

Effects of different forestry management practices on soil mesofauna in the regeneration phase

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ABSTRACT

Forests hold both ecological and economic value, but as the majority are now under human management, there is an increasing need for silvicultural strategies that support biodiversity and ecosystem functioning alongside timber production. Soil mesofauna, which comprise a substantial proportion of forest biodiversity, play vital roles in maintaining soil processes and overall ecosystem health. This study assessed the long-term effects of four forest management treatments, preparation cutting (partial cutting), retention tree group, gap-cutting, and clear-cutting, on various soil mesofauna groups (Acari, Collembola, Protura, Diplura, Symphyla, Pauropoda) in a managed oak forest in Hungary, sampled six and nine years after intervention. The treatments significantly influenced mesofaunal communities, although responses varied by taxon. Acari and Protura displayed the clearest gradients, with densities declining from control plots to more intensively disturbed treatments. Other groups showed more variable patterns, often shaped by seasonal dynamics. Retention tree group and preparation cutting were the most successful at maintaining mesofaunal densities at levels comparable to, or even exceeding, those in undisturbed sites. In contrast, clear-cutting and gap-cutting were associated with lower densities in several taxa, although some recovery was evident due to vegetation regrowth over time. The findings highlight the importance of seasonal timing in ecological assessments, with treatment effects most pronounced in spring and autumn. Taxon-specific responses, particularly those of Protura, Acari, and Collembola, demonstrate the potential of soil mesofauna as sensitive indicators of ecological change and recovery following forest management.

1. Introduction

Forests cover approximately 31 % of the Earth's surface and 39 % within the European Union (FAO, 2020). However, only a small fraction—around 1 %—remains in a natural state (Sabatini et al., 2018). Forests provide critical ecological functions, including carbon sequestration, climate regulation, soil stabilisation, water filtration, and habitat provision, while also supporting high levels of biodiversity (Jandl et al., 2007; Mori et al., 2017). Beyond their ecological roles, forests are an essential economic resource, particularly for timber. The vast majority of the world's forests are now under management (FAO, 2020). Conventional rotation forestry often results in simplified, even-aged monocultures (Bauhus et al., 2009; Franklin et al., 2002), undermining forest biodiversity and resilience. The risks of abiotic and

biotic disturbances are increasing under global changes, which makes it necessary to enhance forest resilience via management including tree species diversity, adaptive capacity and structural heterogeneity (Thom and Seidl, 2016). There is an urgent need for management strategies that support not only timber production but also forest site protection, natural regeneration and biodiversity conservation (Bauhus et al., 2013; Thom and Seidl, 2016). To address this challenge, a range of silvicultural approaches has been developed to reconcile ecological and economic goals. Although rotation-based systems remain dominant, continuous cover forestry (CCF) systems are gaining traction in Hungary and elsewhere, reflecting a shift towards more sustainable forest management (Aszalós et al., 2022). These approaches often mimic natural disturbance regimes and rely on ecosystem-based principles.

Forestry treatments influence forest structure, altering

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environmental conditions such as temperature, soil moisture, and light availability (Kovács et al., 2020). These changes affect habitat heterogeneity and, consequently the diversity of forest-dwelling species (Brockerhoff et al., 2017; Paillet et al., 2010). Among silvicultural methods, rotation systems, particularly clear-cutting and final cutting of shelterwood management, represent the most drastic intervention, producing harsh environmental conditions through increased exposure, temperature extremes, and reduced habitat heterogeneity (Chaudhary et al., 2016; Kovács et al., 2020). To mitigate these negative effects, certain practices have been introduced, such as leaving retention trees, which provide shade for saplings, and leaving retention tree groups, which can act as refuges for forest-dwelling species (Gustafsson et al., 2010). By contrast, CCF systems, of which an important intervention is the gap-cutting, seek to emulate the gap dynamics of natural forests, as caused by treefalls (Aszalós et al., 2022; Attiwill, 1994; Madsen and Hahn, 2008). These methods promote stand-level microclimatic diversity and long-term structural heterogeneity, helping to preserve forest continuity while reducing ecological disruption (Achury et al., 2023; Gustafsson et al., 2010; Lafond et al., 2014; Perry et al., 2018).

As in most terrestrial systems, soil is an important habitat and a hotspot of forest biodiversity (Guerra et al., 2022). It serves as a major carbon reservoir and a medium for numerous ecological processes (Lal, 2005). In forests, one of the most crucial processes is leaf litter decomposition, which is driven and regulated by soil biota. The activity of soil invertebrates plays a key role in energy and nutrient cycling within forest ecosystems (Kudrin et al., 2023). In brief, soil macrofauna (> 2 mm) contribute to decomposition by fragmenting leaf litter and mixing it with mineral soil. This process is further facilitated by soil mesofauna (0.2–2 mm), which break down organic matter into finer particles, while microbial communities complete the degradation (Briones, 2014; Coleman et al., 2017). Mesofauna also influence microbial communities by feeding on fungi and bacteria, thereby stimulating growth, maintaining balance, and aiding propagule dispersal (Culliney, 2013; Grandy et al., 2016; Seastedt, 1984; Visser, 1985).

For a profound understanding of the ecological consequences of forest management, it is essential to assess its impact on the entire decomposition system. Soil mesofauna are abundant, diverse, and sensitive to environmental changes. Their limited mobility and rapid reproduction make them effective bioindicators of habitat disturbances (Boros et al., 2019; Coller et al., 2022; Joimel et al., 2021; Menta and Remelli, 2020; Siepel, 1994; Thakur et al., 2020). They occupy different soil layers. There are surface-dwelling (epigeic), intermediate (hemiedaphic) forms that move both on the surface and retreat into the soil or live in the litter layer, and truly soil-dwelling (euedaphic) forms. Despite their ecological significance, the response of belowground fauna to forest management remains insufficiently studied, especially across multiple taxa. Research has largely focused on aboveground communities, with limited attention to soil and litter communities. When invertebrates are considered, studies typically target surface-dwelling macrofauna, such as carabids and spiders (e.g., Elek et al., 2018; Samu et al., 2021), while soil-living mesofauna receive less attention, although see Boros et al. (2019). The disturbance effect on belowground communities is not fully understood yet, and it can greatly vary according to different taxonomical or functional groups (Sterzyńska et al., 2020). Among mesofauna, Acari and Collembola are the most frequently studied groups. This is due to their diverse life strategies (Table 1). In contrast, groups such as Protura, Diplura, Pauropoda, Symphyla, and Pseudoscorpiones remain underrepresented in ecological and bioindication research (Gonçalves et al., 2021; Menta and Remelli, 2020). This underrepresentation is likely due to their lower population densities and the limited ecological information available. However, these groups also possess distinct life strategies and feeding habits (Table 1). Moreover, existing mesofauna studies often examine isolated disturbance factors, such as burning, soil compaction, or litter removal, rather than comparing different forest management treatments. These comparisons can significantly contribute to evidence-based decision-making

Table 1
Feeding habits and ecological traits of different mesofauna groups.

Group	Feeding	Ecological traits	Reference
Acari	Herbivores, detritivores, fungi/bacteria feeders and predators	Very abundant and diverse in forests and grasslands, and abundant in agroecosystems. Epigeic, hemiedaphic, euedaphic	(Krantz and Walter, 2009; Walter and Proctor, 2013)
Collembola	Mostly fungi and bacteria feeders	Sensitive to soil changes, good bioindicators. Ecological response varies by life-form (epigeic, hemiedaphic, euedaphic).	(Chernova and Kuznetsova, 2000; Hopkin, 1997)
Diplura	Mostly predators, some omnivores/detritivores	Found in all soil types; prefer moist, stable conditions; sensitive to climate and anthropogenic change. Euedaphic.	(Condé, 1956; Sendra et al., 2021)
Pauropoda	Detritivores and fungivores	Prefer undisturbed soils with high organic content and porosity. Euedaphic.	(Scheller and Minor, 2010)
Protura	Mainly mycorrhiza feeders	Sensitive to disturbance, seasonality, moisture, light, and temperature changes. Euedaphic.	(Christian and Szeptycki, 2004; Imadaté, 1973)
Pseudoscorpiones	Predators	Inhabit stable habitats; rare, thus seldom used alone as bioindicators. Hemiedaphic.	(Gerlach et al., 2013; Gonçalves et al., 2021; Menta and Remelli, 2020)
Symphyla	Herbivores and detritivores	Avoid compacted soils; prefer moist, undisturbed soils with stable temperatures. Good disturbance indicators. Euedaphic.	(Gonçalves et al., 2021)

in forestry practice.

Trees influence soil fauna both directly—through inputs like litter, root exudates, and woody debris, and indirectly, by stabilising microclimatic conditions and enhancing habitat heterogeneity (Bluhm et al., 2019; Siira-Pietikäinen and Haimi, 2009). The effects of forestry treatments on soil fauna appear via the total or partial elimination of trees in a given area: changes in soil chemical and physical properties, alteration of leaf litter quantity and quality and changes in microclimatic conditions due to more open canopy structure (Herrera-Alvarez et al., 2020; Renčo et al., 2024). While epigeic species often show immediate responses to disturbances, euedaphic taxa tend to react more slowly due to the buffering effects of the soil (Coyle et al., 2017). Even within euedaphic groups, responses vary widely among taxa, ecosystems and time scales (Chaudhary et al., 2016; Nardi et al., 2023). Thus, studying multiple mesofaunal taxa offers valuable insight into how forest management practices influence soil biodiversity and ecosystem function, and can support the development of more ecologically sound forestry strategies (Burrascano et al., 2018).

In a forest ecological experiment, we assessed the effects of treatments within the conventional rotation forestry system (clear-cutting, retention tree group, and preparation cutting) compared to CCF systems (gap-cutting) and a control (undisturbed forest stand) on soil mesofaunal communities. Given that the impact of forestry treatments is widely acknowledged to be taxon-specific (Elek et al., 2018;

Siira-Pietikäinen and Haimi, 2009), our primary objective was to investigate how different soil mesofaunal groups, namely Acari, Collembola, Protura, Pauropoda, Symphyla, and Diplura, respond to varying levels of disturbance. We expected that even within the decomposer community, responses would differ depending on each group's ecological traits and life-history strategies.

A further aim was to evaluate the relative ecological impact of each forestry treatment through the lens of these mesofaunal groups. Based on earlier research at the same site (Aszalós et al., 2023; Boros et al., 2019; Elek et al., 2018; Kovács et al., 2020; Samu et al., 2021), we hypothesised that preparation cutting would have minimal effects on soil fauna, as it maintains structural and microclimate conditions similar to those of undisturbed forests (Fedrowitz et al., 2014; Kovács et al., 2020; Rosenvald and Lohmus, 2008). Retention tree group was expected to show greater resemblance to clear-cutting areas due to their limited climatic buffering capacity, and previous negative effects on Enchytraeidae (Boros et al., 2019; Elek et al., 2018). Conversely, we predicted stronger negative effects for gap-cutting and clear-cutting plots, with the latter exerting the most substantial impact on soil conditions and fauna. Although gap-cutting also modifies the microclimate, it aims to mimic natural disturbances and thus may preserve more favourable conditions than clear-cutting (Kovács et al., 2020; Schliemann and Bockheim, 2011). Overall, we hypothesised a gradient of declining mesofaunal densities corresponding to the increasing intensity of disturbance: Control (C) > Preparation cutting (P) > Retention tree group (R) > Gap-cutting (G) > Clear-cutting (CC). Finally, we examined how these responses varied seasonally and between years, with the goal of identifying optimal sampling periods for monitoring the ecological effects of forest management on soil mesofauna.

2. Materials and methods

2.1. Study site and design

The study area is located in north-central Hungary, near the village of Pilisszentkereszt, in the Pilis Mountains, on Hosszú-hegy (N47° 40', E18° 54'), at a moderately high elevation of 370–470 m (see Kovács et al., 2018). The annual mean temperature is 9.0–9.5 °C, with an annual precipitation of 600–650 mm. The predominant soil type is lessivage brown forest soil (Luvisol), which has developed on bedrock composed of limestone and red sandstone, with loess deposits. Soil depth varies between 70 cm (upper part of the hill) and 250 cm at lower elevations. The experiment was conducted in an 85-year-old oak-hornbeam forest (40 ha) (Natura 2000 code: 91G0, European Commission, 1992), which had been previously managed by rotation forestry system (shelterwood system) and consisted of an even-aged tree stand. The dominant tree species is sessile oak (*Quercus petraea* (Matt.) Liebl.), with a mean height of 21 m and a mean diameter of 28 cm (for further details see Kovács et al., 2018). Associated tree species of the upper canopy layer include turkey oak (*Quercus cerris* L.), beech (*Fagus sylvatica* L.), and wild cherry (*Prunus avium* L.). The height of the secondary canopy layer is 11 m, and it is composed mainly of hornbeam (*Carpinus betulus* L.) and manna ash (*Fraxinus ornus* L.). The understory, which covers approximately 40 %, is dominated by *Carex pilosa* Scop. and *Melica uniflora* L. (Aszalós et al., 2023).

In December 2014 and January 2015, four treatments and a control were implemented. Control (C): A closed-canopy stand without any intervention. Clear-cutting (CC): A circular clear-cutting area (0.5 ha, 80 m diameter) within the forest. Retention tree group (R): Within the clear-cutting area, a circular group of trees (8–12 individuals of dominant species) and the understory were left intact in a 20 m diameter circular area (300 m²). Preparation cutting (P): 30 % of the dominant tree layer and the entire secondary canopy layer were removed within an 80 m diameter area. Gap-cutting (G): A circular gap (20 m diameter) was created in the closed-canopy stand by removing trees. The diameter of the gap is similar to the mean canopy height. Gap-cutting is a common

intervention tool within CCF systems. The treatments were arranged in a randomised complete block design, with six blocks serving as replicates (Fig. 1).

2.2. Background variables

Two types of environmental variables were measured: microclimatic variables were continuously measured, while vegetation and soil variables were surveyed once a year. Microclimatic variables were continuously recorded at the centre of each plot. Measurements included soil temperature (°C), relative humidity at 130 cm height (%), and volumetric water content (m³ m⁻³) in the upper 20 cm of the soil profile. Instrumentation varied between years. In April 2020, soil temperature was recorded using S-TMB-M0020 sensors, and relative humidity was measured with T/RH sensors (Onset Computer Corporation), both shielded with passively ventilated radiation covers to minimise direct solar effects. Soil moisture was assessed using S-SMD-M0050 probes. These sensors were connected to HOBO H021–0020 data loggers. In subsequent monitoring periods, soil temperature and moisture were recorded using TOMST TMS-4 multi-sensor devices, while relative humidity was monitored with MCC USB-502 sensors. All parameters were logged at 15-minute intervals. To characterise the environmental conditions preceding faunal sampling, daily mean values from each sensor were averaged over the 14 days prior to the fauna collection period. Detailed descriptions of the measurement methods can be found in Kovács et al. (2020).

Vegetation data, including percentage cover, sapling density, and species richness (total number of herb-layer species), were recorded annually between 2014 and 2024 in 2 × 2 m plots located near the microclimatic stations at the centre of each treatment area. Understorey vegetation was surveyed by separating the herb layer and the regeneration layer (saplings). The herb layer comprised all herbaceous species and woody seedlings under 50 cm in height, with cover estimated as the sum of individual species' percentage covers. Saplings included woody individuals taller than 50 cm with a diameter at breast height (DBH) of less than 5 cm.

Soil samples were collected on two occasions. In May 2020, four subsamples per plot were taken from the top 20 cm of the mineral soil layer, near the locations used for litter sampling. A second round of sampling took place in April 2023, during which two subsamples per plot were collected concurrently with faunal assessments. All soil samples were air-dried and sieved to < 2 mm prior to analysis. Soil pH was determined potentiometrically in a 1:2.5 soil-to-distilled water suspension (10 g soil in 25 ml), following the Hungarian Standard (MSZ-08–0205, 1978). For the analysis of total carbon and nitrogen, the < 2 mm fraction was further sieved to < 0.5 mm and combined into a single composite sample per plot. Total carbon content was measured using the dichromate oxidation method with colorimetric detection (MSZ 21470/52, 1983), while nitrogen concentrations were quantified via the Kjeldahl method (Bremner, 2016). Plant-available phosphorus and potassium were extracted using ammonium acetate-lactate (AL) solution (as AL-P₂O₅ and AL-K₂O), according to Egnér et al. (1960). Soil organic matter (SOM) content was determined using the modified Walkley-Black method (FAO, 2020).

2.3. Fauna sampling

Soil mesofauna were sampled in each plot during three seasons: spring (before the vegetation period, 2nd April), summer (during the vegetation period, 10th June), and autumn (after the vegetation period, 10th October) in both 2020 and 2023. Considering five treatments and six replicates, a total of 30 samples were collected at each time, using a metal soil corer (8 cm diameter, 8 cm length; 402 cm³). Six replicates were deemed sufficient to account for heterogeneity.

Soil samples were immediately transported to the laboratory and extracted over one week using a Berlese funnel into 70 % ethanol. All

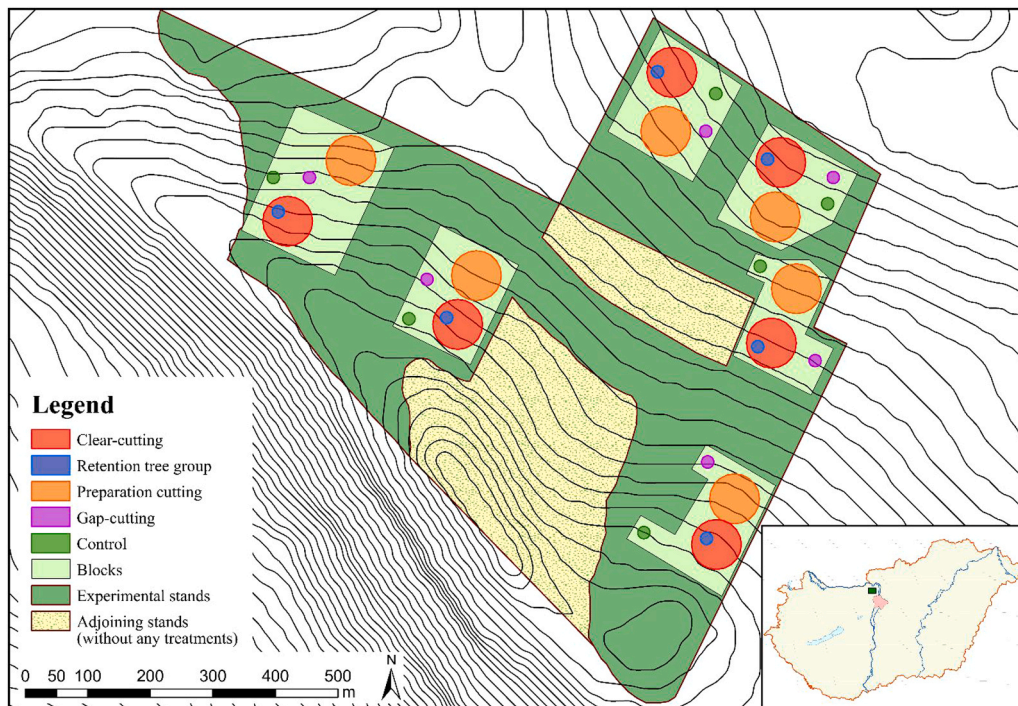


Fig. 1. Layout of the Pilis Forestry Systems Experiment, located in the Pilis Mountains, Hungary.

specimens were manually sorted and identified to major taxonomic groups (Acari, Collembola, Protura, Symphyla, Pauropoda, Diplura, and Pseudoscorpiones) and counted under a Nikon SMZ25 digital microscope. Density data were calculated by dividing the abundance by the area of soil extraction (0.00503 m^2).

2.4. Statistical analyses

All statistical analyses were conducted by R version 4.2.1 (R Core Team, 2020). To analyse the effects of environmental factors, we categorised the environmental variables into two groups: (1) microclimatic data (air- and soil temperature, volumetric water content, and relative humidity), for which the mean values over the two weeks preceding each seasonal sampling were calculated; and (2) vegetation-soil data (vegetation cover, plant species richness, sapling density, and soil variables). The two types of data were analysed separately. To examine differences in environmental conditions across treatments and seasons, we first performed a Permutational Multivariate Analysis of Variance (PERMANOVA, Legendre and Legendre, 1998) using the `adonis2` function from the `vegan` package (Oksanen et al., 2022). This analysis was based on a Euclidean distance matrix of standardised environmental variables, with treatment and season included as explanatory factors. Statistical significance was assessed using 9999 permutations. To identify significant pairwise differences between treatments and seasons (the latter applied only to microclimatic variables), we conducted pairwise comparisons using the `pairwise.adonis` function. Subsequently, one-way ANOVAs (only for treatments) were applied to individual environmental variables, followed by Tukey's Honest Significant Difference (HSD) post-hoc tests, with Bonferroni correction, using the `TukeyHSD` function. To visualise multivariate differences in environmental conditions among treatments, we generated radar charts (spider plots) using the `fmsb` package (Nakazawa, 2024). Based on our data table, for each treatment, median values of the environmental variables were calculated, standardised, and scaled between their respective minimum and maximum values. Separate figures were created for vegetation-soil and microclimatic variables, with the latter further subdivided by season.

Principal Component Analysis (PCA) was employed to explore and

visualise patterns in mesofaunal community composition, and to assess their relationships with treatment and seasonal variation (Borcard et al., 2011). Analyses were conducted separately for the years 2020 and 2023. Prior to PCA, mesofaunal abundance data were Hellinger-transformed using the `decostand` function from the `vegan` package (Oksanen et al., 2022) to minimise the influence of dominant taxa. PCA was performed using the `PCA` function from the `FactoMineR` package (Lê et al., 2008), and the results were visualised with the `fviz_pca_biplot` function from the `factoextra` package (Kassambara, 2021). Biplots display both taxa loadings and sample scores, with individual samples coloured according to treatment and distinguished by season using shape aesthetics. To aid interpretation and assess group separation, 98 % confidence ellipses were added around treatment groups.

For mesofaunal groups with relatively high densities (Acari, Collembola, Protura), statistical analyses were performed using linear mixed-effects models fitted with the `lmer` function from the `lme4` package (Bates et al., 2015). A stepwise model selection procedure was applied, beginning with the most complex model and proceeding to simpler alternatives. Model selection was based on comparisons of Akaike Information Criterion (AIC) values and likelihood ratio tests. Final models included each mesofaunal group as a response variable, treatment as a fixed effect, and both block and season as random intercepts. For taxa with a high frequency of zero counts (Pauropoda, Diplura, Symphyla), we employed zero-inflated generalised linear mixed-effects models (GLMMs) with a negative binomial distribution to address overdispersion and excess zeros. These models were fitted using the `glmmTMB` package (Brooks et al., 2017), with treatment as a fixed effect, block and season as random effects. Model diagnostics were conducted to assess assumptions, including residual inspection and evaluation of dispersion. For seasonal analyses, separate models were fitted for each season following the same model selection approach. In these cases, season was not included as a random effect. Post-hoc comparisons among treatments were conducted using estimated marginal means (EMMs) with Tukey's adjustment for multiple testing, using the `emmeans` package (Searle et al., 2023).

3. Results

3.1. Effects of treatments on environmental variables

Seasonality explained the majority of the variation in microclimatic variables in both 2020 (75 %) and 2023 (85 %) (PERMANOVA, $p < 0.0001$), whereas treatment effects were considerably smaller (4 % in 2020, $p = 0.0034$; 3 % in 2023, $p < 0.0001$; Table S1). All measured microclimatic variables were influenced by treatment to some extent (Table S2), with autumn consistently exhibiting the strongest treatment effects ($R^2 = 0.48$ in 2020; $R^2 = 0.42$ in 2023), followed by spring (significant only in 2023), and summer showing the weakest responses (Tables S1, S3). Although overall management effects were modest, clear-cutting consistently produced the most distinct microclimatic conditions, particularly in autumn (Table S4). Soil temperature was generally lowest in CC and highest in R (Fig. 2; Table S4). By 2023, CC plots exhibited warmer soils in spring and cooler temperatures in summer (Fig. 2), suggesting increasing seasonal buffering linked to vegetation regrowth. In both years, relative humidity was generally highest in CC (Fig. 2). In 2020, soil moisture was significantly lower in P compared to CC ($p = 0.049$) and marginally lower than in G ($p = 0.065$) however, these differences had diminished by 2023 (Table S5).

In the case of vegetation-soil variables, treatment explained 29 % of the variance in 2020 and 26 % in 2023 (Table S1). Significant effects were observed only for vegetation and litter variables (Table S4). Litter quantity was lowest in CC and highest in C and R (Fig. 2; Table S5). Vegetation cover was lowest in C, while understory species richness peaked in R by 2023 (Fig. 2; Tables S5, S6). Sapling density was highest in G, with CC also showing high values, although differences with C were only marginally significant (Tables S5, S6). No significant treatment effects were found for soil chemical parameters (pH, SOM content, P, K, N, C) (Tables S5, S6). A more detailed account of seasonal and treatment effects on environmental variables is provided in the Supplementary material.

3.2. Effects of treatments on mesofaunal communities

PCA revealed distinct patterns in mesofaunal community composition in both years. In 2020, the first three principal components (PC1–PC3) accounted for 59.77 % of the total variance, with PC1 and PC2 explaining 45.44 %. Collembola and Acari dominated PC1, representing the main gradient of variation (Table S8). Along PC1, a separation emerged between C and CC treatments, while the remaining, less intensive treatments (G, P, R) clustered more centrally (Fig. 3). On the PC1 axis, CC plots were positioned to the right, whereas C and the other treatments were grouped to the left. In 2020, Collembola and Symphyla were associated with CC plots, while Acari displayed the opposite pattern, being linked to less disturbed treatments. Protura was associated with the control treatment (Fig. 3).

In 2023, the explanatory power of the first three components increased to 66.37 % (PC1–PC3), with PC1 and PC2 together accounting for 49.78 %, indicating stronger differentiation than in 2020 (Table S7). Seasonal variation was clearly expressed along PC1, with summer samples positioned to the right and spring and autumn samples to the left. Additionally, the G treatment separated distinctly from all others along this axis (Fig. 3). As in 2020, Collembola and Acari remained the dominant contributors to PC1, continuing to define the main variation gradient (Table S8). Diplura showed a much stronger association with PC2 in 2023, in contrast to its weaker role in 2020. Protura, Pauropoda, and Pseudoscorpiones had high loadings on PC2 and PC3, suggesting their variation was influenced more by secondary structuring factors than by treatment effects. Collembola and Symphyla were linked to summer samples, while Acari displayed an inverse pattern. Gap-cutting plots were distinctly separated along PC2 and were associated with Diplura (Fig. 3). No treatment-based separation was evident along PC3.

3.3. Effects of treatments on mesofauna groups

The effects of forestry treatments and seasonal variation on different soil arthropod groups were evaluated using linear mixed-effects models for the years 2020 and 2023. The significance and strength of treatment effects varied across taxa, seasons, and years. For Collembola, in 2020, there was not any significant treatment effect across the full year ($p > 0.05$), although R and G treatments showed marginally lower values compared to the C ($p = 0.058$ and $p = 0.056$, respectively, Table S9). However, significant differences emerged in spring, with both C and CC showing higher densities than the other treatments (Fig. 4). No significant differences were observed in summer or autumn, although the lowest values occurred in gap-cuttings during summer. In 2023, Collembola showed a significant treatment effect ($F = 3.07$, $p < 0.05$), with the lowest values in G. This was significant compared to C ($p = 0.047$) and marginal compared to R ($p = 0.09$). No significant differences were detected seasonally, but G and CC consistently exhibited the lowest values (Fig. 5 Table S9).

Treatment effects on Acari were strong in 2020 ($F = 13.82$, $p < 0.0001$). The control plots had the highest densities, significantly greater than all other treatments. CC had the lowest values, significantly lower than all treatments except G (Fig. 4). This trend remained consistent across the seasons. In spring, G had the lowest densities, significantly different from all other treatments except CC. Although CC had the second lowest values, it differed significantly only from C. In summer, the pattern persisted, but due to high variance, only the C vs. CC comparison remained significant. In autumn, CC had the lowest values, significantly lower than C and G, and marginally lower than P and R (Table S8). In 2023, the overall treatment effect was weaker ($F = 3.11$, $p = 0.054$) than in 2020. CC had the lowest values and differed significantly from R, and marginally from C and P. Seasonal differences were only significant in summer ($p = 0.021$), with CC having the lowest values, significantly different from all treatments except G (Fig. 5, Table S9).

Protura responded significantly to treatments in both years (2020: $F = 11.48$, $p < 0.0001$; 2023: $F = 10.72$, $p < 0.0001$). In 2020, the highest values occurred in the control, significantly exceeding all treatments except R ($p = 0.126$). CC had the lowest densities, differing significantly from R and marginally from P ($p = 0.051$). G also showed low values. Seasonal patterns followed a similar trend, with CC and G consistently showing significantly or marginally lower densities than C. In summer, CC had significantly lower values than all treatments except G, while in autumn, C remained highest and P and CC showed significant declines (Fig. 4, Table S7). A similar pattern was observed in 2023, with the exception that differences between C and P disappeared. Open treatments (CC and G) had the lowest values across all seasons, with significant differences found in spring (G vs. C) and in autumn (G and CC vs. C and R) (Fig. 5, Table S9).

Pauropoda exhibited no significant treatment effects in 2020, but showed significant differences in 2023 (Table S9). Throughout 2023, R had significantly higher values than both C and CC. R reached its highest values in summer and autumn, though these were not statistically significant. (Fig. 5).

Diplura did not show significant treatment effects in either year (Table S9). Seasonal differences were generally non-significant, but in summer 2023, G had the highest values. Symphyla showed no significant treatment effects in 2020, although G and R (in autumn) had lower values than the other treatments (Fig. 4). In contrast, treatment effects were more pronounced in 2023 (Table S9). G had lower annual values than the other treatments. Although not statistically significant, gap-cutting plots tended to show lower densities in spring and summer. In spring, C and G were similarly low. In summer and autumn, G remained the lowest (Fig. 5).

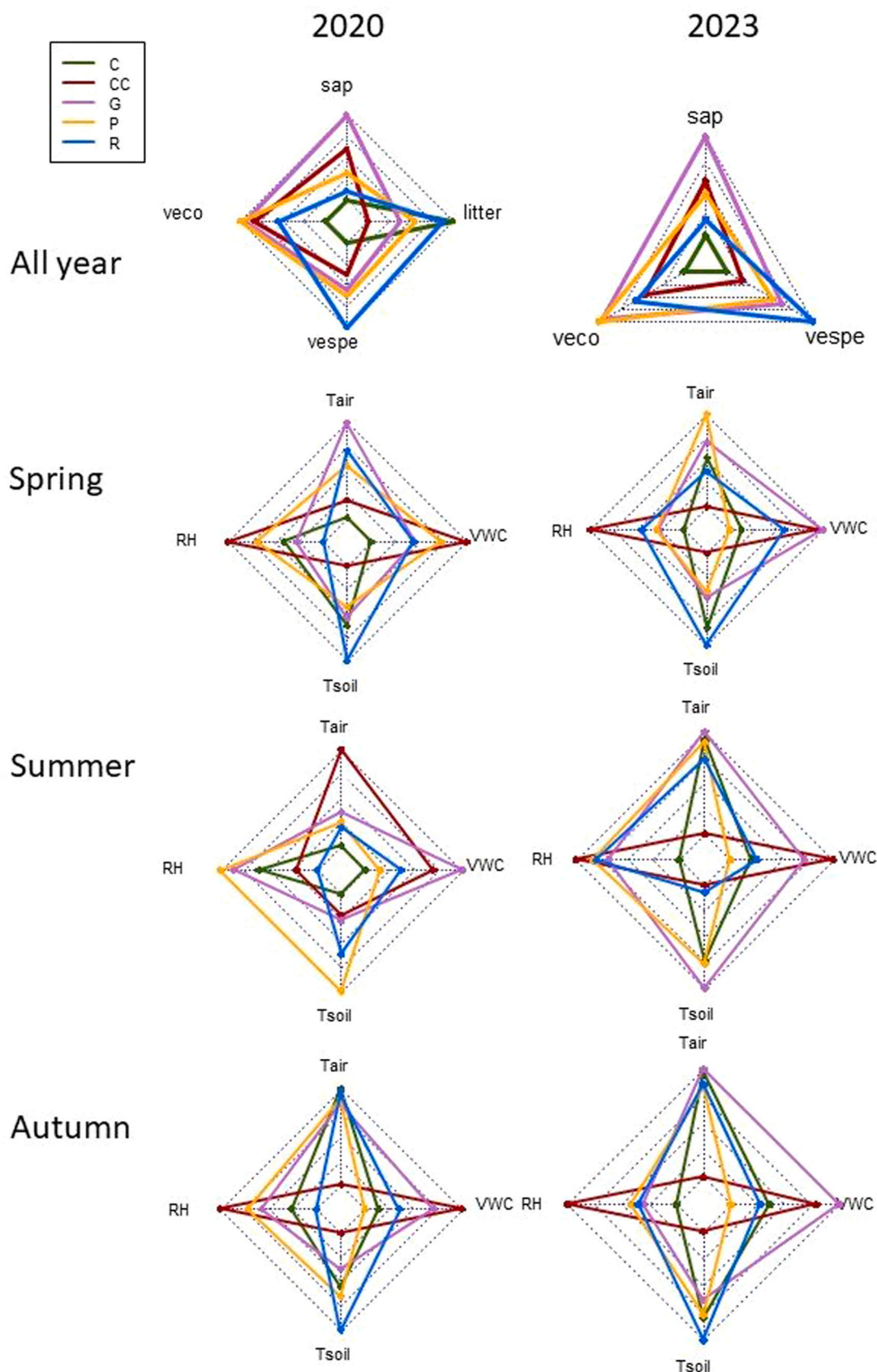


Fig. 2. Radar charts of environmental variables (based on median values) across five treatments in 2020 and 2023 (C: control; CC: clear-cutting; G: gap-cutting; P: preparation cutting; R: retention tree group) annually and by season. Abbreviations: *sap* – number of saplings; *veco* – vegetation cover; *vespe* – vegetation species richness; *litter* – leaf litter weight; *RH* – relative humidity; *Tair* – air temperature; *Tsoil* – soil temperature; *VWC* – volumetric water content.

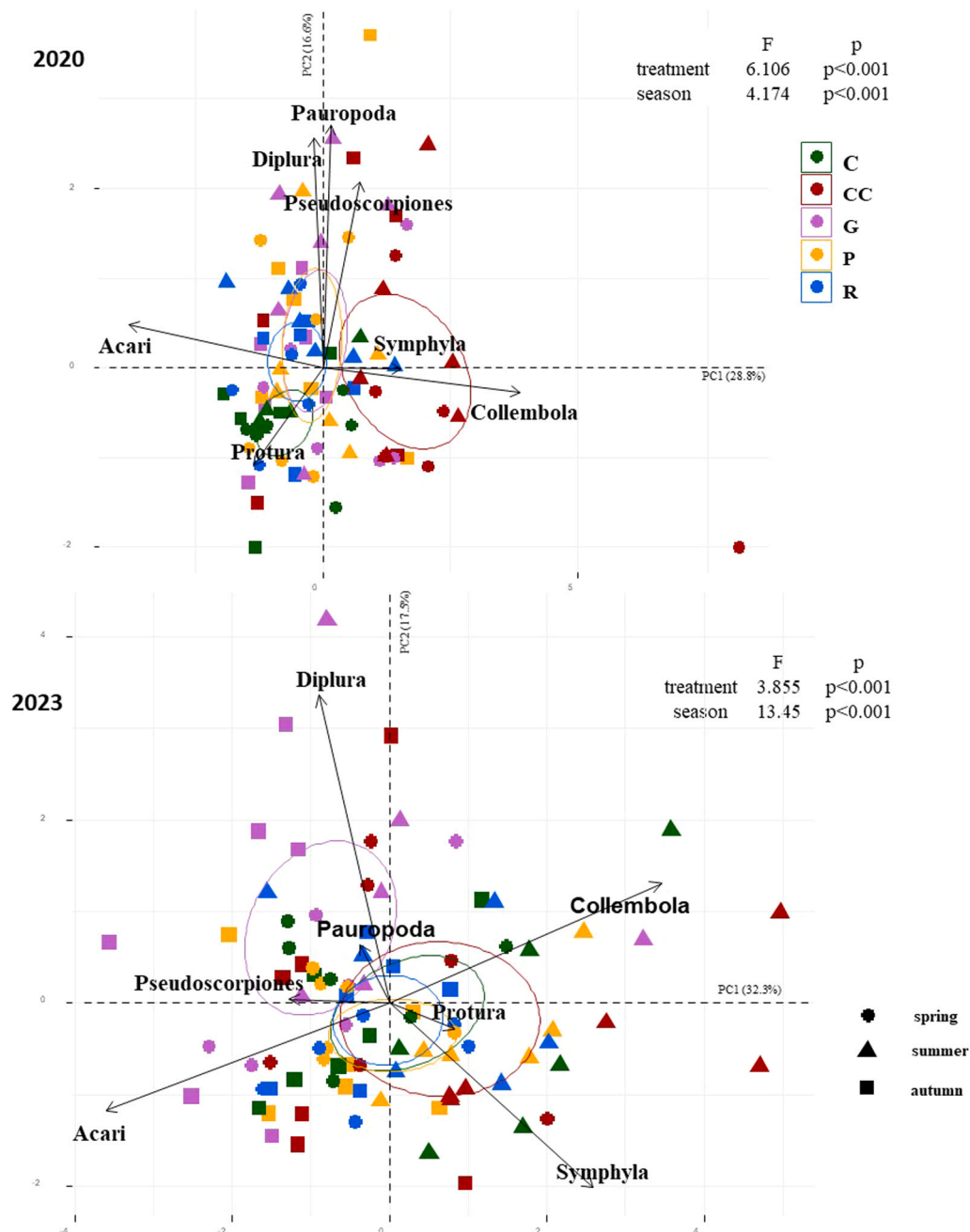


Fig. 3. Principal Component Analysis (PCA) biplots showing the ordination of soil mesofauna communities across different forest management treatments (C: control; CC: clear-cutting; G: gap-cutting; P: preparation cutting; R: retention tree group) and seasons for two years (2020 and 2023). Arrows represent the direction and strength of taxa contributions to the ordination space. Ellipses indicate 95 % confidence intervals for groupings by treatment.

4. Discussion

As living trees shape their surrounding soil biota (Siira-Pietikäinen and Haimi, 2009), the negative effects, with a slow recovery, observed following forest management were expected. Intensive practices, particularly those involving heavy machinery, such as clear-cutting, can exacerbate these effects through biomass removal, forest floor disturbance, soil compaction, and erosion (Bird et al., 2004; Rousseau et al., 2018; Siira-Pietikäinen et al., 2001). Despite some taxonomic, seasonal, and interannual variation, our proposed disturbance gradient ($CC > G > R > P > C$) was generally supported across taxa. As in earlier studies (e.g., Boros et al., 2019; Wehner et al., 2021), forest treatments altered the microclimate and vegetation, indirectly affecting soil mesofauna

composition and abundance. Among the groups studied, Acari and Protura consistently showed lower densities in managed plots compared to controls. Collembola responded most strongly in spring, while responses of Diplura, Symphyla, and Pauropoda were weaker or more variable.

Although control plots were previously managed and did not represent pristine forest conditions (Chauvat et al., 2003), they served as a practical baseline. Mesofaunal densities in these plots aligned with reports from other temperate deciduous forests (Blesić, 1987; Nosek, 1975; Van der Drift, 1951).

Preparation cutting and retention tree group deviated only slightly from controls in vegetation and microclimate, yielding intermediate mesofaunal densities (between control and the most disturbed sites).

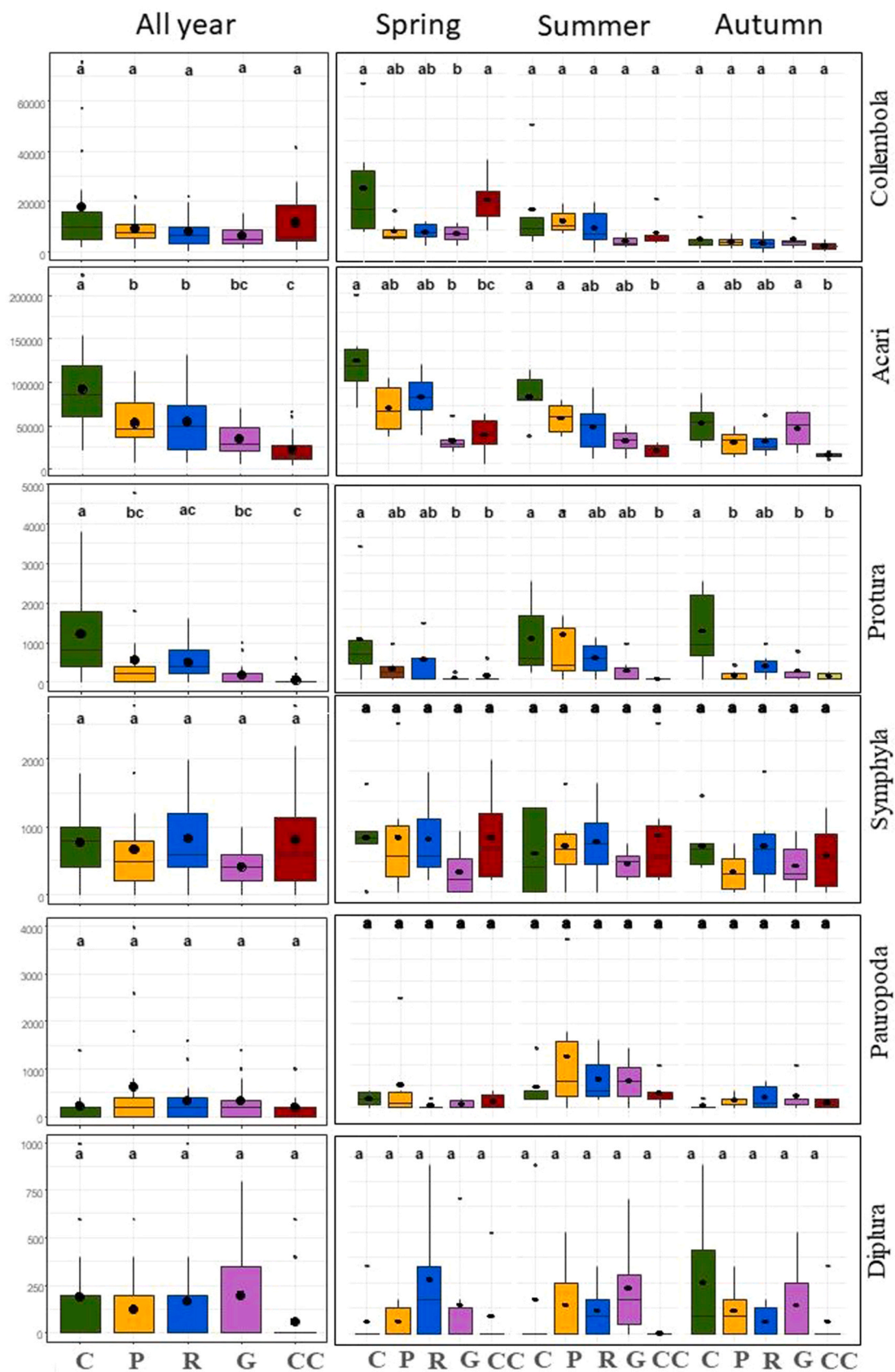


Fig. 4. Densities of different mesofaunal groups across five treatments in 2020 (C: control; CC: clear-cutting; G: gap-cutting; P: preparation cutting; R: retention tree group) annually and by season. Boxplots display the densities of different mesofaunal groups. Dots indicate mean values. Different letters indicate significant differences between groups ($p < 0.05$), separately for the whole year and in seasonal display.

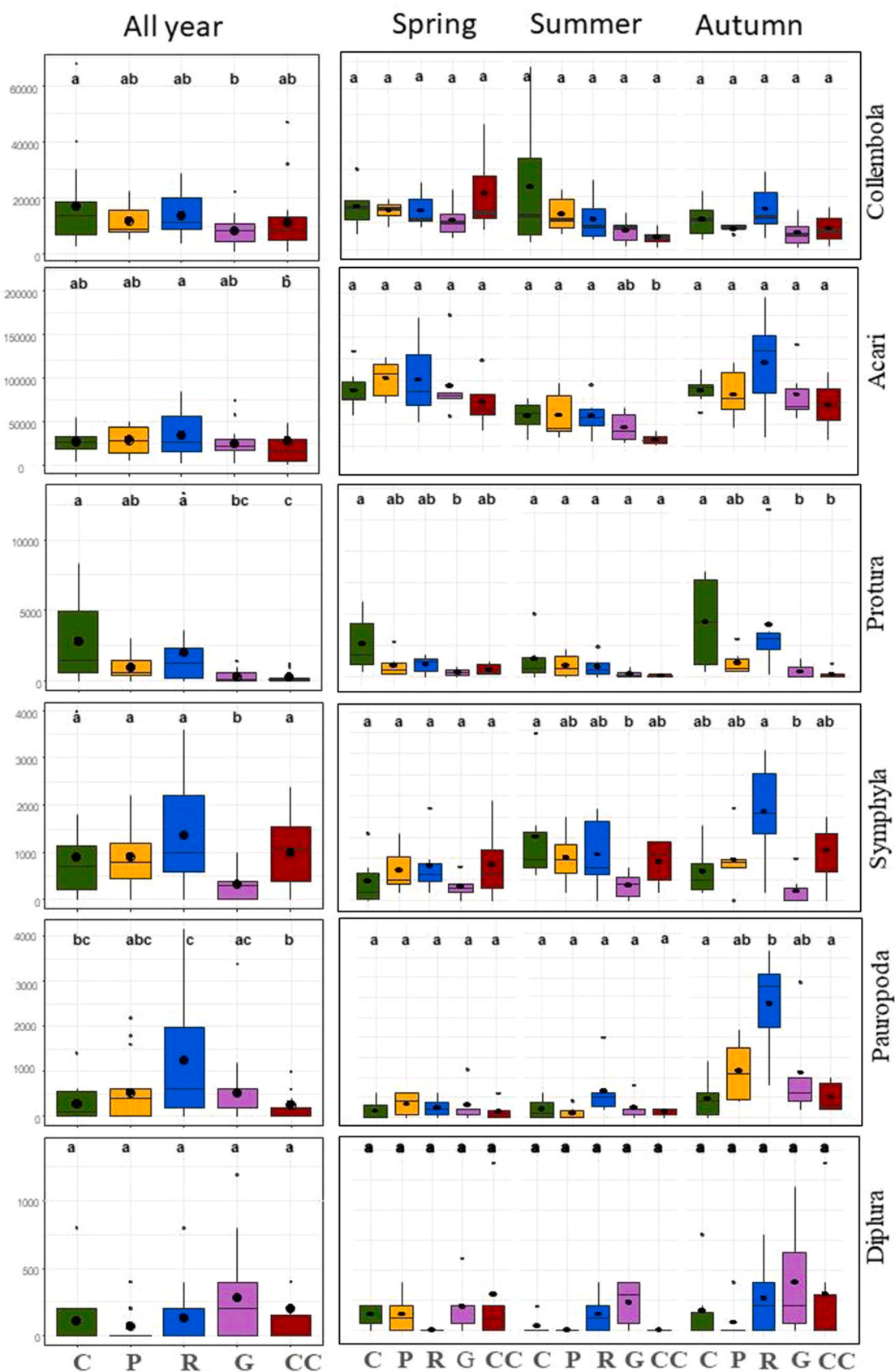


Fig. 5. Densities of different mesofaunal groups across five treatments in 2023 (C: control; CC: clear-cutting; G: gap-cutting; P: preparation cutting; R: retention tree group) annually and by season. Boxplots display the densities of different mesofaunal groups. Dots indicate mean values. Different letters indicate significant differences between groups ($p < 0.05$), separately for the whole year and in seasonal display.

These treatments aim to retain organic matter and support nutrient cycling (Dahlgren and Driscoll, 1994), providing refuge for forest-adapted soil fauna (Elek et al., 2018). Our data support, that preparation cutting as one of the least disruptive practices (Chaudhary et al., 2016; Kudrin et al., 2023), maintaining closed canopies, compared to other cutting treatments and supporting high understory diversity (Aszalós et al., 2023; Kovács et al., 2020).

Retention tree group, designed to maintain forest-dependent species within clear-cutting areas (Fedrowitz et al., 2014; Mori and Kitagawa, 2014; Rosenvald and Lõhmus, 2008), often supported the highest densities of Symphyla, Pauropoda, Diplura, and Protura. Protura, closely associated with moist and ectomycorrhizal fungi-rich soils (Bluhm et al., 2019; Galli et al., 2019; Malmström and Persson, 2011; Minor, 2008; Pass and Szucsich, 2011). This group was most abundant where tree cover and fungal associations persisted (Sterzyńska et al., 2020). Pauropoda and Symphyla likely benefited from dense, diverse herbaceous cover of the retention tree group (Aszalós et al., 2023). Initial findings, based on Enchytraeidae worms suggested retention groups were less favourable for mesofauna (Boros et al., 2019; Elek et al., 2018). The reason of this negative effect was the relatively high soil temperature and low soil moisture in retention tree group, directly after the treatment interventions. However, six years after the interventions, natural regeneration in CC reduced the edge effects (Kovács et al., 2020) and improved habitat quality in retention tree group. By 2023, these plots featured a thick litter layer, high herbaceous cover, and the greatest understory species richness (Aszalós et al., 2023), with seasonal microclimatic buffering, warmer soils in spring and cooler conditions in summer compared to the previous state, may further support mesofaunal activity. In line with Chaudhary et al. (2016), our findings suggest that both selection (e.g., preparation cutting) and retention approaches are effective in sustaining soil biodiversity in managed forests. It is also very important phenomenon that the short and mid-term effect of retention tree group could be different for soil organisms.

Clear-cutting and gap-cutting had the strongest negative impacts, though surprisingly, clear-cutting (CC) did not always produce the most severe effects. CC is typically the most intensive disturbance (Chaudhary et al., 2016), and often results in negative outcomes for decomposer communities (Lindberg and Bengtsson, 2005; Siira-Pietikäinen et al., 2001; Siira-Pietikäinen and Haimi, 2009). In our case, its impact varied across taxa. Acari, Protura, and Diplura densities declined markedly, aligning with previous findings (e.g., Lindo and Visser, 2004; Lóšková et al., 2013; Siira-Pietikäinen and Haimi, 2009; Sterzyńska et al., 2020). For Collembola, the literature is inconsistent, while some studies report obscure effects (Setälä et al., 2000), others—including ours—document notable declines in densities (Blair and Crossley, 1988; Kudrin et al., 2023; Siira-Pietikäinen and Haimi, 2009).

Despite the drastic initial alterations (Kovács et al., 2020), environmental conditions in CC plots became buffered by the time of sampling. Rapid regrowth of disturbance-tolerant species altered vegetation composition, aligning CC with gap-cutting areas (Aszalós et al., 2023). Although, the initial extremes associated with CC likely had lasting impacts, particularly on more sensitive mesofaunal groups, over time. Over time, the observed regrowth may have buffered the extremeities and diminished mesofaunal differences.

One important factor underlying the observed mesofaunal patterns may be the condition of the leaf-litter layer. This is critical for soil fauna through moisture retention, habitat provision, and serving as both a food source and a substrate for microbial communities (Wehner et al., 2016), the other food source of mesofauna (Hopkin, 1997; Remén et al., 2008). Changes in litter quantity and acidity may explain declines in groups like Acari community, especially Oribatida, which dominated our samples and rely on decomposing plant material (Culliney, 2013). Furthermore, shifts in litter characteristics can indirectly influence soil fauna by altering fungal communities (Bååth et al., 1995; Hartmann et al., 2012). Such bottom-up effects have been widely documented (Marshall, 2000), reinforcing the importance of leaf-litter dynamics in

shaping decomposer communities in managed forest ecosystems.

Gap-cutting, while designed to mimic natural disturbances, can have contrasting effects on surface- and soil-dwelling fauna. Surface arthropods often benefit from increased vegetation heterogeneity (Eckert et al., 2021; Perry et al., 2018), yet soil fauna, particularly forest specialists requiring stable conditions, may respond negatively (Zhang et al., 2025). In our study, Diplura, which are sensitive to desiccation and depend on stable soil humidity and temperature (Condé, 1956; Sendra et al., 2021), were more abundant in gap-cuttings. This may be attributed to higher soil moisture levels during the early stages; however, this advantage declined over time as tree roots extended into the gap centre, leading to drier conditions (Kovács et al., 2020). Additionally, the increased cover of regeneration likely reduced rainfall reaching the soil surface and contributed to further moisture loss through transpiration. Furthermore, reduced litter input and slower canopy closure in gaps compared to forest stands, likely increased exposure to environmental fluctuations (Kovács et al., 2020; McCarthy, 2001; Stan and Daniels, 2014).

Interestingly, Collembola in spring and Symphyla in autumn were sometimes more abundant in CC than in gap-cuttings. Similar declines in gaps were observed by Zhang et al. (2025) in moist forests with deep soils, while positive responses occurred in drier sites with shallow soils. In the Pilis Mountains, with 200–250 cm soil depth in some places and 600–650 mm annual precipitation (Dövényi, 2010; Kovács et al., 2018), local edaphic conditions may explain the negative responses observed. This aligns with several earlier findings. For example, Čuchta et al. (2019) found reduced Collembola densities where succession was suppressed. Sabais et al. (2011), observed that dense vegetation improves habitat suitability for Collembola. Hasegawa et al., (2006) similarly reported rapid Collembola recovery within four years, driven by regrowth of disturbance-tolerant species like *Rubus* and *Salix*. Our data may reflect a transitional phase where vegetation recovery in CC plots outpaced that in gap-cuttings. While gap-cutting is often valued for promoting habitat heterogeneity, our sampling, restricted to gap centres, may have captured mostly the less buffered conditions. Future studies incorporating edge-to-centre gradients could provide a more complete picture of mesofaunal responses to gap-cutting.

After harvesting, although the recovery of microclimatic conditions tends to take longer time (Csölleová et al., 2024), deciduous forests typically regenerate rapidly (Hasegawa et al., 2006), which in turn influences soil faunal communities. Long-term effects of forest treatments may diverge significantly from immediate responses. The forest's regeneration capacity is a key factor when evaluating the sustainability of silvicultural practices. Ideally, management should facilitate the rapid recovery of decomposer communities, enabling a return to near pre-disturbance conditions (Siira-Pietikäinen and Haimi, 2009). In our treatments, perennial forb cover peaked by 2018 and declined thereafter as saplings grew (Aszalós et al., 2023). Microclimatic recovery in gap- and clear-cutting areas can take 7–20 years (Baker et al., 2014; Beaudet et al., 2004; Csölleová et al., 2024; Lewandowski et al., 2015), with pine forests recovering in 4–10 years (Casaril et al., 2024). Our mesofaunal data from 2020, five years post-treatment, likely reflect a regeneration phase. The absence of pre-treatment and immediate mesofaunal density data limits direct comparisons to immediate effects.

Response and recovery rates of soil fauna differ among taxa and over time, and knowledge in this area remains limited (Kudrin et al., 2023; Siira-Pietikäinen and Haimi, 2009). For instance, enchytraeid worms in boreal forests may require up to 12 years to return to baseline levels (Huhta, 1976; Siira-Pietikäinen and Haimi, 2009), and Collembola densities have remained suppressed for 10–17 years post-disturbance in some studies (Bengtsson et al., 1998; Slawski and Slawska, 2019), though others have shown no long-term impact (Siira-Pietikäinen and Haimi, 2009). In our case, Acari declined consistently from control to CC in 2020, but differences diminished by 2023, suggesting gradual recovery. Oribatid mites, as K-strategists, with mainly slow reproduction and delayed population responses, recover slowly (Lindberg and

Bengtsson, 2005; Walter and Proctor, 2013) often requiring a decade to that (Kudrin et al., 2023). While Collembola, as r-strategists, rebound quickly due to their high flexibility and dispersal capacity (Marshall, 2000; Petersen, 2002; Rousseau et al., 2018). It may explain the weaker treatment responses observed, especially in later years.

Most mesofaunal groups—excluding Acari and Collembola—remain insufficiently studied (Voigtländer et al., 2016), complicating direct comparisons with previous research. Many of these taxa, including Symphyla and Pauropoda, are predominantly forest-dwelling organisms that prefer undisturbed habitats characterised by high organic matter content, stable temperatures, and uncompact soil substrates (Gonçalves et al., 2021; Voigtländer et al., 2016). For this reason, we expected negative responses to the applied treatments. In line with earlier findings (Gonçalves et al., 2021; Sterzyńska et al., 2020), Protura emerged as reliable indicators of environmental change, with their responses reflecting alterations in mycorrhizal communities and microclimatic conditions (Bluhm et al., 2019; Galli, 2020; Malmström and Persson, 2011). Other mesofaunal groups, such as Diplura, Pauropoda, and Symphyla, exhibited more variable patterns, potentially due to ongoing forest regeneration or limitations associated with sampling limitations. Their typically patchy distributions (Gonçalves et al., 2021), coupled with low overall density, likely constrained statistical detectability. To better capture their ecological responses, more targeted and group-specific sampling approaches may be required.

Despite certain limitations—such as taxonomic resolution within groups—our study provides a broad overview of how forestry treatments impact a key component of the soil decomposer community. These responses may cascade across trophic levels, influencing microbiota and decomposition processes (Marshall, 2000). Overall, our findings underscore the importance of considering life-history strategies and taxon-specific traits when evaluating forest management outcomes.

Seasonal and interannual variability played a pivotal role in shaping both environmental conditions and soil mesofauna responses. Treatment effects on microclimatic variables were most pronounced in autumn, moderate in spring, and least evident during summer. Mesofaunal taxa displayed distinct seasonal response patterns. Collembola and Acari exhibited the clearest treatment-related differences in spring, especially in 2020, while Symphyla and Pauropoda showed more consistent responses in summer and autumn, particularly in 2023. These seasonal dynamics were further modulated by year-to-year climatic variation. Autumn 2023 was unusually warm and dry, likely prolonging vegetation activity and amplifying habitat contrasts among treatments. In contrast, the cooler and wetter autumn of 2020 may have triggered partial dormancy in soil fauna, diminishing the detectability of treatment effects. Notably, dense canopy cover buffered summer extremes, aligning with previous findings (Kovács et al., 2020), and likely contributed to the more subdued seasonal shifts observed under closed-canopy plots.

Spring peaks followed by sharp summer declines in Collembola, particularly evident in 2023, when clear-cutting plots fell below gap-cutting plots, suggest that seasonal stressors such as heat and desiccation induced avoidance behaviours like dormancy or vertical migration (Edwards, 1961; Galli et al., 2013; Hopkin, 1997; Voigtländer et al., 2016). However, these responses cannot be solely attributed to abiotic stress. Although soil moisture was elevated in both springs and temperature patterns were similar across years, Collembola still declined in summer, even when humidity remained stable, as in 2023. This points to additional factors, including vegetation structure, litter quality, and microbial resource availability, which may mediate seasonal population dynamics.

Taken together, these findings highlight the necessity of integrating both seasonal and interannual perspectives into assessments of forest management impacts. The interplay between environmental variability and species-specific ecological traits, such as moisture tolerance, dormancy potential, and microhabitat specificity, underscores the complexity of mesofaunal responses. It is essential to consider seasonal and long-term dynamics when monitoring biodiversity and developing

effective conservation strategies in managed forest ecosystems.

5. Conclusion

Our study highlights that forest management practices significantly affect soil mesofaunal communities, though the magnitude and direction of these effects vary depending on taxon, treatment intensity, and time since intervention. The expected disturbance gradient ($CC > G > P > R > C$) was generally supported, particularly for Acari and Protura, which emerged as the most responsive groups across both years. In contrast, Collembola, Symphyla, Pauropoda, and Diplura showed weaker or more variable responses, often influenced by seasonality and interannual climatic variation.

Retention tree group and preparation cutting proved to be effective in conserving soil biodiversity, often supporting faunal densities close to or even exceeding those of closed managed forests. Conversely, clear-cutting and gap-cutting were associated with reduced densities in several groups, although vegetation regeneration appeared to buffer some negative effects over time.

Our results also underscore the importance of the timing of assessments. Treatment effects were most evident in spring and autumn. These patterns point to the need for temporally explicit monitoring frameworks to capture the full ecological impact of forest interventions. Finally, while some soil mesofaunal taxa remain underexplored, our findings emphasise the importance of incorporating a diversity of taxa and life-history strategies into forest biodiversity assessments and ecologically sustainable forestry practices.

CRedit authorship contribution statement

Péter Ódor: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Norbert Flórián:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **András Bidló:** Data curation, Investigation, Methodology, Writing – review & editing. **Réka Aszalós:** Data curation, Investigation, Writing – review & editing. **Bence Kovács:** Data curation, Formal analysis, Investigation, Validation, Writing – review & editing. **Veronika Gergőcs-Winkler:** Formal analysis, Validation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

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.

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Supplementary data

The supplementary file contains a detailed description of changes in environmental variables and [supporting tables](#) related to the mesofaunal results.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.123196](https://doi.org/10.1016/j.foreco.2025.123196).

Data availability

Data will be made available on request.

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