

Article

Seasonal Drivers Exert Stronger Effects on Mesofauna Communities than Agricultural Management in Two Contrasting Arable Soils

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Abstract

Soil mesofauna play important roles in soil food webs, organic matter decomposition, and nutrient cycling. We quantified mesofauna responses to tillage, liming, fertilisation, and Geo2 biostimulant application at two Croatian experimental sites differing in soil type and land-use history: a long-term arable Stagnosol in Čačinci and a recently converted Gleysol in Križevci. Mesofauna were sampled in spring and autumn 2023 and analysed using generalised linear mixed-effects models (GLMMs). Seasonal dynamics exerted the strongest influence on mesofauna communities, with Collembola and Acari abundances approximately sixfold and sevenfold higher, respectively, in spring than in autumn. A significant Season $\times$ Location interaction for total Acari and Oribatida indicated a stronger spring increase at Križevci. Liming increased Mesostigmata (+94%) and total Acari (+33%), while recommended fertilisation increased Entomobryomorpha (+78%) and total Collembola (+46%). In contrast, tillage treatments did not significantly affect the abundance of Acari, Collembola, or their major subgroups. The Collembola:Acari ratio remained relatively stable (0.56–0.93), suggesting parallel responses of dominant taxa. Overall, site-specific conditions and seasonal variation exerted stronger effects on soil mesofauna communities than the tested management practices, emphasising the importance of local environmental factors and land-use history in shaping mesofauna community dynamics in agricultural soils.

Keywords: soil mesofauna; Acari; Collembola; conservation tillage; GLMM; Croatia



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1. Introduction

Soil is a fundamental component of terrestrial ecosystems, providing habitat, nutrients and water for diverse biota. Essential ecological processes such as organic matter decomposition, nutrient cycling and carbon sequestration depend on soil biota. However, intensive agricultural practices, including deep ploughing and excessive use of agrochemicals, can lead to soil degradation, compaction, loss of organic matter and decreased soil biodiversity [1].

Soil invertebrates interact within complex soil food webs [2] and are commonly grouped according to body size into macrofauna, mesofauna and microfauna. Mesofauna

comprise small (0.1–2 mm) soil-dwelling animals that contribute to the fragmentation of organic matter, facilitate microbial decomposition processes and nutrient cycling [3,4]. Among these organisms, mites (Acari) and springtails (Collembola) represent the most abundant and functionally important groups. These groups are also sensitive to environmental changes, making them widely used as bioindicators of soil condition and land-use intensity [5].

These organisms occupy different trophic positions within soil food webs. Mesostigmata mites are primarily predators and are frequently used as indicators of soil food-web complexity; Oribatid mites contribute to humus formation and nutrient recycling and are often associated with stable soils rich in organic matter, whereas Prostigmata mites represent a functionally diverse group that includes predators, fungivores and detritivores [6–9]. Within springtails, Entomobryomorpha are typically associated with surface litter and respond rapidly to environmental disturbance. Poduromorpha are mainly soil-dwelling organisms sensitive to soil compaction and structural disturbance; Symphypleona are mainly epigeal species associated with vegetation structure and surface moisture [4,9–11].

Agricultural management practices can strongly influence soil mesofauna communities. Intensive soil disturbance associated with conventional tillage can disrupt soil structure and habitat continuity, often leading to reduced abundance and diversity of soil microarthropods [12,13]. Such disturbance also redistributes soil organisms between soil layers and exposes them to unfavourable environmental conditions. In contrast, reduced or conservation tillage systems characterised by reduced soil disturbance and crop residue retention frequently promote higher abundance of mites and springtails owing to improved soil structure, increased organic matter content and greater habitat stability [14–16].

Additionally, soil amendments such as liming, fertilisation and biostimulants may further influence soil fauna communities by modifying soil physicochemical conditions and microbial activity [17]. Increased soil pH may favour predatory mites but reduce some detritivorous microarthropods [18,19], whereas fertilisation and soil biostimulants can indirectly affect mesofauna by altering microbial biomass and nutrient availability [17,20]. However, responses of soil mesofauna to agricultural practices are often context-dependent and may vary according to soil properties, climate conditions and land-use history [13–15]. In particular, experimental evidence regarding the combined effects of multiple agricultural practices on soil mesofauna communities in arable systems remains limited. Understanding how agricultural practices affect soil biodiversity is therefore important for the development of sustainable agricultural systems that maintain soil ecosystem functions [21].

The aim of this study was to investigate the responses of soil mesofauna communities to different agricultural management practices in arable soils. Specifically, we examined the effects of tillage type (conventional, conservation shallow and conservation deep tillage), liming, fertilisation intensity and biostimulant application on the abundance and structure of soil mesofauna communities. Because biostimulants are increasingly incorporated into sustainable crop management, they were included among the management factors evaluated in the present field experiment. We hypothesised that (i) conservation tillage would support higher abundance than conventional tillage, (ii) soil amendments would elicit taxon-specific responses linked to edaphic context and (iii) seasonal and site effects would interact to shape community composition.

2. Materials and Methods

2.1. Research Sites, Experimental Design and Treatments

The split-split-plot experiment was conducted at Čačinci (CA) (45.6137° N, 17.8627° E) and Križevci (KR) (46.0275° N, 16.5590° E), Croatia. The two experimental sites differ in land-use history and soil characteristics (Table 1, Appendix A Table A1). The Čačinci site

has a history of conventional agricultural use, whereas the Križevci site had been managed as grassland and remained undisturbed for at least 15 years before being converted to an experimental agricultural field in 2021. Mesofauna sampling was therefore conducted after three years of cultivation at this location. At Čačinci, soils are classified as silty clay loam corresponding to the Stagnosol reference group according to the World Reference Base for Soil Resources [22]. These soils are characterised by pseudogley horizons with periodic water saturation below the ploughed layer. In contrast, soils at Križevci are classified as silt loam corresponding to the Gleysol reference group, formed under conditions of periodic groundwater influence [22].

Table 1. Measured soil properties of sampling locations at Čačinci (CA) and Križevci (KR). FC—field water capacity; ρ_b —soil bulk density; ci—cumulative infiltration; SOC—soil organic carbon; SOM—soil organic matter.

KR	CA	
7.3	12.07	Sand (%)
82.60	53.35	Silt (%)
10.10	34.58	Clay (%)
Silt	Silty clay loam	Texture
44.59	34.91	FC (% vol)
1.39	1.64	ρ_b (g cm ^{−3})
80.04	57.33	ci (cm h ^{−1})
1.18	1.42	SOC (%)
2.36	2.84	SOM (%)
Hypogley/Gleysol	Pseudogley/Stagnosol	WRB classification

The experimental design has been described in detail by Jug et al. [23]. The experiment followed a split–split plot design in which tillage type was applied at the main plot level, liming at the subplot level, and fertilisation rate and Geo2 application at the sub-subplot level. The experimental scheme and aerial photo are given in Appendix A Figure A1. Each treatment combination was represented by two separate plots within the same experimental area. Briefly, tillage included three treatments: conventional tillage (ST; ploughing to 30 cm), conservation shallow tillage (CTS; loosening to 10 cm with crop residue $\geq 30\%$ retained on the soil surface), and conservation deep tillage (CTD; loosening to 30 cm with crop residue $\geq 30\%$ retained on the soil surface). Within each tillage treatment, liming was either applied (YL) or not applied (NL). Fertilisation treatments consisted of the recommended fertilisation rate (F1) and a reduced rate (F0.5; 50% of the recommended amount). Fertilisers were applied as NPK (0:20:30) and urea (46% N) during autumn in conjunction with primary tillage, while calcium ammonium nitrate (CAN; 27% N) was applied before sowing in spring. The biophysical activator Geo2 was either applied (YG) or not applied (NG). Geo2 is a commercially available granulated mineral soil activator applied according to the manufacturer’s recommendations (150 kg/ha). It is intended to improve soil physicochemical properties and stimulate soil microbial activity, potentially enhancing nutrient availability and soil biological processes. Maize (*Zea mays* L.) was grown at both sites during the 2023 sampling year.

2.2. Sampling

Sampling was conducted according to the hierarchical split–split plot design during two sampling periods, spring (S) and autumn (A) 2023, at both study sites. Each site and season included 48 samples representing all combinations of tillage, liming, fertilisation and Geo2 treatments, with two replicate samples per treatment combination in a full factorial design collected using a metal corer (5 cm diameter). Each core was treated as

an independent biological replicate. For each treatment combination, one soil core was collected from each of the two separate plots with the same treatment combination. Thus, the two replicate samples represented plot-level biological replicates rather than technical subsamples taken from the same plot. A total of 192 samples were processed. All samples were placed in labelled plastic bags and stored at 4 °C until further processing (no longer than ten days). Soil mesofauna was extracted using a Berlese–Tullgren apparatus for 72 h under a temperature gradient of approximately 30–40 °C. Extracted organisms were preserved in 96% ethanol. Each sample was subsequently transferred to a Petri dish (9 cm diameter) and scanned using an EPSON Perfection V600 scanner (Seiko Epson Corporation, Suwa, Nagano, Japan) at a resolution of 3200 dpi [24]. The digital images were analysed using ImageJ software (version 1.54k) [25], and the samples were further analysed under the stereomicroscope.

All organisms were counted and classified into taxonomic groups according to Coleman [4]. The total number of Acari, Collembola, Protura, Diplura, Insecta and Myriapoda were recorded. Some groups were further classified into lower taxonomic levels: mites into Mesostigmata, Oribatida and Prostigmata; springtails into Entomobryomorpha, Poduromorpha and Symphypleona; insects into Coleoptera and Diptera; and Myriapoda into Symphyla, Diplopoda, Pauropoda and Chilopoda.

2.3. Data Analysis

All statistical analyses were conducted in R [26]. Abundance data were analysed using generalised linear mixed-effects models (GLMMs) implemented in the *glmmTMB* package (version 1.1.14) [27]. As the count data exhibited overdispersion, models were fitted using a negative binomial error distribution (*nbinom2*) with a log-link function. Separate models were fitted for total Acari, total Collembola, and each major subgroup (Oribatida, Mesostigmata, Prostigmata, Entomobryomorpha, Poduromorpha, and Symphypleona/Neelipleona).

For each response variable (Y), an initial additive model was fitted:

$$Y \sim \text{Loc} + \text{Sea} + \text{Till} + \text{Fert} + \text{Calc} + \text{Geo2} + (1 \mid \text{Plot}) + (1 \mid \text{ObsID}) \quad (1)$$

where Loc (location: Čačinci, Križevci) and Sea (season: autumn, spring) were included as fixed effects, while tillage, fertilisation, liming (Calc) and GeO₂ application represented management treatments. Plot was included as a random intercept to account for the split–split plot experimental design, representing subplots nested within blocks. An observation-level random effect (ObsID) was included where necessary to account for residual overdispersion.

A Season × Location interaction was tested for each response variable using likelihood-ratio tests and AIC-based model comparison. The interaction term was retained for total Acari ($\Delta\text{AIC} = -4.8$, $p = 0.009$) and Oribatida ($\Delta\text{AIC} = -11.0$, $p < 0.001$), but was not supported for the remaining taxa (all $p > 0.07$; Appendix A Table A2) and was therefore excluded from their final models. Model assumptions were evaluated using the *DHARMa* package (version 0.5.0) [28] by inspecting simulated residuals and testing for overdispersion and zero inflation. No substantial deviations from model assumptions were detected in the final models. Model coefficients are reported on the log scale. For ease of interpretation, percentage changes relative to reference levels were calculated as $(\exp(\beta) - 1) \times 100$. Statistical significance was assessed at $\alpha = 0.05$. Post hoc estimated marginal means (EMMs) with 95% confidence intervals were obtained using the *emmeans* (version 2.0.3) package [29] where relevant for graphical presentation.

3. Results

3.1. Abundance and Community Structure

A total of 4809 individuals were extracted from both study sites. Acari represented the dominant group (56.7%), followed by Collembola (34.4%), whereas other taxa (Insecta, Diplura, Protura and Myriapoda) together accounted for 8.9% of the community (Figure 1A). Within Acari, Oribatida was the dominant subgroup (48.4%), followed by Mesostigmata (4.6%) and Prostigmata (3.7%) (Figure 1B). Among Collembola, Entomobryomorpha was the most abundant subgroup (24.4%), whereas Poduromorpha (7.5%) and Symphypleona + Neelipleona (2.5%) occurred at lower proportions (Figure 1C).

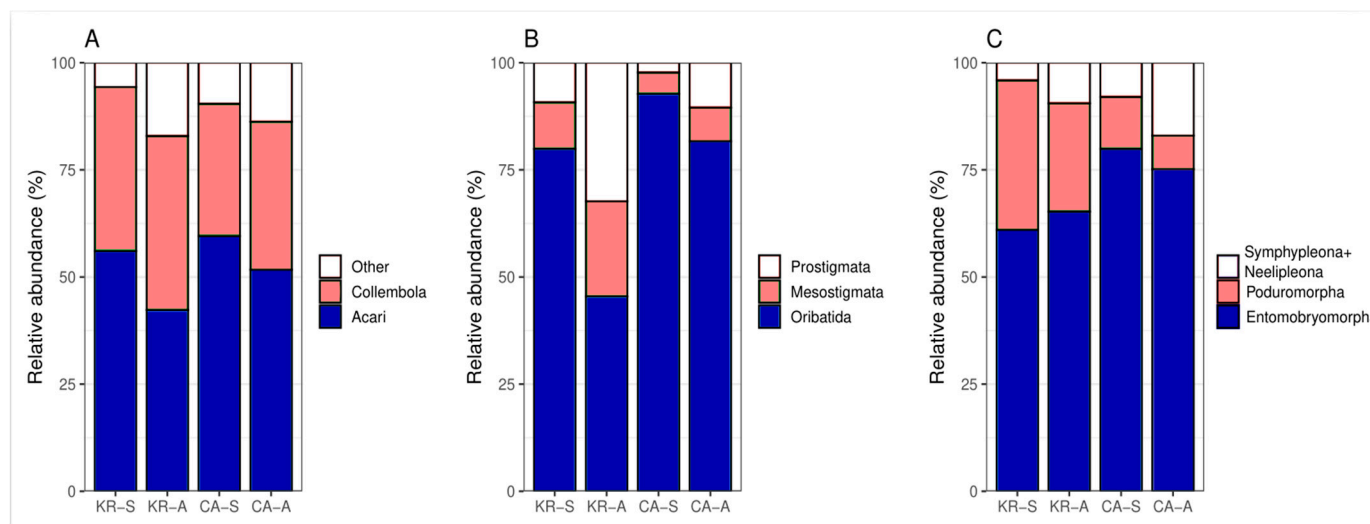


Figure 1. Relative abundance (%) of major soil mesofauna groups across locations and seasons. (A) Relative abundance of Acari, Collembola, and other mesofaunal groups. (B) Relative abundance of the dominant mite groups within Acari (Oribatida, Mesostigmata, and Prostigmata). (C) Relative abundance of the dominant collembolan groups within Collembola (Entomobryomorpha, Poduromorpha, and Symphypleona + Neelipleona). KR = Križevci; CA = Čačinci; S = spring; A = autumn.

Total mesofauna abundance varied significantly with location and season (Figure A2). Abundance was consistently higher in spring than in autumn at both sites ($p < 0.001$), while location also had a significant effect ($p < 0.001$). The interaction between location and season was not significant. Predicted abundances derived from GLMMs revealed pronounced seasonal patterns across taxa (Figure 2). Total Acari abundance was approximately sevenfold higher in spring than in autumn ($\beta = 1.95$, $p < 0.001$), whereas total Collembola abundance was approximately sixfold higher ($\beta = 1.80 \pm 0.16$, $z = 11.49$, $p < 0.001$). Oribatida showed the strongest seasonal response, with abundances approximately ninefold higher in spring ($z = 13.76$, $p < 0.001$).

Site effects were weaker and taxon-specific. Total Acari abundance was significantly lower at Križevci (KR) than at Čačinci (CA) ($p < 0.01$), whereas total Collembola abundance did not differ significantly between sites. Oribatida ($p < 0.001$), Entomobryomorpha ($p < 0.05$) and Symphypleona + Neelipleona ($p < 0.01$) were less abundant at KR, while Poduromorpha and Prostigmata were more abundant at KR ($p < 0.01$) (Figure 1B,C). Mesostigmata showed no significant differences between locations (Figure 1B).

The Collembola/Acari ratio varied only slightly and did not differ significantly among soil management treatments (Table 2). Across treatments, the values indicated relatively balanced abundances of the two dominant groups. Seasonal means ranged from 0.56 to 0.93, with KR showing a slightly higher ratio in autumn (0.93; 95% CI 0.71–1.22). Slightly higher values were observed under conventional tillage than under conservation treat-

ments, whereas liming, fertilisation and Geo2 application produced only minor differences among treatments.

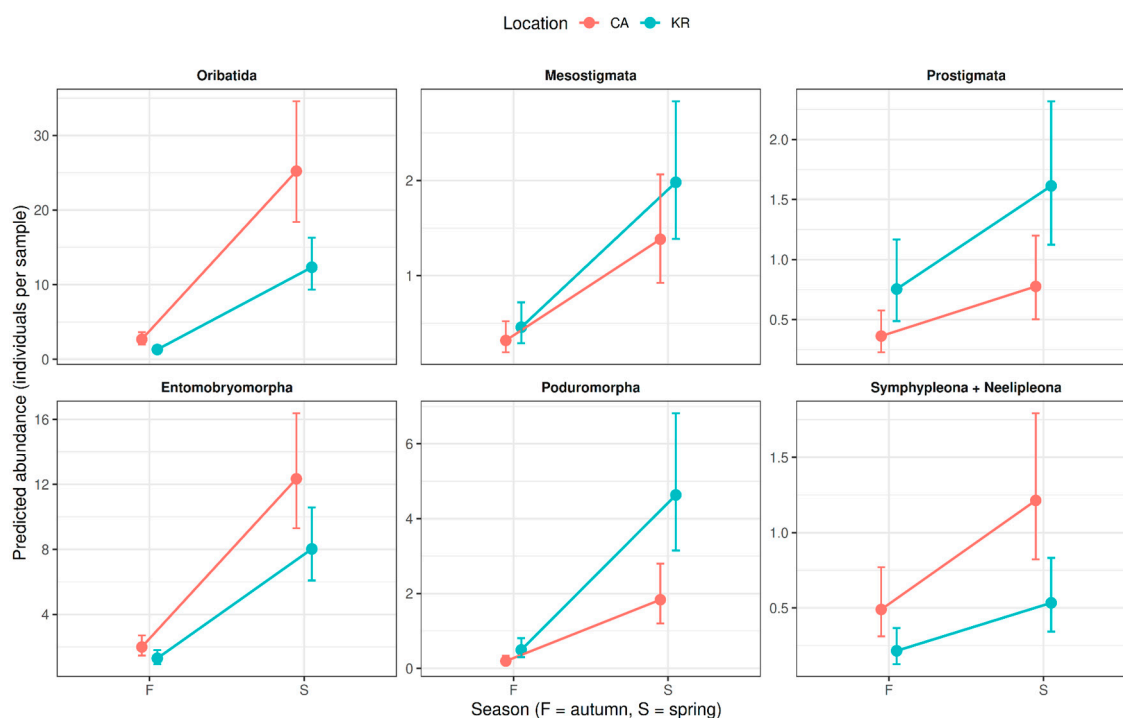


Figure 2. Predicted abundance of Acari and Collembola subgroups across seasons and locations derived from generalised linear mixed-effects models (GLMMs) fitted with a negative binomial distribution (nbinom2, log-link). Models included Location, Season, Tillage, Fertilisation, Liming (Calc), and Geo2 as fixed effects and plot identity as a random intercept. Points represent model-estimated marginal means on the response scale (individuals per sample), and error bars indicate 95% confidence intervals. Location. Čačinci (CA), Križevci (KR).

Table 2. Estimated marginal means (EMMs) of the log-transformed Collembola:Acari ratio and back-transformed values across seasons and locations (CA—Čačinci, KR—Križevci).

Season	Location	EMM (Log Scale)	Ratio (Back-Transformed)
Autumn	CA	-0.43 ± 0.14	0.65 (0.49–0.85)
Spring	CA	-0.58 ± 0.14	0.56 (0.42–0.74)
Autumn	KR	-0.07 ± 0.14	0.93 (0.71–1.22)
Spring	KR	-0.41 ± 0.14	0.66 (0.50–0.87)

3.2. Effect of Tillage

Across all treatments and sites, Acari and Collembola remained the dominant components of the mesofauna community, whereas other taxa occurred at low abundances and frequently exhibited zero counts. Consequently, subsequent analyses focused primarily on these groups and their principal subgroups.

GLMMs detected no significant effects of tillage on total Acari, total Collembola or their subgroups (all $p > 0.05$). Season $\times$ Site EMMs emphasised that seasonal variation dominated observed trends, with tillage contrasts remaining within $\pm 15\%$ of the reference treatment for most taxa.

Descriptive patterns suggested site-specific differences: at CA, CTD generally supported the highest abundances, followed by ST and CTS, whereas at KR the highest values occurred under CTS and the lowest under ST.

3.3. Effects of Soil Amendments

Responses to soil amendments were taxon- and site-specific and generally weaker than seasonal effects (Figure 3). Across both sites, liming significantly increased total Acari abundance ($p < 0.05$), primarily driven by a positive response of Mesostigmata ($z = 2.92$, $p = 0.003$), whereas Poduromorpha decreased significantly under liming ($z = -2.68$, $p = 0.007$) (Appendix A Table A3). At Čačinci (CA), liming was associated with higher abundances of several taxa, including Entomobryomorpha, Mesostigmata, Prostigmata and Oribatida. GLMM analyses confirmed significantly higher abundance of Mesostigmata ($p = 0.046$) and total mesofauna abundance ($p = 0.0021$) in limed plots. In contrast, Poduromorpha and Symphypleona tended to be more abundant in non-limed soil. At Križevci (KR), responses to liming were more variable. Prostigmata showed significantly higher abundance in limed soil ($p = 0.033$), whereas other taxa exhibited only minor differences between treatments.

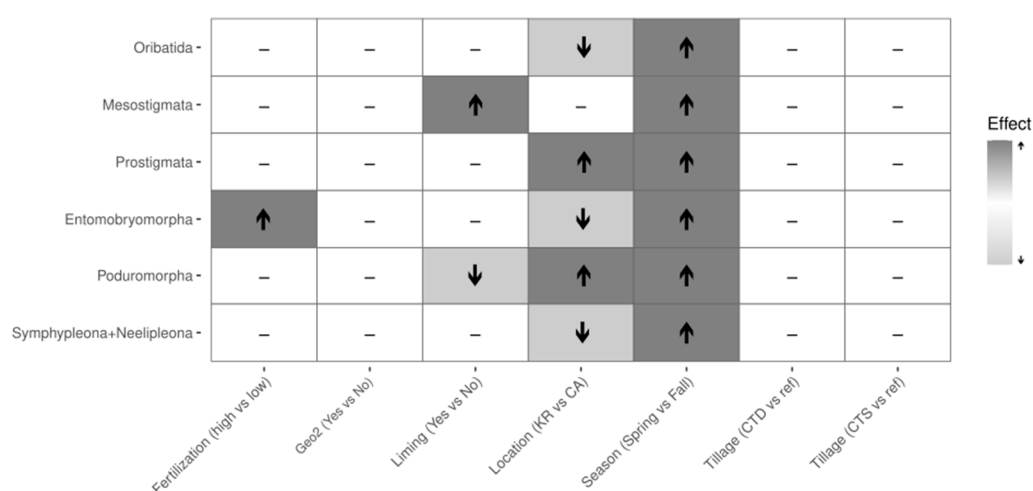


Figure 3. Direction and significance of fixed effects across mesofauna groups based on GLMM analyses. Arrows indicate statistically significant effects ($p < 0.05$): ↑ indicates an increase, ↓ indicates a decrease relative to the referent level, – indicates a non-significant effect. Estimates are derived from models with a negative binomial error structure and plot identity included as a random intercept. Location: Križevci (KR), Čačinci (CA); tillage: ST—convention, CTD—conservation tillage deep, CTS—conservation tillage shallow. Referent levels: location: KR (Križevci), season: F (autumn) and tillage: ST (conventional).

Fertilisation generally increased the abundance of several Collembola groups. Entomobryomorpha abundance was significantly higher under the recommended fertilisation rate (F1) at both sites (CA: $p = 0.021$; KR: $p = 0.0084$), with predicted abundances approximately 78% greater under higher fertilisation ($z = 3.30$, $p = 0.001$). Total mesofauna abundance was also significantly higher under F1 at KR.

In contrast, application of the Geo2 biostimulant produced weak and inconsistent responses and had no significant effects on the major taxa.

4. Discussion

The results indicate that site characteristics and land-use history were important factors shaping soil mesofauna communities. Although both experimental sites were managed under the same experimental design, clear differences in community composition were observed between Čačinci (CA) and Križevci (KR). The KR site generally supported a greater number of taxa. These differences likely reflect contrasting soil properties and previous land management. The CA site has a long history of intensive agricultural use, which may have favoured taxa tolerant of frequent soil disturbance and mechanical soil

inversion. In contrast, the KR site had been managed as grassland for more than 15 years before being converted to agricultural use only three years prior to sampling. Such a relatively recent transition may allow soil communities to retain characteristics associated with less intensively disturbed systems. Previous studies have shown that land-use history can strongly influence soil fauna responses to agricultural management [13,30]. However, because the two study sites differed simultaneously in soil type, physicochemical properties, and land-use history, the present design does not allow the effects of land-use history to be fully separated from those of local edaphic conditions. Therefore, site-related differences should be interpreted as the combined influence of land-use history and soil properties rather than as the effect of either factor alone. We further note that cation exchange capacity and soil organic carbon fractions (labile versus stable) were not determined; soil characterisation was based on texture, pH (H₂O) and total SOC (Appendix A Table A1).

The dominance of Oribatida observed at both sites is consistent with their ecological traits. Oribatid mites are often well adapted to agricultural environments due to their protective cuticle, slow life cycle and ability to tolerate disturbance [6,31]. More generally, soil properties such as texture, bulk density and moisture conditions interact with functional traits of soil organisms and influence mesofauna community composition in agricultural soils [11].

Responses of soil mesofauna to the management practices were generally moderate and taxon-specific. Although descriptive patterns suggested differences among tillage treatments, statistical analyses did not detect significant effects of tillage on total Acari, Collembola or their major subgroups. This suggests that the response of soil mesofauna to tillage may depend strongly on local soil conditions and previous land-use history. Similar context-dependent responses have been reported by Fiera et al. [32], who found that tillage intensity significantly affected the composition and activity density of surface-active Collembola communities in vineyards. Therefore, the absence of significant tillage effects should be interpreted cautiously. The limited number of sampling periods, together with the high spatial and temporal variability typical of soil fauna communities, may have reduced the statistical power to detect small management effects and higher-order interactions. At the KR site, conservation tillage tended to support higher abundance than conventional tillage. Reduced soil disturbance can promote soil fauna by maintaining soil structure, organic matter content and pore connectivity, and similar trends have been reported in studies showing increased abundance of mites and springtails under reduced or no-tillage systems [15,33]. In contrast, at the CA site several dominant taxa showed higher abundances under conventional tillage. This pattern may reflect long-term adaptation of soil communities to repeated disturbance, as intensive management may favour disturbance-tolerant taxa capable of persisting under continuous mechanical soil disturbance [6,34].

Liming and fertilisation showed more taxon-specific responses. Increased Mesostigmata abundance and total mesofauna abundance under liming at CA suggest that increased soil pH (from 6.06 to 6.63) may enhance predator activity and trophic interactions. Changes in soil pH are known to influence the distribution and abundance of soil mites through effects on microbial activity and nutrient availability [19,35]. Fertilisation may indirectly stimulate mesofauna populations by increasing microbial biomass and food availability [36]. However, responses differed among taxa, suggesting that fertilisation effects are mediated by trophic interactions and local soil conditions. These contrasting responses among taxa likely reflect differences in ecological traits and trophic roles. Collembola, particularly Entomobryomorpha, are closely associated with microbial resources and often respond rapidly to increases in microbial biomass. In contrast, predatory mites such as Mesostigmata may respond more indirectly through changes in prey availability within the soil food web.

Soil organic matter and microbial activity represent key drivers of food availability for soil fauna [37], and biostimulants may influence these processes by modifying microbial activity and soil physicochemical properties. However, such responses are often strongly site-dependent [38], which may explain the limited response observed in this study. The Geo2 biostimulant showed negligible effects on all mesofauna groups. This result is consistent with the currently limited experimental evidence on this product's direct and indirect effects on soil biota, as controlled field studies remain sparse. Consequently, the biological mechanisms proposed for this product—stimulation of soil microflora and humification processes—remain insufficiently characterised under field conditions. The absence of a detectable mesofauna response may reflect either a genuine lack of effect at the tested dose and timescale, or the need for longer exposure periods before indirect trophic pathways propagate to the fauna level.

Despite some taxon-specific responses, the overall structure of the mesofauna community remained relatively stable across treatments. The Collembola/Acari ratio showed only minor variation among management treatments, indicating relatively balanced abundances of the two dominant groups. Soil mesofauna communities are often considered relatively resilient to disturbance due to their high functional redundancy, complex trophic interactions and the ability of many taxa to recolonise disturbed habitats [21,39]. Nevertheless, agricultural intensification can influence the abundance of particular soil fauna groups, particularly mites and springtails. Large-scale studies have shown that increasing agricultural intensity may simplify soil food webs and reduce biodiversity in important soil fauna groups such as Collembola and oribatid mites [13]. Differences observed between sites in the present study further highlight that local environmental conditions may influence how soil mesofauna responds to agricultural management. Overall, the results suggest that seasonal dynamics and site-specific conditions acted as stronger effects on mesofauna communities than the tested management practices.

The present study represents a short-term assessment of soil mesofauna responses to experimental agricultural management. Because the KR site was converted from grassland only three years before sampling, the observed community structure likely reflects transitional stages of soil ecosystem development. Soil fauna communities often require several years or even decades to fully respond to land-use changes [13,33]. Soil biodiversity plays a crucial role in maintaining soil food-web stability and ecosystem functioning [39,40]. Therefore, long-term monitoring and broader studies are needed to better understand how agricultural practices influence soil biodiversity and ecosystem processes over time.

5. Conclusions

Seasonal dynamics and site-specific conditions had stronger effects on soil mesofauna communities than the tested management practices. Tillage did not significantly influence the abundance of Acari, Collembola or their subgroups, although conservation tillage tended to support higher abundance at one site. Soil amendments showed taxon-specific responses: liming increased Acari abundance, particularly that of Mesostigmata, while fertilisation increased Entomobryomorpha abundance. In contrast, the Geo2 biostimulant produced weak and inconsistent effects. Overall, the results indicate that agricultural practices in the short term primarily influence the dominance of individual taxa rather than causing major shifts in mesofauna community structure. These findings highlight the importance of local environmental conditions when evaluating the effects of soil management on soil mesofauna communities.

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analysis, writing—review and editing, B.H.K.; supervision, formal analysis, writing—original draft, D.H.K. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Processed data and R scripts are available from the corresponding author upon reasonable request.

Conflicts of Interest: Author Branimir Hackenberger Kutuzović was employed by the company SCION. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A

Table A1. Soil physico-chemical parameters included soil texture (sand, silt, clay), soil pH (H₂O), and soil organic carbon (SOC) at two experimental sites: Čačinci (CA) and Križevci (KR), and under different tillage—conventional tillage system (ST), conservation tillage system-deep (CTD), and conservation tillage system-shallow (CTS), with the application of liming (YL) or without (NL). Fertilisation comprised the recommended quantity of NPK, urea and CAN (calcium ammonium nitrate) (F1) and 50% of the recommended amount (F0.5). The biophysiological soil activator Geo2 was either applied (YG) or not (NG). Parameters are measured at three depths: 0–10, 10–20 and 20–30 cm.

Location	Field	Depth (cm)	Tillage	Liming	Fertilisation	Geo2	Sand (%)	Silt (%)	Clay (%)	pH (H ₂ O)	SOC (%)
CA	1	0–10	ST	NL	F0.5	NG	12.36	55.82	31.82	5.95	1.25
CA	1	10–20	ST	NL	F0.5	NG	12.33	54.13	33.54	6	1.35
CA	1	20–30	ST	NL	F0.5	NG	12.33	54.13	33.54	6	1.35
CA	2	0–10	ST	NL	F1	NG	12.36	55.82	31.82	6.04	1.33
CA	2	10–20	ST	NL	F1	NG	12.33	54.13	33.54	5.95	1.53
CA	2	20–30	ST	NL	F1	NG	12.33	54.13	33.54	5.95	1.53
CA	3	0–10	ST	NL	F0.5	YG	12.36	55.82	31.82	5.95	1.44
CA	3	10–20	ST	NL	F0.5	YG	12.33	54.13	33.54	6.05	1.44
CA	3	20–30	ST	NL	F0.5	YG	12.33	54.13	33.54	6.05	1.44
CA	4	0–10	ST	NL	F1	YG	12.36	55.82	31.82	6.17	1.53
CA	4	10–20	ST	NL	F1	YG	12.33	54.13	33.54	6.18	1.48
CA	4	20–30	ST	NL	F1	YG	12.33	54.13	33.54	6.18	1.48
CA	5	0–10	CTD	NL	F0.5	NG	11.81	54.14	34.05	6.18	1.55
CA	5	10–20	CTD	NL	F0.5	NG	12.18	52.59	35.23	6.25	1.38
CA	5	20–30	CTD	NL	F0.5	NG	12.18	52.59	35.23	6.25	1.38
CA	6	0–10	CTD	NL	F1	NG	11.81	54.14	34.05	6.38	1.46
CA	6	10–20	CTD	NL	F1	NG	12.18	52.59	35.23	6.27	1.38
CA	6	20–30	CTD	NL	F1	NG	12.18	52.59	35.23	6.27	1.38
CA	7	0–10	CTD	NL	F0.5	YG	11.81	54.14	34.05	6.24	1.55
CA	7	10–20	CTD	NL	F0.5	YG	12.18	52.59	35.23	6.27	1.55
CA	7	20–30	CTD	NL	F0.5	YG	12.18	52.59	35.23	6.27	1.55
CA	8	0–10	CTD	NL	F1	YG	11.81	54.14	34.05	6.26	1.42
CA	8	10–20	CTD	NL	F1	YG	12.18	52.59	35.23	6.24	1.23
CA	8	20–30	CTD	NL	F1	YG	12.18	52.59	35.23	6.24	1.23
CA	9	0–10	CTS	NL	F0.5	NG	11.55	54.64	33.81	6.02	1.63
CA	9	10–20	CTS	NL	F0.5	NG	11.29	54.49	34.22	5.98	1.47
CA	9	20–30	CTS	NL	F0.5	NG	11.29	54.49	34.22	5.98	1.47
CA	10	0–10	CTS	NL	F1	NG	11.55	54.64	33.81	5.73	1.35
CA	10	10–20	CTS	NL	F1	NG	11.29	54.49	34.22	5.82	1.25
CA	10	20–30	CTS	NL	F1	NG	11.29	54.49	34.22	5.82	1.25
CA	11	0–10	CTS	NL	F0.5	YG	11.55	54.64	33.81	5.83	1.32
CA	11	10–20	CTS	NL	F0.5	YG	11.29	54.49	34.22	5.75	1.29
CA	11	20–30	CTS	NL	F0.5	YG	11.29	54.49	34.22	5.75	1.29

Table A1. Cont.

Location	Field	Depth (cm)	Tillage	Liming	Fertilisation	Geo2	Sand (%)	Silt (%)	Clay (%)	pH (H ₂ O)	SOC (%)
CA	12	0–10	CTS	NL	F1	YG	11.55	54.64	33.81	5.89	1.13
CA	12	10–20	CTS	NL	F1	YG	11.29	54.49	34.22	5.93	1.12
CA	12	20–30	CTS	NL	F1	YG	11.29	54.49	34.22	5.93	1.12
CA	13	0–10	CTS	YL	F1	YG	11.55	54.64	33.81	6.72	1.26
CA	13	10–20	CTS	YL	F1	YG	11.29	54.49	34.22	6.87	1.24
CA	13	20–30	CTS	YL	F1	YG	11.29	54.49	34.22	6.87	1.24
CA	14	0–10	CTS	YL	F0.5	YG	11.55	54.64	33.81	7.72	1.33
CA	14	10–20	CTS	YL	F0.5	YG	11.29	54.49	34.22	7.60	1.32
CA	14	20–30	CTS	YL	F0.5	YG	11.29	54.49	34.22	7.60	1.32
CA	15	0–10	CTS	YL	F1	NG	11.55	54.64	33.81	6.23	1.51
CA	15	10–20	CTS	YL	F1	NG	11.29	54.49	34.22	6.65	1.47
CA	15	20–30	CTS	YL	F1	NG	11.29	54.49	34.22	6.65	1.47
CA	16	0–10	CTS	YL	F0.5	NG	11.55	54.64	33.81	6.17	1.50
CA	16	10–20	CTS	YL	F0.5	NG	11.29	54.49	34.22	6.29	1.52
CA	16	20–30	CTS	YL	F0.5	NG	11.29	54.49	34.22	6.29	1.52
CA	17	0–10	CTD	YL	F1	YG	11.81	54.14	34.05	6.51	1.43
CA	17	10–20	CTD	YL	F1	YG	12.18	52.59	35.23	6.61	1.47
CA	17	20–30	CTD	YL	F1	YG	12.18	52.59	35.23	6.61	1.47
CA	18	0–10	CTD	YL	F0.5	YG	11.81	54.14	34.05	6.45	1.57
CA	18	10–20	CTD	YL	F0.5	YG	12.18	52.59	35.23	6.41	1.55
CA	18	20–30	CTD	YL	F0.5	YG	12.18	52.59	35.23	6.41	1.55
CA	19	0–10	CTD	YL	F1	NG	11.81	54.14	34.05	7.04	1.40
CA	19	10–20	CTD	YL	F1	NG	12.18	52.59	35.23	7.07	1.38
CA	19	20–30	CTD	YL	F1	NG	12.18	52.59	35.23	7.07	1.38
CA	20	0–10	CTD	YL	F0.5	NG	11.81	54.14	34.05	6.46	1.38
CA	20	10–20	CTD	YL	F0.5	NG	12.18	52.59	35.23	6.49	1.36
CA	20	20–30	CTD	YL	F0.5	NG	12.18	52.59	35.23	6.49	1.36
CA	21	0–10	ST	YL	F1	YG	12.36	55.82	31.82	6.44	1.43
CA	21	10–20	ST	YL	F1	YG	12.33	54.13	33.54	6.44	1.36
CA	21	20–30	ST	YL	F1	YG	12.33	54.13	33.54	6.44	1.36
CA	22	0–10	ST	YL	F0.5	YG	12.36	55.82	31.82	6.32	1.48
CA	22	10–20	ST	YL	F0.5	YG	12.33	54.13	33.54	7.01	1.56
CA	22	20–30	ST	YL	F0.5	YG	12.33	54.13	33.54	7.01	1.56
CA	23	0–10	ST	YL	F1	NG	12.36	55.82	31.82	6.42	1.66
CA	23	10–20	ST	YL	F1	NG	12.33	54.13	33.54	6.34	1.44
CA	23	20–30	ST	YL	F1	NG	12.33	54.13	33.54	6.34	1.44
CA	24	0–10	ST	YL	F0.5	NG	12.36	55.82	31.82	6.21	1.58
CA	24	10–20	ST	YL	F0.5	NG	12.33	54.13	33.54	6.28	1.56
CA	24	20–30	ST	YL	F0.5	NG	12.33	54.13	33.54	6.28	1.56
KR	1	0–10	ST	NL	F0.5	NG	7.84	82.20	9.97	7.44	0.98
KR	1	10–20	ST	NL	F0.5	NG	7.57	82.06	10.37	7.11	1.12
KR	1	20–30	ST	NL	F0.5	NG	7.57	82.06	10.37	7.11	1.12
KR	2	0–10	ST	NL	F1	NG	7.84	82.20	9.97	7.24	1.07
KR	2	10–20	ST	NL	F1	NG	7.57	82.06	10.37	7.35	0.95
KR	2	20–30	ST	NL	F1	NG	7.57	82.06	10.37	7.35	0.95
KR	3	0–10	ST	NL	F0.5	YG	7.84	82.20	9.97	6.79	1.07
KR	3	10–20	ST	NL	F0.5	YG	7.57	82.06	10.37	6.41	1.17
KR	3	20–30	ST	NL	F0.5	YG	7.57	82.06	10.37	6.41	1.17
KR	4	0–10	ST	NL	F1	YG	7.84	82.20	9.97	6.46	1.21
KR	4	10–20	ST	NL	F1	YG	7.57	82.06	10.37	6.41	1.11
KR	4	20–30	ST	NL	F1	YG	7.57	82.06	10.37	6.41	1.11
KR	5	0–10	CTD	NL	F0.5	NG	7.91	82.36	9.73	6.22	1.07
KR	5	10–20	CTD	NL	F0.5	NG	7.86	82.27	9.87	6.20	1.08
KR	5	20–30	CTD	NL	F0.5	NG	7.86	82.27	9.87	6.20	1.08
KR	6	0–10	CTD	NL	F1	NG	7.91	82.36	9.73	5.95	1.08
KR	6	10–20	CTD	NL	F1	NG	7.86	82.27	9.87	6.60	1.04
KR	6	20–30	CTD	NL	F1	NG	7.86	82.27	9.87	6.60	1.04

Table A1. Cont.

Location	Field	Depth (cm)	Tillage	Liming	Fertilisation	Geo2	Sand (%)	Silt (%)	Clay (%)	pH (H ₂ O)	SOC (%)
KR	7	0–10	CTD	NL	F0.5	YG	7.91	82.36	9.73	6.07	1.26
KR	7	10–20	CTD	NL	F0.5	YG	7.86	82.27	9.87	6.42	1.20
KR	7	20–30	CTD	NL	F0.5	YG	7.86	82.27	9.87	6.42	1.20
KR	8	0–10	CTD	NL	F1	YG	7.91	82.36	9.73	6.57	1.06
KR	8	10–20	CTD	NL	F1	YG	7.86	82.27	9.87	6.70	1.26
KR	8	20–30	CTD	NL	F1	YG	7.86	82.27	9.87	6.70	1.26
KR	9	0–10	CTS	NL	F0.5	NG	7.55	83.61	8.84	6.99	1.21
KR	9	10–20	CTS	NL	F0.5	NG	6.82	83.11	10.06	7	1.29
KR	9	20–30	CTS	NL	F0.5	NG	6.82	83.11	10.06	7	1.29
KR	10	0–10	CTS	NL	F1	NG	7.55	83.61	8.84	7.01	1.23
KR	10	10–20	CTS	NL	F1	NG	6.82	83.11	10.06	6.61	1.24
KR	10	20–30	CTS	NL	F1	NG	6.82	83.11	10.06	6.61	1.24
KR	11	0–10	CTS	NL	F0.5	YG	7.55	83.61	8.84	6.68	1.13
KR	11	10–20	CTS	NL	F0.5	YG	6.82	83.11	10.06	6.77	1.24
KR	11	20–30	CTS	NL	F0.5	YG	6.82	83.11	10.06	6.77	1.24
KR	12	0–10	CTS	NL	F1	YG	7.55	83.61	8.84	6.85	1.32
KR	12	10–20	CTS	NL	F1	YG	6.82	83.11	10.06	6.75	1.22
KR	12	20–30	CTS	NL	F1	YG	6.82	83.11	10.06	6.75	1.22
KR	13	0–10	CTS	YL	F1	YG	7.55	83.61	8.84	6.45	1.14
KR	13	10–20	CTS	YL	F1	YG	6.82	83.11	10.06	6.32	1.20
KR	13	20–30	CTS	YL	F1	YG	6.82	83.11	10.06	6.32	1.20
KR	14	0–10	CTS	YL	F0.5	YG	7.55	83.61	8.84	6.36	1.24
KR	14	10–20	CTS	YL	F0.5	YG	6.82	83.11	10.06	6.45	1.15
KR	14	20–30	CTS	YL	F0.5	YG	6.82	83.11	10.06	6.45	1.15
KR	15	0–10	CTS	YL	F1	NG	7.55	83.61	8.84	6.55	1.21
KR	15	10–20	CTS	YL	F1	NG	6.82	83.11	10.06	6.47	1.47
KR	15	20–30	CTS	YL	F1	NG	6.82	83.11	10.06	6.47	1.47
KR	16	0–10	CTS	YL	F0.5	NG	7.55	83.61	8.84	6.53	1.50
KR	16	10–20	CTS	YL	F0.5	NG	6.82	83.11	10.06	6.47	1.35
KR	16	20–30	CTS	YL	F0.5	NG	6.82	83.11	10.06	6.47	1.35
KR	17	0–10	CTD	YL	F1	YG	7.91	82.36	9.73	6.49	1.29
KR	17	10–20	CTD	YL	F1	YG	7.86	82.27	9.87	6.61	1.23
KR	17	20–30	CTD	YL	F1	YG	7.86	82.27	9.87	6.61	1.23
KR	18	0–10	CTD	YL	F0.5	YG	7.91	82.36	9.73	6.61	1.15
KR	18	10–20	CTD	YL	F0.5	YG	7.86	82.27	9.87	6.67	1.18
KR	18	20–30	CTD	YL	F0.5	YG	7.86	82.27	9.87	6.67	1.18
KR	19	0–10	CTD	YL	F1	NG	7.91	82.36	9.73	6.74	1.25
KR	19	10–20	CTD	YL	F1	NG	7.86	82.27	9.87	6.61	1.23
KR	19	20–30	CTD	YL	F1	NG	7.86	82.27	9.87	6.61	1.23
KR	20	0–10	CTD	YL	F0.5	NG	7.91	82.36	9.73	6.47	1.20
KR	20	10–20	CTD	YL	F0.5	NG	7.86	82.27	9.87	6.63	1.24
KR	20	20–30	CTD	YL	F0.5	NG	7.86	82.27	9.87	6.63	1.24
KR	21	0–10	ST	YL	F1	YG	7.84	82.20	9.97	6.74	1.07
KR	21	10–20	ST	YL	F1	YG	7.57	82.06	10.37	6.68	0.97
KR	21	20–30	ST	YL	F1	YG	7.57	82.06	10.37	6.68	0.97
KR	22	0–10	ST	YL	F0.5	YG	7.84	82.20	9.97	6.63	1.03
KR	22	10–20	ST	YL	F0.5	YG	7.57	82.06	10.37	6.74	1.07
KR	22	20–30	ST	YL	F0.5	YG	7.57	82.06	10.37	6.74	1.07
KR	23	0–10	ST	YL	F1	NG	7.84	82.20	9.97	7.90	1.25
KR	23	10–20	ST	YL	F1	NG	7.57	82.06	10.37	7.67	1.17
KR	23	20–30	ST	YL	F1	NG	7.57	82.06	10.37	7.67	1.17
KR	24	0–10	ST	YL	F0.5	NG	7.84	82.20	9.97	7.03	1.20
KR	24	10–20	ST	YL	F0.5	NG	7.57	82.06	10.37	6.93	1.19
KR	24	20–30	ST	YL	F0.5	NG	7.57	82.06	10.37	6.93	1.19

Table A2. Likelihood-ratio tests of the Season $\times$ Location interaction for each analysed mesofauna response variable. Each interaction model was compared with the corresponding additive model (Location + Season + Tillage + Fertilisation + Liming + Geo2) fitted with the same random-effects structure. χ^2 = likelihood-ratio test statistic; df = degrees of freedom; Δ AIC = AIC (interaction) – AIC (additive), with negative values indicating support for the interaction. The interaction was retained in the final models only for total Acari and Oribatida ($p < 0.05$).

Response Variable	χ^2	df	p -Value	Δ AIC	Interaction Retained
Total Acari	6.84	1	0.009	−4.8	Yes
Oribatida	12.97	1	<0.001	−11.0	Yes
Mesostigmata	0.42	1	0.518	+1.6	No
Prostigmata	3.19	1	0.074	−1.2	No
Total Collembola	1.74	1	0.188	+0.3	No
Entomobryomorpha	0.27	1	0.603	+1.7	No
Poduromorpha	0.57	1	0.450	+1.4	No
Symphyleona + Neelipleona	0.62	1	0.431	+1.4	No

Table A3. Parameter estimates of the generalised linear mixed-effects models (GLMMs) fitted for each analysed mesofauna group. Estimates are presented on the log scale together with their standard errors (SE), z-values and associated p -values.

Group	Term	Estimate	Std. Error	z Value	Pr(> z)
Oribatida	(Intercept)	0.7213605401	0.2480277136	2.908386848	0.003632986221
Oribatida	LocationKR	−0.7154306348	0.1602310127	−4.464994778	8.01×10^{-6}
Oribatida	SeasonS	2.244076444	0.1630573197	13.7625005	4.28×10^{-43}
Oribatida	TillageCTD	0.1865259186	0.1940189653	0.9613798234	0.3363612254
Oribatida	TillageCTS	0.04120048493	0.1960177714	0.2101874979	0.8335213368
Oribatida	Fert1	0.1782673653	0.1598821887	1.114992024	0.2648538395
Oribatida	LimYes	0.1276534062	0.1584674268	0.8055498143	0.4205024725
Oribatida	Geo2Yes	0.06650884076	0.158449583	0.4197476542	0.6746698084
Mesostigmata	(Intercept)	−1.653664454	0.397561087	−4.159522921	3.19×10^{-5}
Mesostigmata	LocationKR	0.3595781424	0.2224241155	1.616632898	0.1059575462
Mesostigmata	SeasonS	1.463208171	0.2372690068	6.166874428	6.97×10^{-10}
Mesostigmata	TillageCTD	0.1259237439	0.3098326794	0.4064249909	0.6844303604
Mesostigmata	TillageCTS	0.3527322543	0.2928201426	1.204603793	0.2283562919
Mesostigmata	Fert1	−0.2701467383	0.2231300687	−1.210714181	0.2260049656
Mesostigmata	LimYes	0.6611677557	0.2262041274	2.922881042	0.003468089867
Mesostigmata	Geo2Yes	0.3189842045	0.2248406773	1.418712167	0.1559829486
Prostigmata	(Intercept)	−1.447608506	0.3806724491	−3.802766681	0.0001430891039
Prostigmata	LocationKR	0.7318187138	0.2486257719	2.943454768	0.003245712485
Prostigmata	SeasonS	0.7607002154	0.2508421477	3.032585323	0.002424685407
Prostigmata	TillageCTD	0.136501791	0.3060170791	0.4460593879	0.6555543478
Prostigmata	TillageCTS	0.3445771856	0.2982116229	1.155478724	0.2478944403
Prostigmata	Fert1	−0.3018258941	0.2468558693	−1.222680648	0.2214503391
Prostigmata	CalcYes	0.4001582393	0.251551999	1.590757541	0.1116641518
Prostigmata	Geo2Yes	0.4480645726	0.2463963661	1.818470701	0.0689922208
Entomobryomorpha	(Intercept)	0.1016110495	0.2549926122	0.3984862487	0.6902717927
Entomobryomorpha	LocationKR	−0.4305362442	0.175899851	−2.447621427	0.01438026607
Entomobryomorpha	SeasonS	1.823095811	0.1778962487	10.24808462	1.21×10^{-24}
Entomobryomorpha	TillageCTD	0.3528142381	0.2103009076	1.677663887	0.09341273318
Entomobryomorpha	TillageCTS	0.2118561735	0.2161316518	0.9802181763	0.3269784342
Entomobryomorpha	Fert1	0.5763581671	0.1745854847	3.301294882	0.0009623967569

Table A3. *Cont.*

Group	Term	Estimate	Std. Error	z Value	Pr(> z)
Entomobryomorpha	LimYes	0.3253588392	0.1729257261	1.881494712	0.05990465389
Entomobryomorpha	Geo2Yes	−0.1013264967	0.1711720994	−0.5919568494	0.5538794839
Poduromorpha	(Intercept)	−1.319653044	0.4117503039	−3.204983777	0.001350700932
Poduromorpha	LocationKR	0.9264604604	0.265089965	3.494890727	0.000474255879
Poduromorpha	SeasonS	2.241220273	0.2839851033	7.892034641	2.97 × 10 ^{−15}
Poduromorpha	TillageCTD	0.1154238164	0.322934243	0.3574220414	0.7207758784
Poduromorpha	TillageCTS	0.1134762845	0.3262851568	0.347782552	0.7280034941
Poduromorpha	Fert1	−0.1827951507	0.2625240126	−0.6962987838	0.4862417347
Poduromorpha	LimYes	−0.7194322725	0.2684313614	−2.680134946	0.007359248567
Poduromorpha	Geo2Yes	0.1192755887	0.266732395	0.4471732378	0.6547499827
Symphypleona + Neelipleona	(Intercept)	−1.130481166	0.3983493007	−2.837914273	0.004540937678
Symphypleona + Neelipleona	LocationKR	−0.8212798007	0.2664931686	−3.081804329	0.00205750037
Symphypleona + Neelipleona	SeasonS	0.9074372406	0.2671684911	3.396497981	0.0006825406091
Symphypleona + Neelipleona	TillageCTD	0.2872702757	0.3162932801	0.9082402118	0.363751323
Symphypleona + Neelipleona	TillageCTS	0.04698201533	0.3288957757	0.1428477311	0.8864104396
Symphypleona + Neelipleona	Fert1	0.3321582226	0.2615536873	1.269942803	0.2041050051
Symphypleona + Neelipleona	LimYes	0.06796789721	0.2593840006	0.262035812	0.7932938326
Symphypleona + Neelipleona	Geo2Yes	0.2109456923	0.2624618744	0.8037193698	0.4215590649

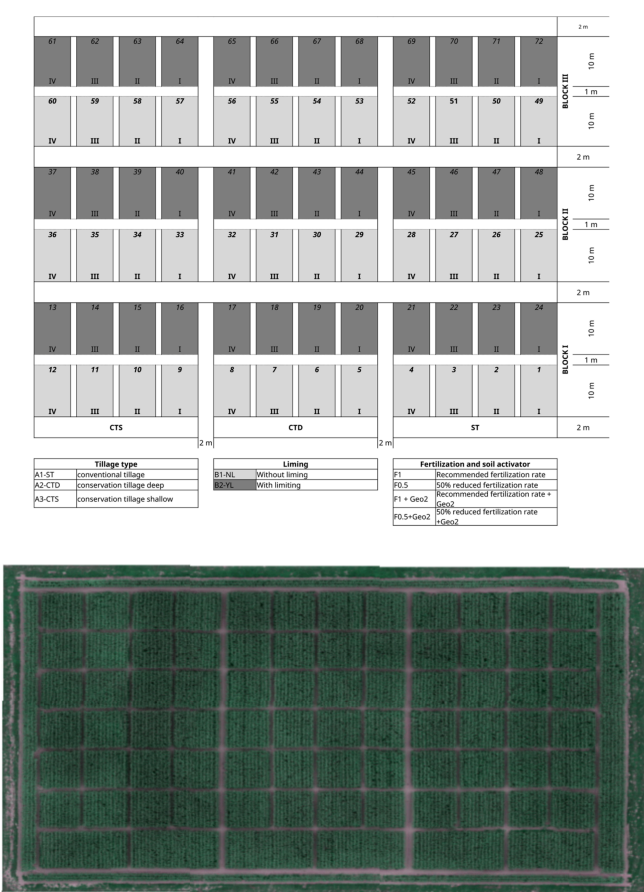


Figure A1. Experimental scheme and aerial photo of the experimental sites. Both locations had the same experimental scheme.

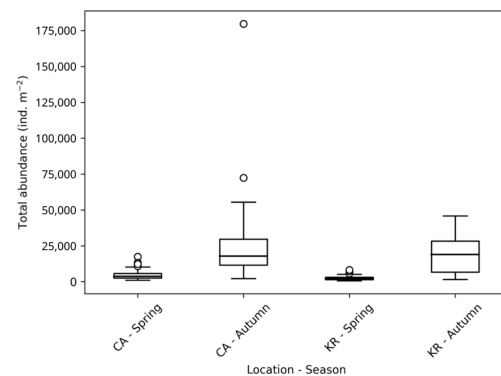


Figure A2. Total abundance of soil mesofauna per location and season expressed as the number of individuals per m². CA—Čačinci, KR—Križevci.

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