Collembola as a metric of soil health remains poorly characterized.

Therefore, our study aimed at investigating the effects of PPT on physicochemical soil properties and mesofauna using Collembola as bioindicator species in smallholder farms. Further, we investigated the effects of PPT on biological quality of the soil using Collembola as indicator species [“Qualità biologica del suolo” (QBS-c) index] [46] as a measure of soil health. We hypothesized that soil conditioned by the push-pull cropping system had better soil physicochemical properties and higher Collembola abundance and diversity compared to soil conditioned by maize monoculture. Additionally, we anticipated a positive correlation between Collembola abundance and key soil physiochemical properties as well as higher QBS-index scores in the push-pull cropping system than in maize monoculture, indicating better soil health.

2. Materials and methods

2.1. Description of the study site

The study was conducted in 5 different smallholder farms, each farm with a pair of push-pull and maize monoculture cropping system fields, situated in Vihiga County, western Kenya (Fig. 1). The County is a highland region located at 0.0768° N, 34.7078° E, with a mean altitude of 1594 m above sea level (masl). The region experiences a mean daily temperature of 24.0 °C and binomial rainfall, with long rains occurring between April and July and short rains between October and December, with mean annual rainfall of 1900 mm [47]. The County was chosen due to dominance of agricultural activities with push-pull and maize monoculture cropping systems commonly practiced. Information regarding cultivation practices on each farm was obtained from farmers prior to collection of soil samples.

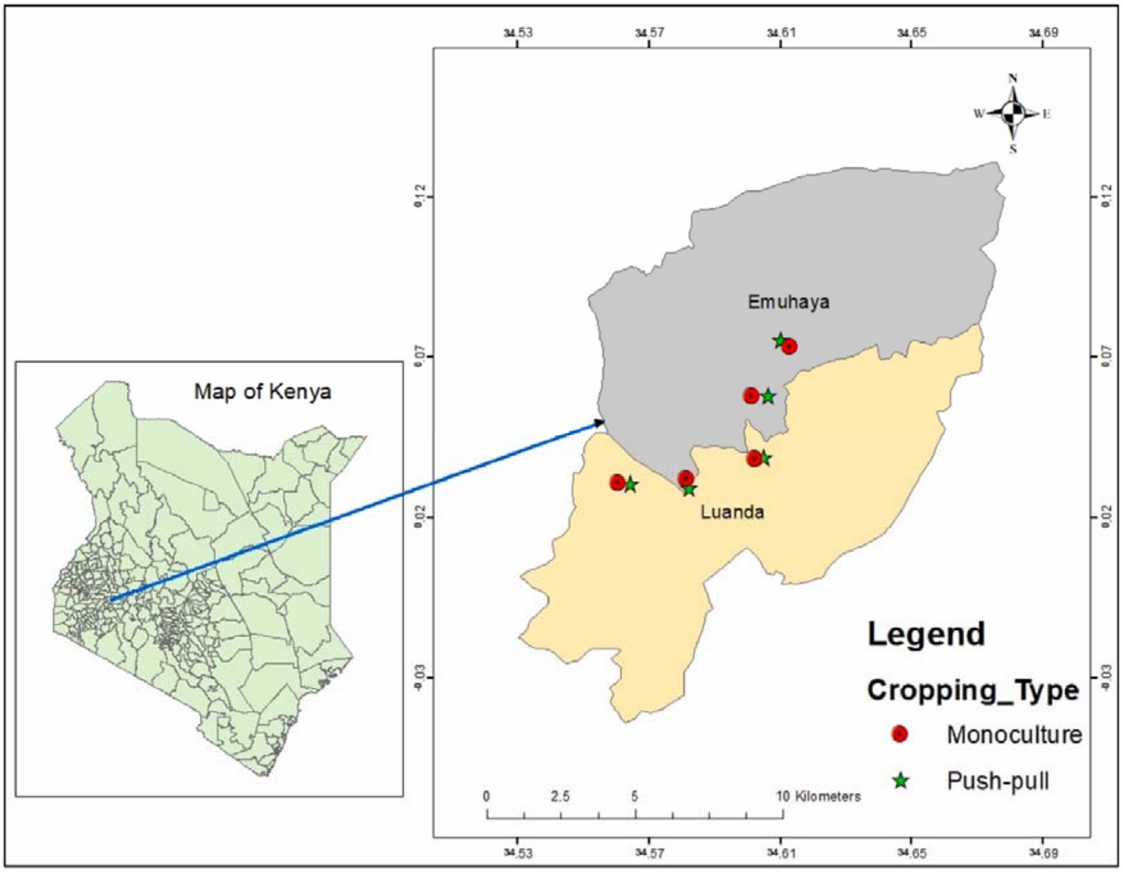


Fig. 1. Map of Kenya showing Vihiga County, where soil samples were collected for physicochemical analysis and Collembola extraction.

2.2. Soil sampling

Soil sampling was conducted in May 2022 to coincide with periods of long rains and the highest activity of soil microarthropods [48]. Farms with both push-pull and maize monoculture cropping systems fields, situated adjacent to each other (at least 100m apart) and established between three to seven years, were selected for soil sampling [49]. On each field, five sampling points at distance of 10m apart from each other were selected making a total of 10 sampling points per farm. Using a metal core sampler (5.8 cm diameter), soil samples were bored at depths of 15 cm, since this soil layer is conducive for Collembola communities [50]. From each cropping system field, the soil samples were pulled together and mixed thoroughly to attain homogeneity. The soil samples were packaged separately from each field in 3 L khaki paper bags (Paper bags Ltd., Nairobi, Kenya) and transported to the laboratory for Collembola extraction and identification. At the same time, a similar set of soil samples were collected for analysis of physicochemical properties. In the push-pull cropping system fields, soil samples were collected between *Desmodium* and maize rows, and the inter-row spacing of the *Desmodium*-maize was 30 cm each. In the maize monoculture cropping system fields, samples were collected between maize rows. No sampling occurred within the last two rows from the border rows. In total, soil was collected from 100 sampling points, 50 each from push-pull and maize monoculture fields.

2.3. Soil physicochemical properties

Soil physicochemical properties were analysed at Société Générale de Surveillance (SGS) Kenya Multi-laboratory, Nairobi, Kenya. Soil chemical nutrients, including nitrogen (N), phosphorus (P), sodium (Na), calcium (Ca), potassium (K), zinc (Zn), boron (B), cupper (Cu), iron (Fe), manganese (Mg), and electrical conductivity (EC), were analysed following the protocol developed by Ref. [50]. Soil texture (silt, clay and sand) was determined through Bouyoucos hygrometer protocol as described by Ref. [51]. Soil organic carbon (C) was quantified using the Walkley-Black method [52]. Soil pH was determined using a glass electrode pH meter (Hach, Loveland, Colorado, United States) following the procedure outlined in Ref. [53].

2.4. Collembola extraction

Collembola extraction and identification were conducted at Duduville Campus (1.2921° S, 36.8219° E; 1616 masl) of the International Center of Insect Physiology and Ecology (*icipe*) located in Kasarani, Nairobi City, Kenya. Soil samples were kept at 4 °C for not more than three days and Collembola extracted using the modified Berlese-Tüllgren funnel method [54]. Funnels (2 L, 15 cm diameter plastic containers fitted with 1.5 mm wire mesh) were fitted 30 cm apart and supported by claps and a stand to hold soil samples. To ensure maximum penetration of light into the soil, each soil sample was divided into two portions and gently placed into the funnel. Collembola were extracted from each soil portion for 48 h. A 500 mL collection container with 70 % ethanol was placed below the funnel to collect Collembola. An incandescent lamp (9 W, 240 V) was placed 10 cm above the soil sample. Using a Pasteur pipette, collected Collembola were transferred into 30 mL glass vials containing 70 % ethanol solution and stored at −4 °C before identification.

2.5. Collembola morphological characterization

Collected Collembola were counted and identified using phase contrast microscope (Carl Zeiss Microscopy GmbH, Göttingen, Germany) at 40X with a fixed digital microscope camera. Collembola were placed on a glass slide and identified to genus level using existing identification keys. Due to scarcity of literature regarding identification of Collembola communities in Africa, morphological keys to identify Collembola were extracted from http://www.collembola.org/ [55] and (https://www.chaosofdelight.org).

Six major morphological features (body length, body shape, number of ocelli, presence of sensorial organ (post-antennal), pigmentation level, and development of furca and scales) were selected to identify Collembola to genus level [[56], [57], [58]] (Fig. S1). Collembola from soil samples of each cropping system per farm were pooled prior to analysis.

2.6. Collembola functional characterization

Functional classification of Collembola was evaluated using “Qualità biologica del suolo” (QBS) index that applies the principle that Collembola are highly sensitive and develop specific morphological features for adaptation to soil habitat [[58], [59], [60]]. Originally proposed by Parisi et al. [60], the method assumes the criteria that different species are classified on the basis of their morphological traits using a simplified eco-morphologic index (EMI). As recommended by Parisi et al. [60], EMI values were assigned to Collembola morphological features used during identification process (Table 1). The EMI scores ranged between 1 (poor adaptation) and 20 (best adaptation). QBS-c index values were computed by totaling EMI values for each Collembola collected.

Table 1. The morphological features of Collembola used to assign eco-morphological index score as developed by Parisi et al. [60].

Features	**EMI-score**
Middle to large size (>2 mm), complex pigmentation, long and well-developed furca, well-developed visual structures (ocelli) (epigeous adaptation).	1
Well-developed appendages (possible), well-developed setae or protective cover of scales, well-developed ocelli (epigeous adaptation).	2
Small size (<2 mm), moderate pigmentation, average length of appendages, developed visual apparatus (epigeous adaptation).	4
Developed ocelli, no elongated appendages, cuticle with pigmentation (hemi-edaphic adaptations).	6
Scarcely developed appendages, often short or absent furca, pigmentation present (hemi-edaphic adaptations).	8
No pigmentation, reduction or absence of ocelli, furca present but reduced (eu-edaphic adaptation).	10
No pigmentation, absent furca, short appendages (eu-edaphic adaptation).	20

2.7. Collembola abundance and diversity

To determine effects of the cropping systems on Collembola diversity, the species richness Shannon-Wiener index was computed using equations (i) and (ii) [61]. In addition, the impact of cropping systems on individuals in the taxa (evenness) was evaluated by Pielou's evenness index (equation iii) [62]. Collembolan abundance was calculated by counting the total number of Collembola in each soil sample. The abundance and diversity of Collembola were expressed as the total genus per meter square.

$$\text{Species richness} = S = \text{number of species} \qquad \text{(i)}$$

$$\text{Shannon Wiener's index} = H' = -\sum [(\text{pi}) * \ln(\text{pi})] \qquad \text{(ii)}$$

$$\text{Pielou's evenness index} = J = \frac{H}{Hmax} \qquad \text{(iii)}$$

Where:

Pi = proportion of total sample represented by species i obtained by dividing no. of individuals of species i by total number of samples.

Hmax = ln(S) = Maximum diversity possible.

ln = is the natural logarithm.

To investigate relationship between soil physiochemical properties and Collembola abundance, a Pearson's correlation coefficient was performed and correlograms were constructed for the compared variables.

2.8. Data analysis

Before analysis, all quantitative data were tested for normality using Shapiro-Wilk's test and for homogeneity of variances using Bartlett's test ($\alpha > 0.05$). Effect of cropping systems on soil physicochemical properties was determined using student *t*-test. A principal component analysis (PCA) was performed to determine the effects of cropping systems on soil physicochemical properties using 'FactoMineR', 'factoextra', and 'corrplot' packages in R software [63]. Mann-Whitney *U* test was used to analyse differences in Collembola abundance and QBS-c index values between PPT and maize monoculture cropping systems. The diversity of Collembola communities in push-pull and maize monoculture cropping systems was analysed using Shannon-Wiener and Pielou's index [64,65]. One-way analysis of similarities (ANOSIM) was carried out to determine effects of cropping systems on composition of Collembola taxa using the Bray–Curtis dissimilarity index [66]. Dissimilarity indices on Collembola taxonomical structure between push-pull and maize monoculture cropping systems were represented by a permutation test using non-metric multidimensional scaling (NMDS). Individual number of Collembola orders, families and genera of each cropping system were plotted on a non-metric multidimensional scaling (NMDS) ordination diagram. We used Pearson correlation coefficient in 'ggpubr' R package [63] to investigate relationship between soil physicochemical properties and Collembola abundance. Analysis of permutation tests (ANOSIM and NMDS) were performed using the paleontological statistics software (PAST, v.4.13) [67]. All other analyses were performed using R Software v4.2.2 with α set at 0.05 [68].

3. Results

3.1. Soil physicochemical properties

The first two axes of the PCA for soil physicochemical properties explained 42 % and 24 % of the total data variability, totaling to 66 % of soil physicochemical properties variability. (Fig. 2). Soil pH, EC, C, and N appeared to be positively correlated in PCA axis 1, while P was positively correlated in PCA axis 2 of push pull cropping system. Conversely, Na, Mg, Ca, K, Clay and silt negatively correlated in PCA axis 1 and sand positively associated in PCA axis 2 of push pull cropping system (Fig. 2). Whereas sand positively associated in PCA axis 1; Na, Mg, Ca, K, Clay, and silt negatively correlated in PCA axis 2 of monoculture cropping system (Fig. 2). Soils from PPT fields had higher pH, N, and C content than in maize monoculture soils (Table 2). Electrical conductivity, phosphorous, potassium, calcium, magnesium, clay, silt, and sand, were not significantly different between PPT and maize monoculture fields (Table 2).

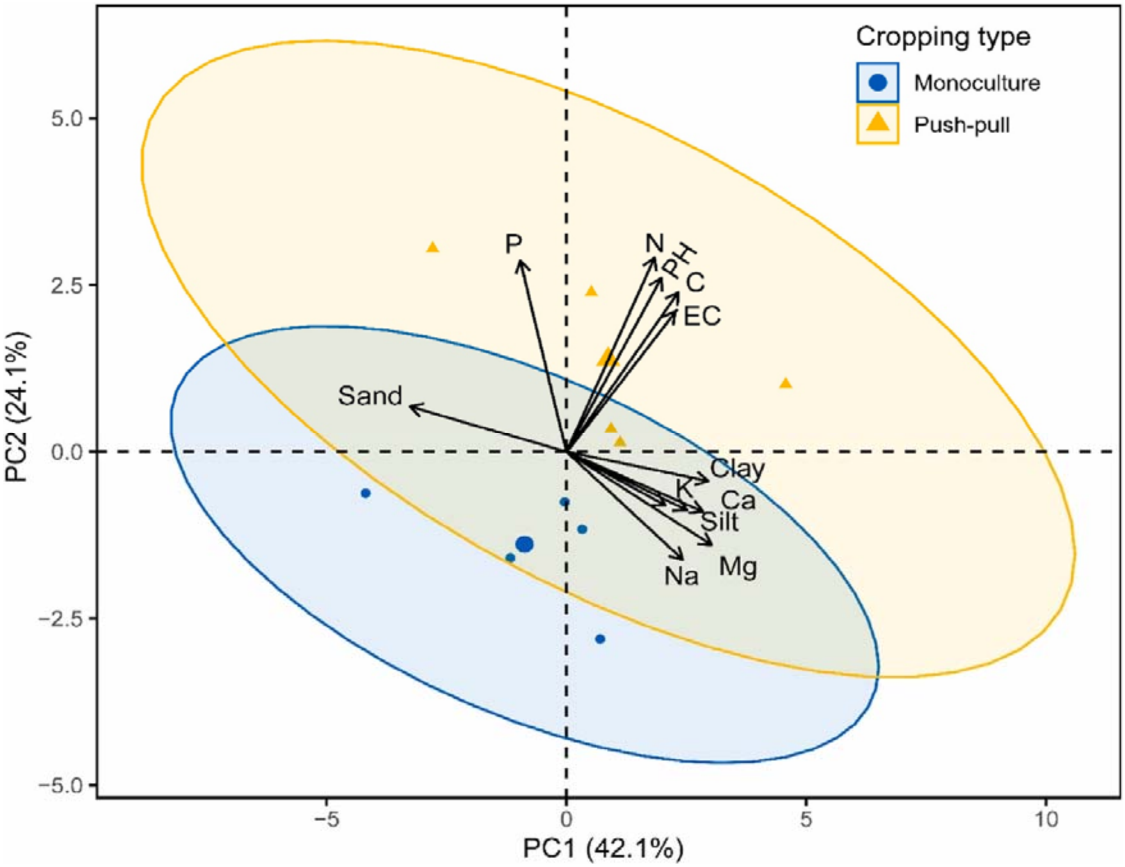


Fig. 2. Principal component analysis (PCA) for the relationship between soil physicochemical properties and cropping type. Principal components 1 = PC1 and principal components 2 = PC2. pH, potential of hydrogen; EC, electrical conductivity; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; C, carbon; N, nitrogen.

Table 2. Soil physicochemical characteristics of soil conditioned by push-pull and maize monoculture cropping systems from smallholder farmer fields in Vihiga county, Kenya.

Cropping system	**pH (H_2O)**	**EC (mmhoscm^{-1})**	**P (mgkg^{-1})**	**K (mg kg^{-1})**	**Na (mg kg^{-1})**	**Ca (mg kg^{-1})**	**Mg (mg kg^{-1})**	**N (%)**	**C (%)**	**Clay (%)**	**Silt (%)**	**Sand (%)**
Push-pull	5.68 ± 0.09	0.09± 0.03	22.95 ± 4.15	93.73 ±8.25	9.56 ±0.23	742.68 ± 176.64	135.23 ± 26.20	0.15 ±0.02	1.54 ±0.19	30.75 ±4.61	20.01 ± 4.25	49.23 ± 8.46
Maize monoculture	4.92 ± 0.12	0.03 ± 0.01	16.6 ± 2.49	92.09 ±19.55	9.81 ± 0.41	704.50 ± 161.24	140.03 ± 31.26	0.06 ± 0.02	0.60 ± 0.15	23.53 ±6.54	19.59 ± 0.50	56.88 ± 6.38
***t* value**	−4.98	−1.85	−1.30	−0.07	0.53	−0.15	0.11	−4.10	−3.83	−0.90	−0.10	0.72
df	7.37	4.22	6.55	5.38	6.38	7.93	7.76	7.91	7.60	7.18	4.11	7.43
***P* value**	**0.001**	0.100	0.229	0.940	0.607	0.877	0.909	**0.003**	**0.004**	0.394	0.922	0.491

pH, potential of hydrogen; EC, electrical conductivity; mmhoscm^{-1}, millimhos per centimeter; mg kg^{-1}, milligrams per kilogram; %, percentage; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; N, nitrogen; C, carbon.

3.2. Collembola abundance and diversity

A total 495 (371 and 124 in PPT and Mono respectively) individual Collembola were collected and identified from the soil samples (Table S1). These individuals consisted of four orders, eight families and 12 genera. This represented a density of 110,750 ind. m^{-2}. A significantly higher Collembola density of 82,974 ind. m^{-2} was obtained from soil from PPT fields compared to soil from maize monoculture fields at 27,776 ind. m^{-2} ($P = 0.04$) (Table 3; Table S1). Soil from PPT cropping system had significantly higher Collembola relative abundance across all four orders (Fig. 3). In these orders, Poduromopha had the highest number of Collembola, followed by Entomorbryomorpha, Symphyleona, and Neelipleaona had the least (Fig. 3). Similarly, eight families, including Hypogastruridae, Neanuridae, Isotomidae, Paronellidae, Dicyrtomidae, Arrhopalitidae, Sminthuridae, and Neelidae, were relatively abundant in the soil of the PPT cropping system compared to that of maize monoculture soil (Fig. 3).

Table 3. Collembola abundance (per meter square), diversity and richness in push-pull and maize monoculture cropping systems.

Collembola classification			**Cropping system**			
			Push-pull		**Maize monoculture**	
Order	**Family**	**Genus**	**No. of individuals**	**Prevalence percentage**	**No. of individuals**	**Prevalence percentage**
Poduromopha	Hypogastruridae	*Hypogastrura*	90,720	21.83	22,400	16.13
		Xenylla	28,000	6.75	12,320	8.87
		Ceratophysella	11,200	2.71	0	0
	Neanuridae	*Neanura*	24,640	5.94	0	0
Entomorbryomorpha	Isotomidae	*Desoria*	13,440	3.23	8960	6.45
		Isotomurus	35,840	8.63	5600	4.03
		Folsomia	13,440	17.79	36,960	26.61
	Paronellidae	*Cyphoderus*	2240	0.54	1120	0.81
Symphyleona	Dicyrtomidae	*Dicyrtomina*	73,920	3.23	11,200	8.07
	Arrhopalitidae	*Pygmarrhopalites*	1120	0.27	0	0
	Sminthuridae	*Sminthurides*	76,160	18.33	24,640	17.74
Neelipleaona	Neelidae	*Neelus*	44,800	10.78	15,680	11.29
		Abundance	**415,520 ± 8825.84**		**138,880 ± 3375.05**	
		Genera Richness	**12**		**9**	
		Shannon index	**2.11 ± 0.03**		**1.96 ± 0.04**	
		Pielou index	**0.86 ± 0.01**		**0.78 ± 0.01**	

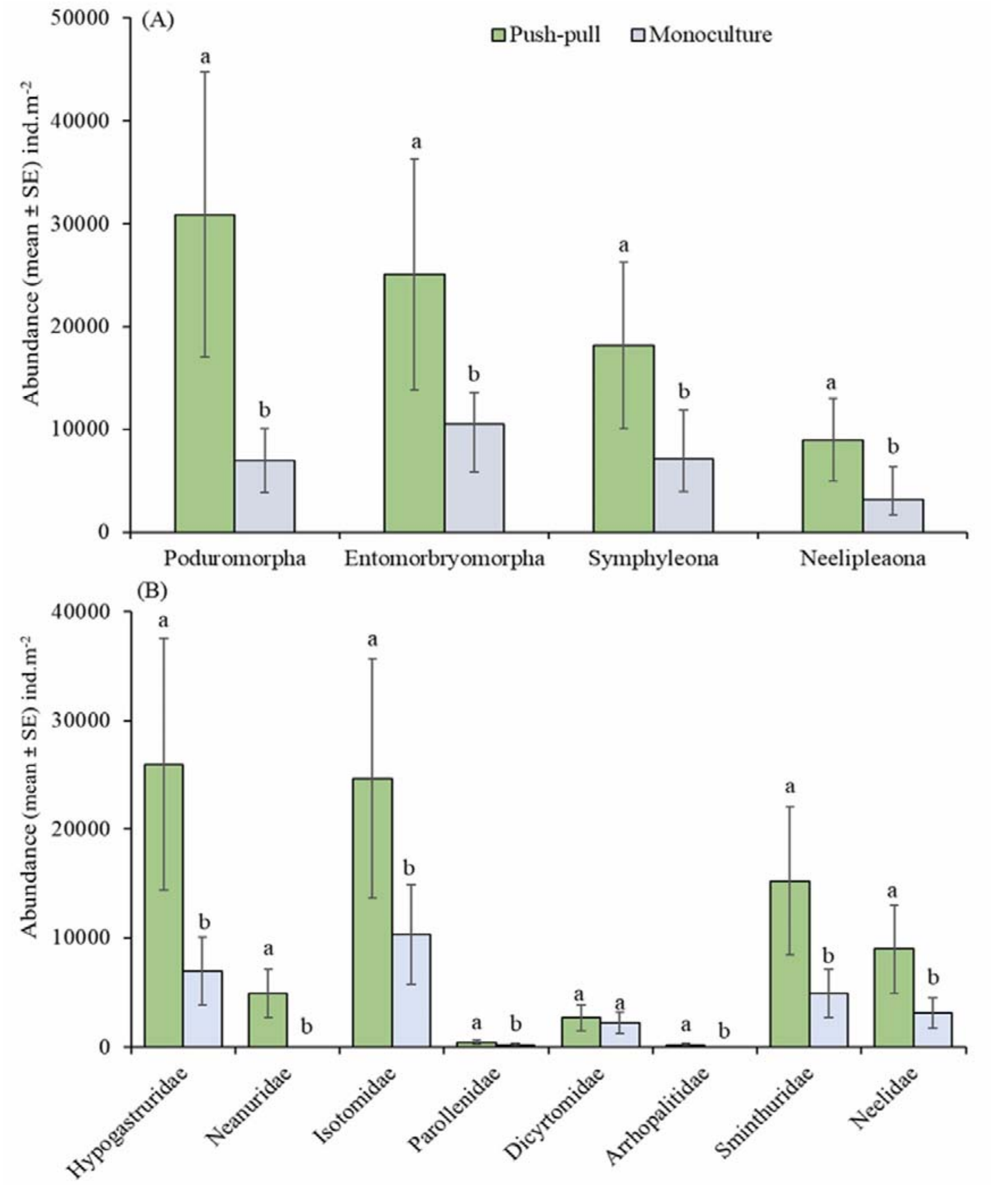


Fig. 3. Population density of identified collembolan orders (A) and families (B) on push-pull and maize monoculture cropping system conditioned soils. Different small letters above the error bars indicate significant differences between the cropping systems.

Cropping systems significantly influenced Collembola genera richness and diversity, as indicated by the Shannon and Pielou indices (Table 3). Overall, Collembola diversity, measured by the Shannon-Wiener index, was higher in PPT soil (2.11) than in maize monoculture soil (1.96) (Table 3). Similarly, Collembola evenness, demonstrated by the Pielou index was higher in PPT soils (0.86) than in maize monoculture soils (0.78) (Table 3). *Ceratophysella, Neanura* and *Pygmarrhopalites* genera were exclusively present in push-pull cropping system-conditioned soil (Table 3). *Hypogastrura* (21.83 %) was the most relatively abundant genus in the push-pull cropping system, while in maize monoculture, *Folsomia* genus dominated (26.61 %) (Table 3).

In addition, ANOSIM results of *R* = 0.80, *P* = 0.008 for Collembola genera, demonstrated overall significant dissimilarity in the population structure of Collembola between the two cropping systems. These differences were also evident in the ordination discrimination for Collembola taxonomic groups for the two cropping systems on the NMDS spaces (Fig. 4; S2).

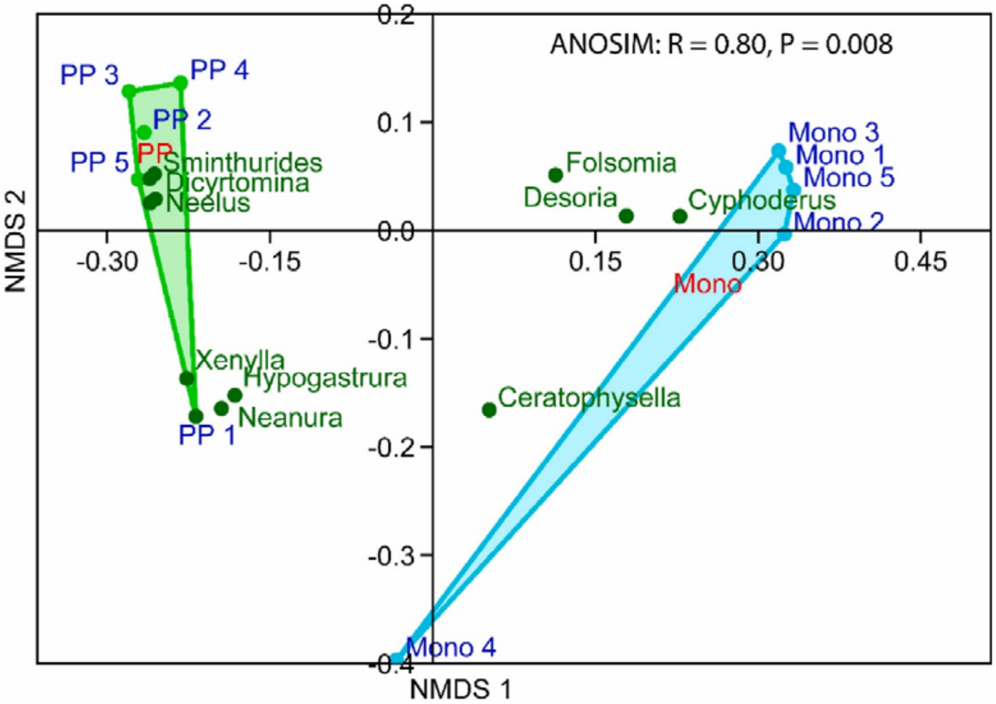


Fig. 4. Ranking by non-metric multidimensional scaling (NMDS) of Collembola genera from push-pull technology cropping system (PP) and maize monoculture (Mono) fields.

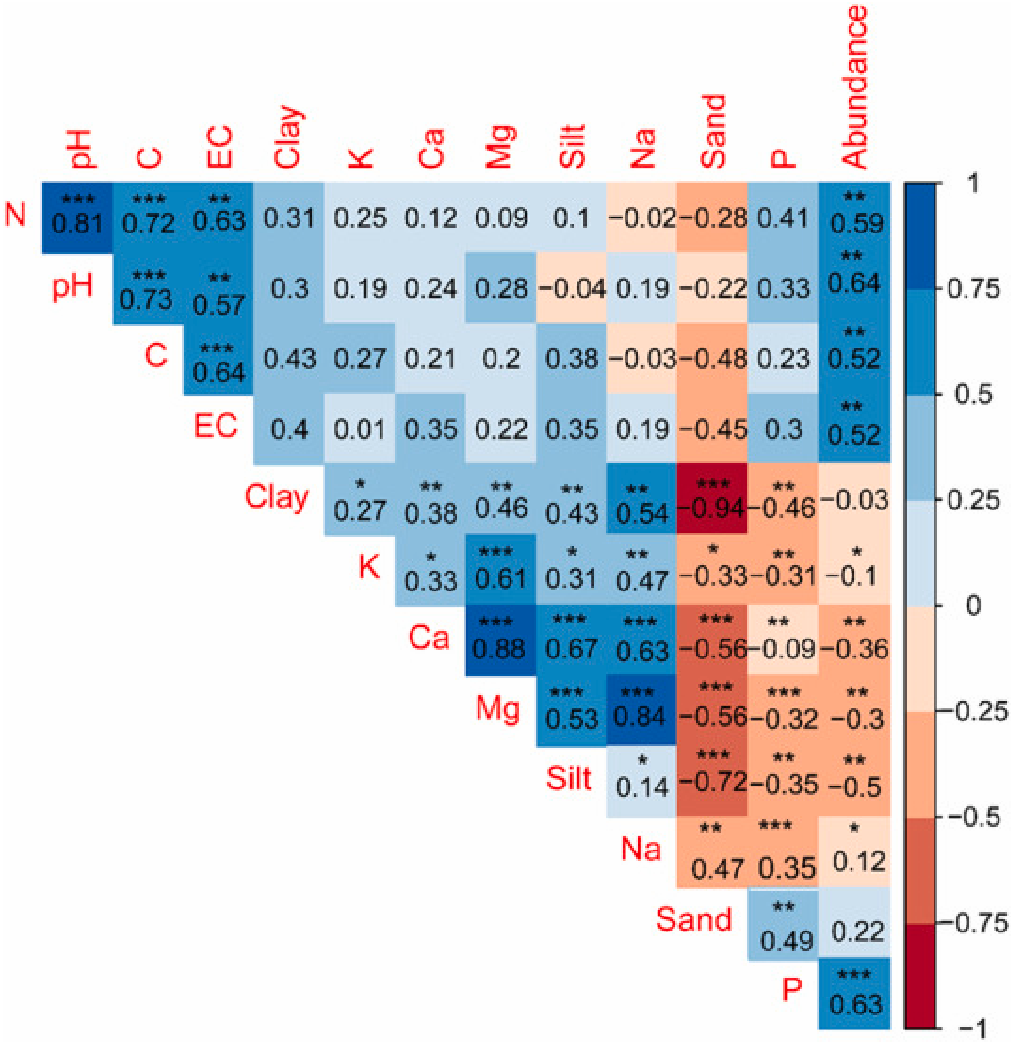
3.3. Functional classification of collembola

Total EMI scores of individual genera differed between soil from PPT and maize monoculture cropping systems (Table 4). There was a significant difference in QBS-c index values between PPT and maize monoculture cropping system ((395.33 ± 117.78 and 125.17 ± 38.76) respectively, *P* = 0.040). The highest EMI score (18) was assigned to *Hypogastrura* genus since it had multiple features for optimum adaption to euedaphic environment. The *Neelus* genus was given the lowest EMI value (8) due to morphological characteristics for adaptation in epigeous soil profiles. Medium EMI scores (10–16) were assigned to *Neanura, Desoria, Isotomurus* and *Folsomia* due to their hemiedaphic adaptations.

Table 4. Eco-morphologic index (EMI) scores of Collembola genera identified in soil samples from push-pull and maize monoculture cropping systems.

Classification	**Push-pull cropping system**			**Maize monoculture cropping system**		
Genus	**Individual EMI-score**	**No. of genera**	**Total EMI-score**	**Individual EMI-score**	**No. of genera**	**Total EMI-score**
Hypogastrura	18	81	1458	18	20	360
Xenylla	16	25	400	16	11	176
Ceratophysella	16	10	160	16	0	0
Neanura	12	22	264	12	0	0
Desoria	14	12	168	14	8	112
Isotomurus	16	32	512	16	5	80
Folsomia	12	66	792	12	33	396
Cyphoderus	10	2	20	10	1	10
Dicyrtomina	8	12	96	8	10	80
Pygmarrhopalites	10	1	10	10	0	0
Sminthurides	8	68	544	8	22	176
Neelus	8	40	320	8	14	112
Total QBS-c score			**4744**			**1502**
Mean QBS-c score±SE			**395.33 ± 117.78**			**125.17 ± 38.76**

Soil chemical parameters such as pH, P, N, C, and EC, were positively correlated with Collembola abundance ($R = 0.59$, $P < 0.01$, $R = 0.64$, $P < 0.01$, R = 0.63, $P < 0.01$, $R = 0.52$, and $R = 0.52$, $P < 0.05$, respectively, Fig. 5). Conversely, clay and sand showed weak correlations with Collembola abundance ($R = 0.03$, $P > 0.05$, and $R = 0.22$, $P > 0.05$, respectively, Fig. 5). On the other hand, parameters such as Mg, Ca, Na, K, and silt were negatively correlated with Collembola abundance ($R = -0.30$, $P < 0.01$, $R = -0.36$, $P < 0.01$, $R = -0.5$, $P < 0.05$, $R = -0.10$, $P < 0.05$, and $R = -0.50$, $P < 0.01$ respectively, Fig. 5).



	pH	C	EC	Clay	K	Ca	Mg	Silt	Na	Sand	P	Abundance
N	*** 0.81	*** 0.72	** 0.63	0.31	0.25	0.12	0.09	0.1	−0.02	−0.28	0.41	** 0.59
pH		*** 0.73	** 0.57	0.3	0.19	0.24	0.28	−0.04	0.19	−0.22	0.33	** 0.64
C			*** 0.64	0.43	0.27	0.21	0.2	0.38	−0.03	−0.48	0.23	** 0.52
EC				0.4	0.01	0.35	0.22	0.35	0.19	−0.45	0.3	** 0.52
Clay					* 0.27	** 0.38	** 0.46	** 0.43	** 0.54	*** −0.94	** −0.46	−0.03
K						* 0.33	*** 0.61	* 0.31	** 0.47	* −0.33	** −0.31	* −0.1
Ca							*** 0.88	*** 0.67	*** 0.63	*** −0.56	** −0.09	** −0.36
Mg								*** 0.53	*** 0.84	*** −0.56	*** −0.32	** −0.3
Silt									* 0.14	*** −0.72	** −0.35	** −0.5
Na										** 0.47	*** 0.35	* 0.12
Sand											** 0.49	0.22
P												*** 0.63

Fig. 5. Correlogram indicating correlations between Collembola abundance (genera) and soil physiochemical properties. Asterisks within the boxes represent significant relationships (*** for P < 0.001, ** for *P* < 0.01, and * for *P* < 0.05) while numbers represent Pearson correlation coefficients (*R*) between the compared variables. pH, potential of hydrogen; EC, electrical conductivity; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; C, carbon; N, nitrogen.

4. Discussion

Results from our study show that PPT positively impacts soil chemical properties and the abundance and diversity of Collembola communities in smallholder farms where this cropping system is practised. The higher diversity and abundance of Collembola associated with the push-pull cropping system are indicators of better soil health than in monoculture cropping systems. This study demonstrates considerable increase in soil mesofauna under the PPT cropping system in smallholder farms, highlighting another ecosystem service offered by this cropping system where it is practiced. We discuss our results in light of these ecosystem services and previous publications.

Agricultural practices such as monoculture and inorganic fertilization often lead to soil acidification; these practices add hydrogen and increase sequestration of soil cations such as Mg, Ca, and K to biomass without any replenishment from the organic matter [69,70]. These farming practices result in changes in soil physiochemical properties and associated soil arthropod diversity and abundance [4,33,71]. We found moderately acidic soils in maize monoculture fields compared to slightly acidic to neutral soil conditions in push-pull fields. It is well established that soil pH can cause great changes in Collembola species survival and reproduction, affecting community composition, with different species having varying tolerance to soil pH change [69]. When the cropping systems' conditioned soil was examined together with the Collembola species, *Desoria* and *Folsomia* species tended to be more closely associated with the monoculture cropping system than any other collembolan genera (Fig. 3). Indeed, *Folsomia* species, such as *Folsomia manoclachei*, are reported to be pH-dependent collembolan species [72].

In addition, the relationship between Collembola and soil physiochemical properties are indicated by the results of correlogram in this study (Fig. 4). The fluctuating patterns in relationship between soil physicochemical properties and Collembola abundance are largely attributed to the intercropped plant (*Desmodium*) which is known to provide organic matter, retain soil moisture, solubilize phosphorous and fix nitrogen in the soil [7,10,71,72]. On the other hand, the insignificant role played by the cropping system to determine presence of minor soil parameters such as K, Na, Ca, and Mg could explain the phenomenon of their low abundance and negative correlation with Collembola occurrences. Based on these findings, soil physicochemical properties and cropping systems are mutually inclusive and complement each other to determine overall impact on abundance and diversity of Collembola as a metric of soil health.

The maize-*Desmodium* cropping system had higher total organic carbon than in maize monoculture cropping. Previous studies have reported higher soil phosphorous, nitrogen, carbon, and organic matter in PPT fields than in maize monoculture fields [10,73,74]. Although both PPT and maize monoculture fields had minimum tillage being practiced, the lack of inorganic fertilizers and pesticides application in the push-pull fields and the accruing organic matter from the shoot and roots of companion plants (*Desmodium* and *Brachiaria* grass) alter the soil structure and chemistry of the push-pull fields compared to that of the maize monoculture. Furthermore, the companion plants are grown as permaculture cover crops and prevent soil degradation through soil erosion prevention and moisture retention, providing suitable habitat for soil microarthropods, including Collembola [75,76]. Monoculture cropping practices cause soil organic carbon loss [77] as shown in the total organic carbon in maize monoculture fields compared to push-pull fields. Low soil organic matter is associated with poor soil moisture retention, as indicated by low soil plasticity (K_A) values. These conditions create unfavourable habitats for Collembola, resulting in decreased abundance, species richness and diversity, as observed in maize monoculture fields compared to push-pull cropping system fields [69].

The overall mean Collembola density (82,974 ind. m^{-2}) observed in PPT fields in our investigation is greater than those previously reported regarding mesofauna densities in tropical forests and agroecosystems while the collembolan density in maize monoculture fields (27,776 ind. m^{-2}) is within the range of some of the reported densities in agricultural soils both in tropics and temperate areas [44,78]. Previous studies have reported varying densities of soil microarthropods in tropical soils compared to temperate ones. Low Collembola densities of ∼38,000 ind. m^{-2} in African pasture lands [78], ∼13,000 ind. m^{-2} in tropical forests, <4000 ind. m^{-2} in forested tropical sites [79] while Petersen and Luxton [80] showed that Collembola densities are lower in tropical soil in comparison to temperate ones. However, other studies in tropical areas have reported higher densities of Collembola. Culik et al. [44] reported high Collembola densities of 60,600 ind. m^{-2} in tropical agroecosystems in Brazil, while Badejo et al. [81] reported high Collembola densities of 72,000–82,000, and 271,000–556,000 ind. m^{-2} in grass, forest, and agroforestry soils, respectively, in Nigeria. Our current study provides additional evidence that high Collembola densities can also occur in tropical agroecosystems under ecological intensification farming systems.

The diversity and relative abundances of Collembola communities typically vary with changes in soil profiles due to agricultural practices [41,82,83]. Agricultural soils both in tropics and temperate areas, have demonstrated relatively low Collembola densities (<20,000 ind. m^{-2}) [38,84]. However, variations in tropical soils have also revealed high Collembola densities (>50,000 ind. m^{-2}) in cultivated soils within temperate and tropic environments [44,85]. Our findings show that maize monoculture cropping systems harbour a low Collembola density of 27,792 ind. m^{-2}. In contrast, the PPT system exhibits a higher density (82,974 ind. m^{-2}) of Collembola, surpassing reported densities from tropical agricultural environments. This suggests that crop diversification in agroecosystems significantly contributes to soil biodiversity conservation. Moreover, positive correlation was observed between Collembola abundance and major soil elements such as pH, electrical conductivity, phosphorous, nitrogen, and carbon. It is well documented that soil variation in soil arthropod populations are associated with soil parameters such as carbon, moisture, pH, and nitrogen [86]. Given that these soil parameters differed significantly between PPT and maize monoculture cropping soils, this positive correlation between these soil physicochemical properties and collembola abundance is likely associated with the type of cropping system.

We observed differences in Collembola richness and diversity between the two cropping practices, with PPT dominating in genera richness, Shannon, and Pielou indices compared to that of maize monoculture. These differences in Collembola diversity confirm that cropping systems play a crucial role in determining ecological diversity. Consequently, the push-pull system appears to have a less detrimental impact on collembola communities compared to maize monoculture systems. Perhaps, the more favorable euedaphic environment provided by the push-pull cropping system could explain such discrepancies in Collembola richness and diversity. These findings concur with Menta et al. [85], who noted that soil-inhabiting communities are determined by soil type and management practices.

We further noted that in the generic composition and dominance of Collembola communities differed between the two cropping systems. Out of a total of 415,520 ind. m^{-2} genera identified, the *Hypogastrura* genus dominated in PPT, while out of 138,880 ind. m^{-2} genera, *Folsomia* dominated in the maize monoculture cropping systems. The higher diversity of Collembola community in push-pull could also be attributed to other ecological services, such as the reduction in plant pathogenic and mycotoxin fungal communities [29]. Collembola have been shown to predate and graze on plant pathogenic fungi, reducing their abundance in the soils [86]. Nonetheless, some genera, such as *Ceratophysella*, *Neanura*, and

Pygmarrhopalites, were absent in maize monoculture soils but present in PPT. Push-pull companion plants (*Desmodium* and *Brachiaria*) sequester carbon and fix nitrogen [10] and build up organic matter in the soil [73]. Although beyond the scope of this study, the role of each genus in the soil habitat could further explain this phenomenon.

The differences in QBS-c values demonstrated in the study are, therefore, linked to the capability of cropping systems to support adaptive Collembola communities. Collembola genera with the highest EMI score, such as *Hypogastrura,* tended to be more relatively abundant in PPT, while those with low EMI-scores, such as *Folsomia*, were enriched in maize monoculture. The higher the number of Collembola, the higher the QBS-c values, indicating better soil biological quality [59]. Due to the high population of Collembola communities with eu-edaphic adaptations, the PPT system demonstrates its ability to positively impact soil quality. These findings are in agreement with Parisi et al. [60], who demonstrated changes in QBS-c values and Collembola abundance with agricultural activities. Future studies should endeavour to back-up morphological identification to species level using molecular techniques. These findings confirm that the PPT cropping system enhances soil health by increasing QBS-c index values, which are good indicators of soil quality, thereby contributing to the knowledge of the PPT cropping system beyond its well-known impact on soil physicochemical properties.

5. Conclusions

This study has shown that conditioning soil with PPT companion cropping system positively impacts soil physicochemical properties and mesofauna, by improving the soil habitat for the survival and biological activity of collembolan microarthropods. Collembola communities had higher genera abundance, richness, and diversity in fields practicing PPT. As a metric of soil health using biological indicators, higher QBS-c index scores were found more in PPT fields than in maize monoculture fields. Our results provide evidence of another ecosystem service: the conservation and enhancement of soil biota as an additional mechanism contributing to economic benefits observed in smallholder farms practising this cropping system. The current findings contribute to the diversification of ecosystem services provided by this cropping system where it is practiced, enhancing the system's resilience and functionality. While soil for this study was collected in May when the region experienced long rains, successive study to highlight Collembola abundance and diversity at different time and seasons provides deeper understanding of effectiveness of push-pull cropping system in soil biota conservation.

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Data availability

Data will be made available up on request. The number of individuals per genera, for each sample, in both PPT and monoculture systems are provided as Table S1.

CRediT authorship contribution statement

Daniel Munyao Mutyambai: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Johnstone Mutiso Mutua:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Abdul A. Jalloh:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Saliou Niassy:** Writing – review & editing, Resources, Methodology, Conceptualization. **Thomas Dubois:** Writing – review & editing, Supervision, Resources, Investigation. **Zeyaur Khan:** Writing – review & editing, Validation, Project administration, Conceptualization. **Sevgan Subramanian:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition.

Declaration of competing interest

All the authors declare that they have no conflict of interest.

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