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Intermediate disturbance and regeneration: Long-term Collembola responses to forest management in an oak-hornbeam forest

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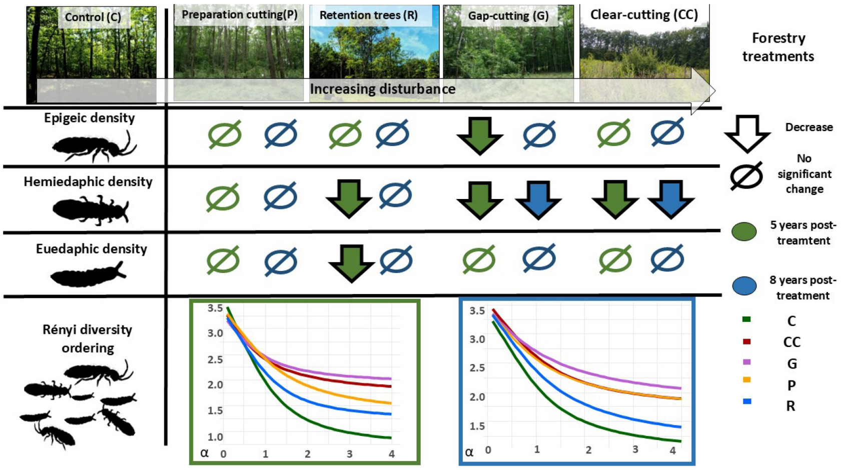
ABSTRACT

- Collembola responses varied across ecomorphological groups and seasons.
- Epigeic densities were lowest in gap-cutting in 2020 but showed recovery by 2023.
- Hemiedaphic Collembola peaked in controls with strong seasonal trends.
- Euedaphic responses were strongest in 2020 but faded by 2023.
- Vegetation structure emerged as the key driver of communities over time.



Balancing timber production with biodiversity conservation is challenging. Collembola, a key soil mesofauna group, contribute significantly to forest ecosystem functioning and bioindication. We examined long-term, seasonal effects of four management treatments, gap-cutting (G), clear-cutting (CC), retention tree group (R), and preparation cutting (P), in an 80-year-old oak forest, with untreated controls (C), after five and eight years. Collembola responses differed by ecomorphological group and season. Epigeic densities were lowest in G plots after five years but recovered in the eighth year. Hemiedaphic forms were most abundant in C plots, while G and CC plots remained reduced. Euedaphic Collembola responded in the fifth year, particularly in R during spring, but differences largely disappeared by the eighth year. By year eight, G supported the most diverse and even communities, whereas diversity declined in C and R plots. Seasonal differences were strongest in spring but weakened over time. Our findings highlight Collembola's capacity to recover after disturbance, supporting their use as indicators of ecological recovery. Treatments with limited canopy opening: G and P maintained community structure and enhanced diversity. As succession advanced, vegetation structure became a stronger driver than soil or seasonal factors. Collembola inform monitoring of forest regeneration and guiding sustainable management.

Keywords ecomorphological groups, rotation forestry, mesofauna assemblages, community recovery, continuous cover forestry, indicator species analysis

1 Introduction

Forests harbour the highest biodiversity of any terrestrial ecosystem and support numerous species dependent on continuous forest cover (Aerts and Honnay, 2011; Nordén et al., 2014; FAO, 2020). Much of this forest area is under human management (FAO and UNEP, 2020). In European broadleaved temperate forests, the prevailing silvicultural system is rotation forestry (Aszalós et al., 2022). Regeneration is achieved either artificially after clear-cutting or naturally through shelterwood systems, where one or two preparation cuttings precede final removal (Gonçalves and Fonseca,

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2023). Both approaches produce even-aged stands with rotation periods of 100–140 years for native deciduous hardwood tree species (e.g., oak species and beech). Within the framework of rotation forestry, the negative effects of these systems can be compensated by the retention of tree individuals or groups from the mature stand during final cutting (Gustafsson et al., 2012).

Although forestry practices can substantially modify forest structure, sustainable management is essential for maintaining ecological integrity while supporting the renewable use of forest resources. Modern silviculture aims to balance economic objectives with biodiversity conservation by retaining key forest functions and structures (Gustafsson et al., 2020). In recent decades, continuous cover forestry has gained prominence in these ecosystems. These systems maintain canopy continuity through low-intensity interventions, such as gap-cutting and overstorey thinning, applied within single- or group-selection systems (Pommerening and Murphy, 2004; Mason et al., 2022). Assessing the ecological effects of these contrasting management approaches requires reliable bioindicators, which are crucial for informing evidence-based policy and identifying practices that either support or compromise forest ecosystem health and biodiversity.

Much of forest diversity is found below ground, where stable, organic-rich soils host complex communities of organisms sustained by litter and deadwood (Bardgett and van der Putten, 2014). Collembola are among the most abundant soil mesofauna groups (Petersen and Luxton, 1982; Hopkin, 1997), with temperate forest densities of 10 000–40 000 individuals per m^2 (Pollierer and Scheu, 2017; Flórián et al., 2025; Junggebauer et al., 2025). Collembola provide essential ecosystem functions. They contribute to nutrient cycling and organic-matter decomposition through direct feeding activity (Visser, 1985; Filser, 2002; Kaneda and Kaneko, 2008; Potapov et al., 2016) and indirectly by regulating microbial communities and stimulating microbial processes (Verhoef and Brussaard, 1990; Coulibaly et al., 2019). They disperse fungal and bacterial propagules (Seastedt, 1984; Monteux et al., 2022) and form an important prey resource in soil food webs (Bilde et al., 2000; Potapov et al., 2022). Their diverse ecological traits generate species-specific responses to environmental variation. Collembola occupy distinct vertical layers linked to ecomorphology and display diverse ecological roles. Epigeic species live on the litter surface and vegetation, mainly consuming plant material and surface microbes (Hopkin, 1997; Potapov et al., 2016). Hemiedaphic species move between litter and mineral soil, and euedaphic species inhabit deeper soil layers, both groups feeding primarily on soil microorganisms (Potapov et al., 2016). Active dispersal is limited (Ojala and Huhta, 2001; Ponge and Salmon, 2013), so most species are relatively sedentary and strongly associated with their microhabitats. Disturbance may trigger dormancy, downward movement, or mortality (Frampton et al., 2001; Ponge, 2020). Owing to this sensitivity, Collembola often respond to subtle environmental changes before other soil physical or chemical indicators (Hopkin, 1997; van Straalen, 1998; Parisi et al., 2001). So, beyond their ecological importance, this group functions as a reliable indicator of forest management impacts (Ponge et al., 2003; Burrascano et al., 2021; Oettel and Lapin, 2021). Understanding their responses is essential for predicting shifts in soil processes under contrasting silvicultural regimes.

Silvicultural interventions alter Collembola communities primarily by modifying soil organic matter, nutrient dynamics, and microhabitat structure (Heiniger et al., 2015; Russell and Gergócs, 2019). Tree removal reduces both current and future detritus input, lowering the quantity and quality of organic matter that supports soil biota. Subsequent shifts in soil nutrient availability and microbial communities can trigger bottom-up effects on Collembola populations (Berch et al., 2011; Rousseau et al., 2018). Management practices also reshape physical and chemical soil conditions, such as pH, compaction, and porosity, and disrupt the fine-scale habitat structure on which many species depend (Kudrin et al., 2023). The canopy openings created by these interventions further intensify microclimatic fluctuations, increasing light and temperature while reducing air humidity (Kovács et al., 2020). These interacting environmental changes make the drivers of Collembola responses difficult to isolate. Moreover, local factors, including soil type, topography, and time since intervention, add further complexity (Salamon et al., 2008; Zhang et al., 2025b).

The magnitude of these effects varies widely across silvicultural practices. Low-intensity interventions such as irregular thinning often produce negligible changes in Collembolan density and diversity (Kudrin et al., 2023). Preparation (partial) cutting or retention tree groups similarly tend to maintain soil mesofaunal integrity (Kudrin et al., 2023). Gap-cutting generally causes moderate impacts, whereas more severe interventions, particularly clear-cutting, frequently result in substantial reductions in Collembola abundance (Siira-Pietikäinen and Haimi, 2009; Kudrin et al., 2023). Natural disturbance analogues reinforce this pattern: large-scale windthrows in the Tatra Mountains, comparable to clear-cutting, also led to marked declines in Collembola populations (Čuchta et al., 2019). Relatively few studies have assessed a broad spectrum of forest management treatments, with most work concentrating on clear-cutting. Broader experimental evidence is therefore needed to evaluate how contrasting silvicultural systems affect Collembola communities and to identify practices that best sustain soil biodiversity and function. This study compares four treatments representing two contrasting forestry systems widely used in Central Europe: clear-cutting (CC), preparation cutting (P) and retention tree groups (R) within rotation forestry, and gap-cutting (G) within continuous cover forestry. The experimental design also represents a gradient of disturbance intensity, ranging from undisturbed control plots to P and R, with G and CC representing stronger canopy openings. To our knowledge, this is the first experiment to assess the effects of this diverse set of treatments on Collembola communities within a single framework.

Previous works in the same experimental plots showed that several soil mesofaunal groups (e.g., Oribatida, Protura) declined with increasing disturbance from the control to P and R, with CC and G showing the strongest negative effects (Flórián et al., 2025; Gergócs-Winkler et al., 2025). Collembola analysed at a coarse taxonomic level showed slightly reduced densities in G, no significant changes in P and R, and seasonally variable but overall positive responses in CC (Flórián et al., 2025). Environmental changes influence collembolan life forms differently in forest ecosystems (Sławski and Sławska, 2019). As both clear-cutting and gap-cutting impose strong disturbance on the litter layer, we first hypothesised that the finer-resolution analyses would show reduced densities of hemiedaphic species in these treatments. Given the increased ground vegetation typically observed in CC, we further hypothesised that the previously reported high total densities of the group Collembola (Flórián et al., 2025) would be driven largely by the epigeic group. Third, euedaphic taxa, which generally respond more slowly to environmental change, were expected to remain negatively affected by CC and G. However, as vegetation richness often increases following canopy opening (Aszalós et al., 2023), we additionally hypothesised higher overall Collembola diversity in both CC and G. Because gap-cutting tends to preserve forest microclimatic conditions more effectively than clear-cutting (Kovács et al., 2020), we further predicted higher relative abundances of both epigeic and hemiedaphic species in G than in CC. Finally, based on our earlier findings, we hypothesised the least intensive interventions, P and R, to induce only minor changes in community structure and overall diversity. Thus, these treatments were predicted to maintain Collembola assemblages most similar to the untreated control, particularly by the final year of the two-year study, when vegetation regeneration had progressed further.

2 Materials and methods

2.1 Study site and design

The research was carried out on the Hosszú-hegy (Pilis Mts., Hungary, 47°40′ N, 18°54′ E), at an elevation ranging from 370 to 470 metres above sea level (see Kovács et al., 2018). The region experiences an annual mean temperature between 9.0 and 9.5 °C, with yearly precipitation levels of approximately 600–650 mm (Zoltán, 2010). The soil in the area is classified as lessivated brown forest soil (Luvisol), formed over a geological base of limestone and red sandstone, with loess deposits contributing to surface layers. Soil depth in the area varies along the slight topographic gradient from approximately 70 cm near the ridge to more than 200 cm in lower positions (Kovács et al., 2020). The study took place in a managed, even-aged oak–hornbeam forest spanning 40 hectares, which was 80 years old at the start of the experiment (2014). The area is part of the Natura 2000 network (habitat code: 91G0; European Commission, 1992). Sessile oak (*Quercus petraea* (Matt.) Liebl.) dominates the overstorey, with average tree height and diameter at breast height (DBH) measuring 21 m and 28 cm, respectively (for more details see Kovács et al., 2018). Other common canopy species include turkey oak (*Quercus cerris* L.), European beech (*Fagus sylvatica* L.), and wild cherry (*Prunus avium* L.), while the secondary layer is primarily composed of hornbeam (*Carpinus betulus* L.) and manna ash (*Fraxinus ornus* L.). The herbaceous understorey, which covers roughly 30% of the forest floor, is mostly dominated by *Carex pilosa* Scop. and *Melica uniflora* L. (Tinya et al., 2019; Aszalós et al., 2023).

Forestry treatments were implemented between December 2014 and January 2015. A total of five treatments were established, including a control, and were applied in a randomised complete block design across six replicate blocks (Fig. 1). These treatments represent an increasing gradient of disturbance intensity to forest structure and the soil environment, ranging from intact forest conditions to large canopy openings:

Control (C): A closed-canopy forest segment left intact without intervention.

Retention tree group (R): Within the clear-cuts, a circular patch of former forest (20 m diameter) containing 8–12 mature trees and the understorey was left untouched.

Preparation cutting (P): A partial cutting (regular thinning) where approximately 30% of the dominant overstorey and all trees in the secondary canopy were removed within an 80 m diameter area.

Gap-cutting (G): A small, circular gap (20 m diameter, circa one tree height) was created by removing trees from the closed-canopy stand. This treatment mimics the selective harvesting approaches used in continuous cover forestry systems.

Clear-cutting (CC): A complete removal of trees in a circular 0.5 hectare area (80 m in diameter).

2.2 Background variables

Vegetation was assessed within each plot using a 2 m × 2 m quadrat each year, during two survey periods: once in

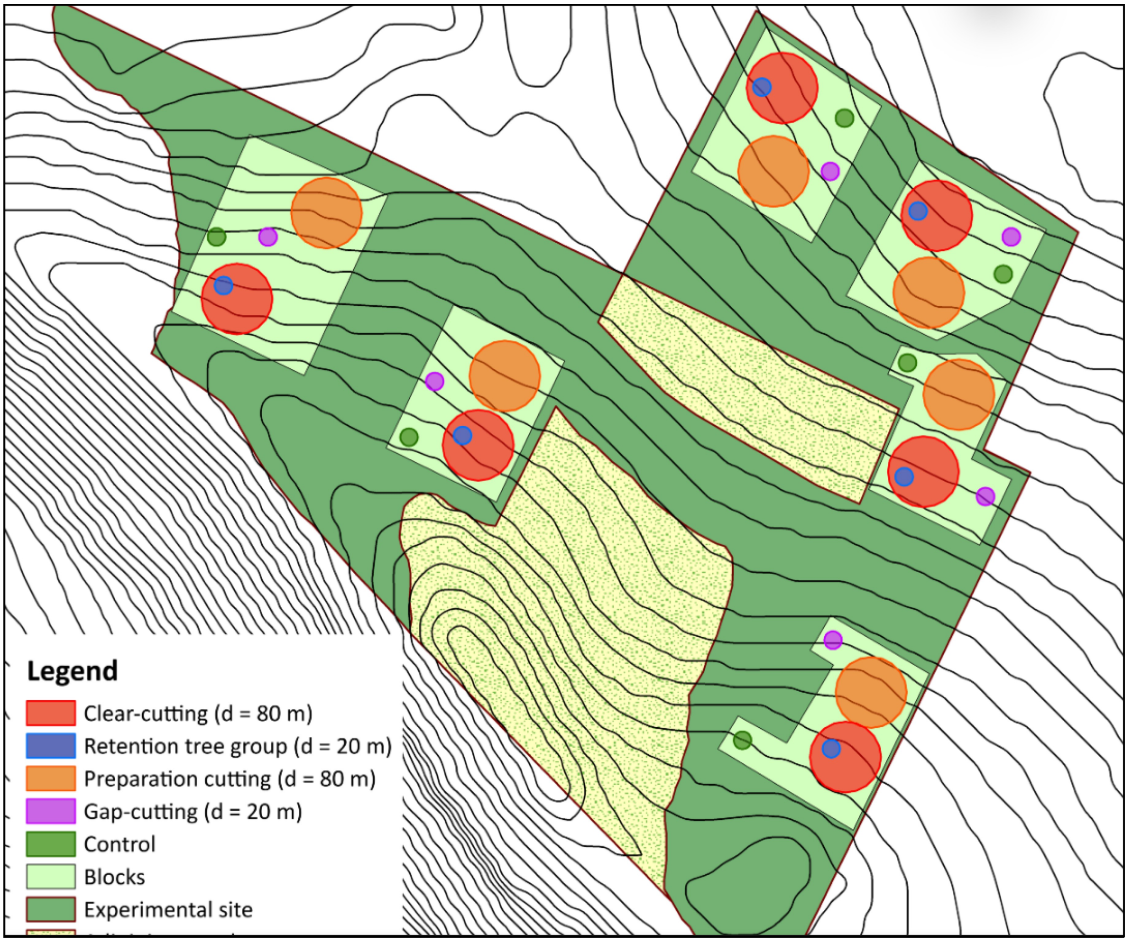

Fig. 1 Layout of the Pilis Forestry Systems Experiment conducted in the Pilis Mountains, Hungary.

April to document early spring flora, and again in June. Within each quadrat, the percentage cover of all herbaceous plants and woody individuals shorter than 50 cm was visually estimated. Overall vegetation cover was calculated by summing the cover percentages of all species, and species richness was recorded as the total number of species per quadrat. Sapling density, defined as the number of woody individuals taller than 50 cm with a diameter at breast height (DBH) of less than 5 cm, was also recorded. Additionally, four litter samples (each 30 cm × 30 cm) were collected near the vegetation quadrats in May 2020 within each plot. These samples were oven-dried, and litter mass (g m^{-2}) was calculated based on dry weight.

Soil sampling was conducted on two occasions. The first campaign took place in May 2020, when four subsamples were collected per plot from the upper 20 cm of the mineral soil, close to the points used for litter collection. The second campaign was carried out in April 2023, with two subsamples per plot taken simultaneously with faunal sampling. All samples were air-dried and passed through a 2 mm sieve prior to laboratory analyses.

Soil pH was assessed potentiometrically using a 1:2.5 suspension of soil and distilled water (10 g soil in 25 mL), following the Hungarian Standard (MSZ-08-0205, 1978). For total carbon and nitrogen determination, the <2 mm fraction was further sieved to <0.5 mm, and subsamples from each plot were pooled into one composite. Total carbon content was measured by dichromate oxidation with colorimetric detection (MSZ 21470/52, 1983), while nitrogen concentrations were obtained using the Kjeldahl digestion method (Bremner, 1965). Available phosphorus and potassium were extracted with an ammonium acetate–lactate (AL) solution and expressed as AL-P_2O_5 and AL-K_2O (Egnér et al., 1960). Soil organic matter (SOM) was quantified with the modified Walkley-Black method (FAO, 2019).

Microclimatic conditions were continuously monitored in the centre of each plot. Variables included soil temperature (°C), relative air humidity (%) at 130 cm above ground level, and volumetric soil water content ($m^3 m^{-3}$) in the top 20 cm of the soil. Different instruments were used in April 2020 versus the later months. In April, soil temperature and relative humidity were recorded using Onset S-TMB-M0020 and T/RH sensors, respectively. Sensors were housed in passively ventilated radiation shields to minimise solar interference. Soil water content was measured with S-SMD-M0050 moisture sensors, and all sensors were connected to

HOBO H021-0020 loggers. Subsequently, TOMST TMS-4 devices were used to record both soil temperature and moisture (Wild et al., 2019), while MCC USB-502 loggers measured relative humidity. Data were logged every 15 minutes. For background environmental variables in our study, mean values for each plot were calculated based on the daily means over the 14 days preceding the soil fauna sampling.

2.3 Fauna sampling

Soil mesofaunal communities were sampled from each plot during three distinct seasonal periods in both 2020 and 2023: spring (pre-vegetation phase; 2 April), summer (vegetation peak; 10 June), and autumn (post-vegetation; 10 October). At each time point, 30 samples were collected, corresponding to one sample per plot (five treatments × six replicate plots). Samples were taken from the centre of each plot using a cylindrical metal corer (8 cm in diameter, 8 cm deep; 402 cm^3 volume) to minimise edge effects. The six replicate plots were considered adequate to capture spatial heterogeneity within treatments. Immediately following collection, samples were transported to the laboratory for faunal extraction using Berlese funnels over one week, with 70% ethanol as the collection and preservation fluid. Specimens were then sorted under a stereomicroscope and assigned to major mesofaunal groups and counted, as reported in a previous paper (Flórián et al., 2025).

Collembola were identified at the species level, using identification keys (Stach, 1960; Fjellberg, 1998; Bretfeld and Dunger, 1999; Potapov, 2001; Thibaud et al., 2004; Hopkin, 2007; Jordana, 2012) under a Nikon SMZ25 digital microscope, and if further details were necessary, under Nikon Eclipse Ts2R microscope. In cases where precise species identification was not possible, individuals were classified as morphospecies. Each Collembola species was further categorised into one of three ecomorphological groups (epigeic, hemiedaphic, euedaphic), based on information from the literature data (Dányi and Traser, 2008; Potapov et al., 2016; Sławski and Sławska, 2019; Yin et al., 2019) (see Supplementary Table S1). Where no ecological data were available for a given species, inferences were made based on the ecology of closely related taxa, or morphometrical measurements were made on those individuals. Faunal density was standardised to 1 m^2 area (individuals m^{-2}), by dividing the total abundance by the surface area of the corer (0.005 03 m^2). Species occurring in fewer than five samples or less than ten specimens were excluded from the following analyses, which are based on species-level data (RDA, indicator species analysis, Rényi diversity), but presented in the ecomorphological group concepts (Supplementary Table S1).

2.4 Statistical analyses

All statistical analyses were conducted in R version 4.5.1 (R Core Team, 2025). To characterise environmental variation among forestry treatments and across seasons, we performed principal component analyses (PCA) using the PCA function in the ‘vegan’ package (Oksanen et al., 2025), where environmental variables were used as variables and plots as objects. Data were analysed separately for 2020 and 2023. Two categories of environmental variables were examined: (i) continuously measured parameters (soil temperature, relative humidity, volumetric water content) and (ii) variables measured once per year (vegetation species richness, vegetation cover, sapling density, soil pH, humus content, litter weight and hygroscopicity; the latter two available only for 2020). All environmental variables were standardised prior to analysis (z-transformation). For continuously measured variables, seasonal trends were removed by regressing each variable against season (spring, summer, autumn) and extracting model residuals. These season-corrected residuals were used as PCA input to isolate treatment-related environmental structure from seasonal fluctuations.

To evaluate how continuously measured microclimatic variables differed between years (2020 vs. 2023) and among seasons, we applied two-way ANOVA models with year, season, and their interaction as fixed factors. In the case of annually measured variables, we fitted separate one-way ANOVA models for each environmental variable. For each model, we assessed the main effect of year or season, and conducted post-hoc pairwise comparisons using estimated marginal means with Tukey adjustment, using the *emmeans* function of the ‘emmeans’ package (Lenth and Piaskowski, 2025). To evaluate differences in environmental conditions between years (2020 vs. 2023) and among seasons, we fitted separate one-way ANOVA models for each environmental variable.

To examine how Collembola community composition responded to forestry treatments and seasonal variation, we applied redundancy analysis (RDA) using the ‘vegan’ package. Separate RDAs were again conducted for 2020 and 2023. Species data were Hellinger-transformed (Legendre and Gallagher, 2001) to account for the compositional nature of community data. Treatment (five levels) and season (three levels) were included as explanatory variables in the constrained ordinations. RDA models were fitted using the *rda* function of ‘vegan’, and significance was assessed with permutation tests (999 permutations) for the overall model, individual terms, and canonical axes (using the *anova.cca* function). To identify the species most strongly associated with the main RDA gradients, Euclidean distances of species scores from the origin were calculated, and the ten species with the strongest axis correlations were retained for interpretation.

When analysing the data of the three ecomorphological groups, due to the right-skewed distribution of different densities, data were log(x+1) transformed to achieve normality prior to statistical evaluation. Linear mixed-effects models were implemented using the *lmer* function of the 'lme4' package (Bates et al., 2015). Each model considered the density of an ecomorphological group as the response variable, with treatment as a fixed effect and block as a random intercept. For models covering all years, season was included as an additional random intercept, whereas seasonal models excluded this term. Model assumptions were evaluated through diagnostic checks of residuals and dispersion. Pairwise treatment differences were evaluated using estimated marginal means with Tukey's correction for multiple comparisons, implemented using the 'emmeans' package (Lenth and Piaskowski, 2025).

To identify species significantly associated with different treatments, we performed an indicator species analysis using the group-equalised indicator value method (IndVal.g; De Cáceres and Legendre, 2009). The analysis was conducted using the *multipatt* function from the 'indicspecies' package (De Cáceres et al., 2025). The significance of species associations was tested using 9999 permutations, and species with $p < 0.05$ were considered significant indicators of their respective treatment groups. The IndVal.g index represents the strength of association, ranging from 0 to 1, where higher values indicate stronger species-group relationships.

To assess species diversity across treatments, Rényi diversity profiles were calculated separately for the two years, and also three seasons within them, using the renyi() function from the vegan package. Rényi diversity is a generalisation of diversity indices, incorporating different sensitivity levels to rare and dominant species (Tóthmérész, 1997). The analysis was performed on species density data using a range of alpha values (0.1 to 4) to capture different aspects of diversity. The results were plotted as diversity profiles, where lower alpha values emphasise rare species, and higher alpha values approach dominance-based measures.

3 Results

In total, 10 306 specimens representing 82 Collembola species were identified (Supplementary Table S1). Of these, 40.3% were classified as epigeic, 43.5% as hemiedaphic, and 16.2% as euedaphic. Despite the high species richness, a small subset, 10 species, accounted for 90% of all individuals sampled (Supplementary Table S1), indicating a highly uneven distribution in community composition.

3.1 Environmental effects of forest management treatments

The four different PCAs (2 years, two types of variables) showed distinct environmental patterns between the treatments. In each case, the first two PCA axes explained a high amount of total variance (Fig. 2, Supplementary Table S2). For continuously measured variables, after removing seasonal effects, PC1 represented a humidity–temperature gradient in both years, with high positive loadings for relative humidity (RH) and strong negative loadings for soil temperature. PC2 was dominated by volumetric water content (VWC) (Supplementary Table S3). Treatment differences were consistent between years: CC plots aligned most strongly with high RH and VWC, while G plots again showed the closest association with high VWC. R plots were moderately associated with soil temperature (it decreased in 2023), whereas C and P plots remained nearer the multivariate centre (Fig. 2A, 2B, Supplementary Table S4).

For variables measured once per year (annually), similar patterns were detected both years as well. N, P, humus, pH, and vegetation cover and species richness were among the strongest contributors to PC1 and PC2 (Supplementary Table S3). The main treatment separation was evident along PC2 in both years (Fig. 2C, 2D). Leaf litter (data were missing from 2023) was the main factor associated with C and R treatments. Vegetation cover and sapling density separated along positive PC2, associated with CC and G. P and R occupied the middle position, while these separations were not so evident in 2023 (Fig. 2C, 2D).

Based on the key environmental variables, clear seasonal and interannual differences were detected (Supplementary Tables S5–S6). Compared with 2020, spring conditions in 2023 were generally more humid, while summer exhibited higher soil moisture and both summer and autumn were warmer. In contrast, autumn 2023 showed lower relative humidity and reduced soil moisture relative to autumn 2020, indicating that late-season conditions in 2023 were overall warmer and drier.

3.2 Collembola composition across forest management treatments

The RDA analyses revealed consistent effects of forest treatment and season on Collembola communities in both 2020 and 2023. In both years, treatment and season emerged as significant predictors (Tables S7, S8). In both years CC and G were separated from P, R and C, mainly along the RDA2 scores (Fig. 3). In 2020 CC and C had negative scores, while P and R positive scores. Strong species contributors to this axis included *Lepidocyrtus lignorum, Isotomiella minor*, *Isotoma caerulea*, *Mesaphorura macrochaeta* and *Sphaeridia pumilis*. RDA2 reflected seasonal structuring, with spring and summer plots positioned

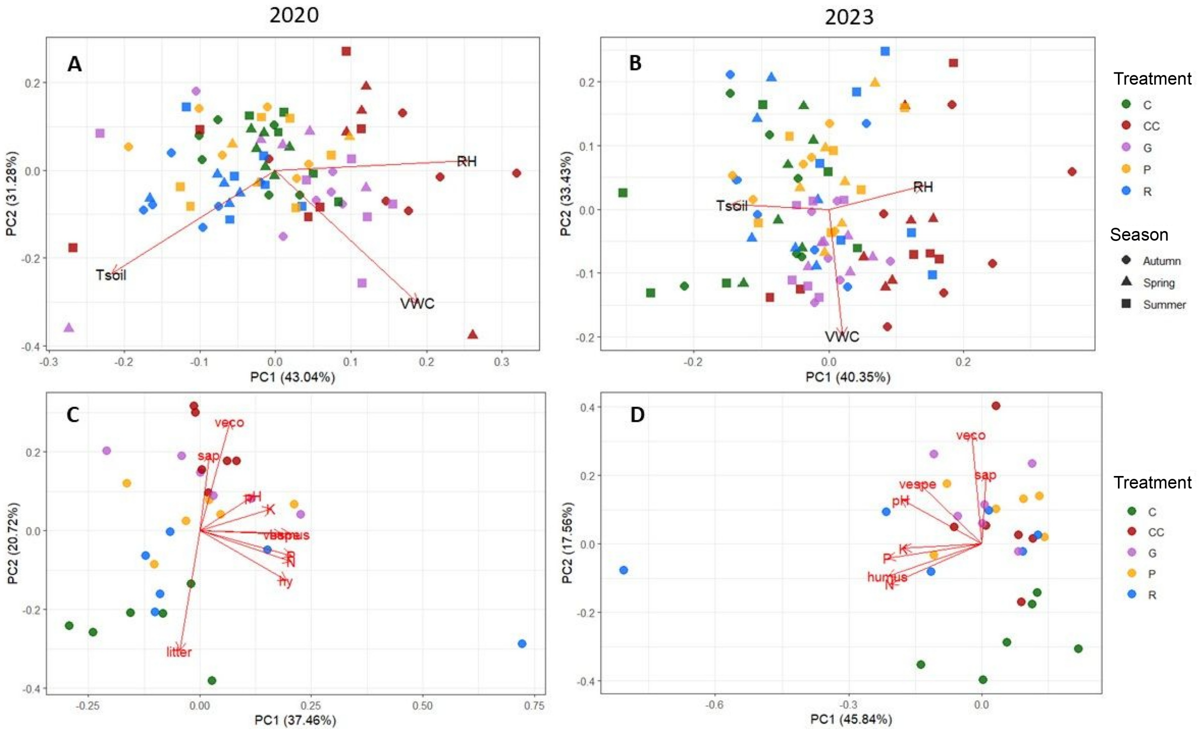

Fig. 2 Principal Component Analyses (PCA) of environmental variables across Forestry Treatments, four distinct PCAs for continuously measured variables from 2020 (A) and 2023 (B) (seasonal effects were removed), and for annually measured environmental variables in 2020 (C) and 2023 (D). Treatments: C, Control; CC, clear-cutting; R, retention tree group; P, preparation cutting; G, gap-cutting. Environmental variables: RH, relative humidity; Tsoil, soil temperature; VWC, volumetric water content; sap, number of saplings; veco, vegetation cover; vespe, vegetation species richness; litter, leaf litter weight; hy, hygroscopicity.

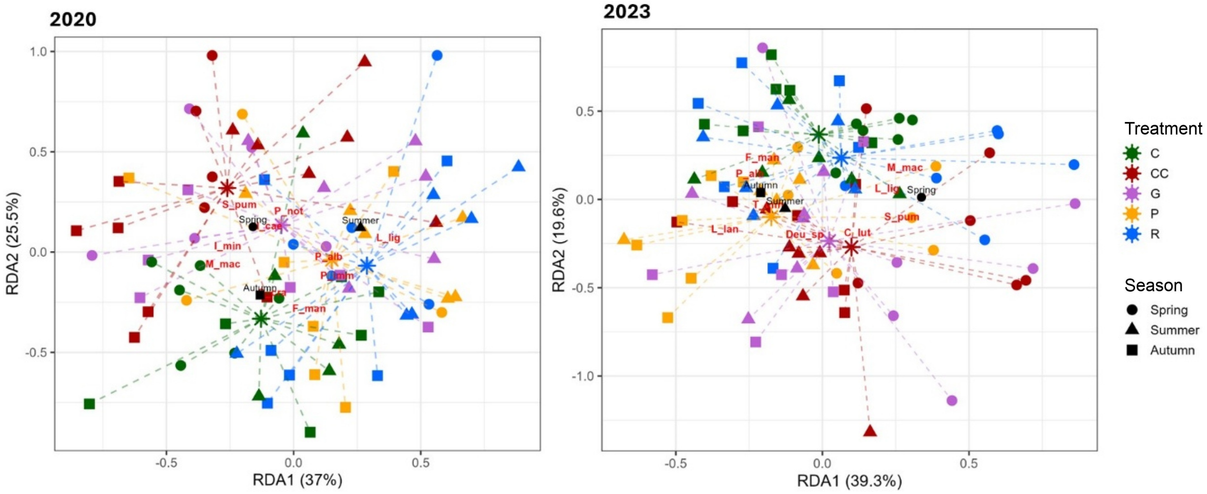

Fig. 3 Redundancy analysis (RDA) of dominant Collembola species in 2020 and 2023. Explanatory variables are season and treatment. Species abbreviations are listed in Supplementary Table S1; only key species are shown in the figure: C_lut, *Ceratophysella luteospina*; Deu_sp., *Deuteraphorura* sp.; F_man, *Folsomia manolachei*; I_min, *Isotomiella minor*; L_lan, *Lepidocyrtus lanuginosus*; L_lig, *Lepidocyrtus lignorum*; M_mac, *Mesaphorura macrochaeta*; O_cra, *Oncopodura crassicornis*; P_alb, *Pseudosinella alba*; P_imm, *Pseudosinella immaculate*; P_not, *Parisotoma notabilis*; P_pan, *Protaphorura pannonica*; *S_pum*, *Sphaeridia pumilis*; T_min, *Tomocerus minutus*. Treatments are as follows: C, control; CC, clear-cutting; G, gap-cutting; P, preparation cutting; R, retention tree groups.

higher on this axis. Species such as *Parisotoma notabilis*, *S. pumilis*, and *I. caerulea* showed positive correlations with RDA2, while *Folsomia manolachei* and *Oncopodura crassicornis* were associated with negative values (Table S9). In 2023, RDA1 represented a seasonal gradient, spring had positive scores, while summer and autumn had negative scores. Here, species such as *Mesaphorura macrochaeta, Sphaeridia pumilis*, and *Lepidocyrtus lignorum* were associated with positive scores, whereas *Lepidocyrtus lanuginosus*, *Tomocerus minutus*, and *Pseudosinella alba* were aligned with negative scores (Fig. 3, Table S9). RDA2 showed a treatment effect, CC and G had negative values, C and R positive values and P had a central position. Species strongly positively associated with RDA2 included *F. manolachei*, *M. macrochaeta*, *P. alba*, and *Pseudachorutes parvulus*, while *Deuteraphorura* sp. and *Ceratophysella luteospina* showed negative associations (Fig. 3, Table S9). Both ordinations indicated separation of C and R from CC and G, while P occupied intermediate positions, although this separation was stronger in 2023 (Fig. 3).

3.3 Effects of forest management treatments on ecomorphological groups

In the case of epigeic Collembola, treatments significantly influenced densities in 2020 (Supplementary Table S10). For the whole year, post hoc comparisons showed that CC and P supported significantly higher densities than the G treatment, while C and R displayed intermediate values (Fig. 4A, Supplementary Table S10). In spring, the lowest densities occurred in G, which was significantly lower than CC. In the later months, no significant differences were detected, although in summer, P had the highest densities and G the lowest (Fig. 4B). In 2023, treatment effects were not significant, although P and G exhibited the highest values (Fig. 4C, Supplementary Table S10). Despite the generally low densities in 2020, spring 2023 recorded the highest densities in G (Fig. 4D, Supplementary Tables S10, S11).

For hemiedaphic species, treatments significantly affected densities in both years (Supplementary Table S10). In both years, the C plots supported significantly higher densities than CC, G, and (in 2020) R, while P showed intermediate values (Fig. 4E, G). In 2020, spring revealed the clearest treatment effects (Fig. 4F, Supplementary Table S10): C plots supported the highest densities, significantly exceeding those in G and P, and CC also had higher densities than G. In 2023, this pattern was not evident; however, in both summers, a similar trend persisted, with C showing the highest mean values. In autumn 2023, a non-significant treatment effect was observed, with C and R exhibiting the highest mean densities (Fig. 4H, Supplementary Table S10).

Considering euedaphic Collembola, the two years displayed different patterns (Fig. 4I–4L). Overall, in 2020, the C plots supported significantly higher densities than the R plots, although this difference was absent in 2023 (Fig. 4I, 4K; Supplementary Table S10). When analysed seasonally, significant differences occurred only in spring 2020: R exhibited the lowest densities, significantly lower than those of C and CC, while P had significantly lower densities than CC. In 2023, the opposite non-significant trend appeared, with G showing the lowest densities and R among the highest (Fig. 4L, Supplementary Table S10).

3.4 Indicator species of forest management treatments

Indicator species analysis revealed distinct associations between specific taxa and forestry treatments, consistent across years and seasons (Table 1). Across both years, several species showed significant treatment specificity. Control plots were characterised by *F. manolachei* while *P. parvulus* was indicative of R plots as well, suggesting some overlap in favourable conditions for this species across less disturbed treatments. Preparation cutting had strong associations with *Arrhopalites pygmaeus* and *C. luteospina*. *Sminthurinus aureus* was an indicator of CC in both years. Some yearly differences occurred as well. In 2020, *T. minutus* was characteristic of C, while in 2023 it was indicative of P as well, where *Lepidocyrtus curvicollis*, another epigeic species, became an indicator species. This was the case for *M. macrochaeta* as well, which in 2023 became indicative of R and CC as well. In 2023, *Lepidocyrtus cyaneus* was an additional indicator in C, while *Deuteraphorura* sp. appeared in treatment combinations CC+P. It is also notable that G lacked an indicator species, reflecting its intermediate composition. C had the highest number of indicator species (Table 1). When considering seasonality, several species appeared in spring (*S. pumilis*, *M. macrochaeta*, *I. minor*, *I. caerulea*, *Deuteraphorura* sp., and *Pseudosinella wahlgreni*) and summer (*T. minutus*, *Isotoma viridis*, and *Pseudosinella immaculata*) or the combination of both seasons (*Megalothorax minimus*, *Lepidocyrtus lignorum*, *Homidia koreana*, and *P. notabilis)* as indicators, whereas no indicator of autumn was found (Table 1D).

3.5 Rényi diversity profiles

Rényi diversity profiles characterise changes in community structure across a continuum of sensitivity parameters (α = 0.1–4). In these profiles, higher curves indicate greater diversity, while intersecting curves suggest that diversity rankings depend on the relative contribution of rare versus dominant species. Low α values (≈0–1) give more weight to rare species, whereas higher α values (>1) increasingly emphasize dominant species and evenness. The profiles differed among treatments, years, and seasons (Fig. 5, Supplementary Fig. S1). In both years, the diversity curves for most treatments intersected, making distinct patterns difficult to distinguish (Fig. 5). Nevertheless, several general trends were apparent. In 2020, the C treatment displayed the highest diversity at low α values, indicating a community rich in rare species; however, in 2023, it showed the lowest values (Fig. 5A). In both years, its curve dropped most strongly at low α (⩽1) and then flattened, indicating that evenness decreases as α increases and a smaller set of taxa becomes increasingly influential. By 2023, the C treatment consistently exhibited the lowest diversity across the

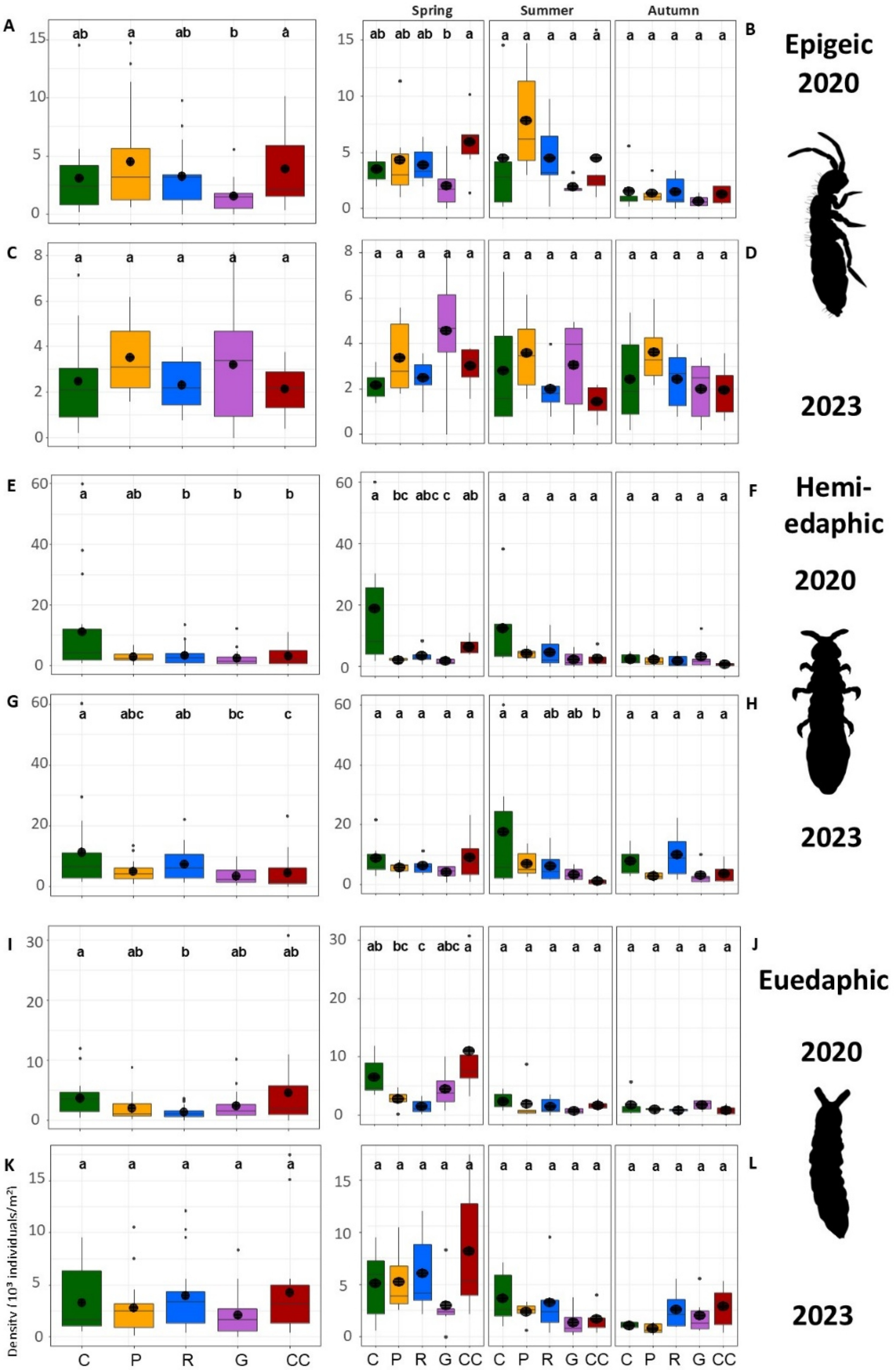

Fig. 4 Densities (10^3 individuals m^{-2}) of different Collembola groups across five treatments in 2020 and 2023, shown annually and by season. Treatments are as follows: C, control; CC, clear-cutting; G, gap-cutting; P, preparation cutting; R, retention tree groups. Dots represent mean values. Different letters indicate significant differences between treatments ($p < 0.05$), assessed separately for the annual and seasonal data.

entire α range (Fig. 5B), reflecting a marked decline in both richness and evenness over time. In contrast, the CC and G treatments showed relatively high and stable diversity across the full α spectrum. From α = 1 onward, G maintained the highest profile of all treatments, suggesting that it supported a well-balanced community with both rare and dominant species present in comparatively even proportions. The P treatment displayed high diversity, similar to C

Table 1 Indicator species associated with forest management treatments overall (A), across years 2020 (B) and 2023 (C), and seasons (D), based on indicator species analysis.

Treatment group	Species	Indicator value (IndVal.g)	*p*-value
A. Indicator species associated with forest management treatments across both years (2020 and 2023).			
C	*Folsomia manolachei*	0.352	<0.01
	Pseudachorutes parvulus	0.279	0.02
P	*Arrhopalites pygmaeus*	0.485	<0.01
	Ceratophysella luteospina	0.248	0.033
C+R	*Pseudachorutes parvulus*	0.303	0.049
B. Indicator species associated with forest management in 2020			
C	*Folsomia manolachei*	0.397	<0.01
	Tomocerus minutus	0.348	<0.01
	Mesaphorura macrochaeta	0.300	0.04
CC	*Sminthurinus aureus*	0.422	<0.01
P	*Arrhopalites pygmaeus*	0.485	<0.01
	Ceratophysella luteospina	0.248	0.03
C+R	*Pseudachorutes parvulus*	0.303	0.05
C. Indicator species associated with forest management in 2023			
C	*Folsomia manolachei*	0.352	<0.01
	Pseudachorutes parvulus	0.279	<0.01
	Lepidocyrtus cyaneus	0.205	0.05
CC	*Sminthurinus aureus*	0.292	<0.01
P	*Arrhopalites pygmaeus*	0.234	0.03
C+P	*Lepidocyrtus curvicollis*	0.264	<0.01
	Tomocerus minutus	0.215	0.04
CC+P	*Deuteraphorura* sp.	0.296	<0.01
C+CC+R	*Mesaphorura macrochaeta*	0.218	0.03
D. Indicator species associated with seasons across both years (2020 and 2023).			
Spring	*Sphaeridia pumilis*	0.438	<0.01
	Mesaphorura macrochaeta	0.379	<0.01
	Isotomiella minor	0.278	<0.01
	Isotoma caerulea	0.199	<0.01
	Deuteraphorura sp.	0.190	0.03
	Pseudosinella wahlgreni	0.171	0.05
Summer	*Tomocerus minutus*	0.246	<0.01
	Isotoma viridis	0.221	<0.01
	Pseudosinella immaculata	0.168	<0.01
Spring+summer	*Megalothorax minimus*	0.228	<0.01
	Lepidocyrtus lignorum	0.213	<0.01
	Homidia cf. koreana	0.210	0.01
	Parisotoma notabilis	0.180	0.03

Significant species-treatment or species-season associations ($p < 0.05$) are listed with their corresponding indicator values and p-values. Results are shown for each year, for both years combined, and across seasons. Treatment abbreviations: C, control; P, preparation cutting; R, retention tree group; CC, clear-cutting; G, gap-cutting. Combined treatments or seasons (e.g., C+R, C+CC+R, and spring+summer) indicate species associated with more than one factor level simultaneously.

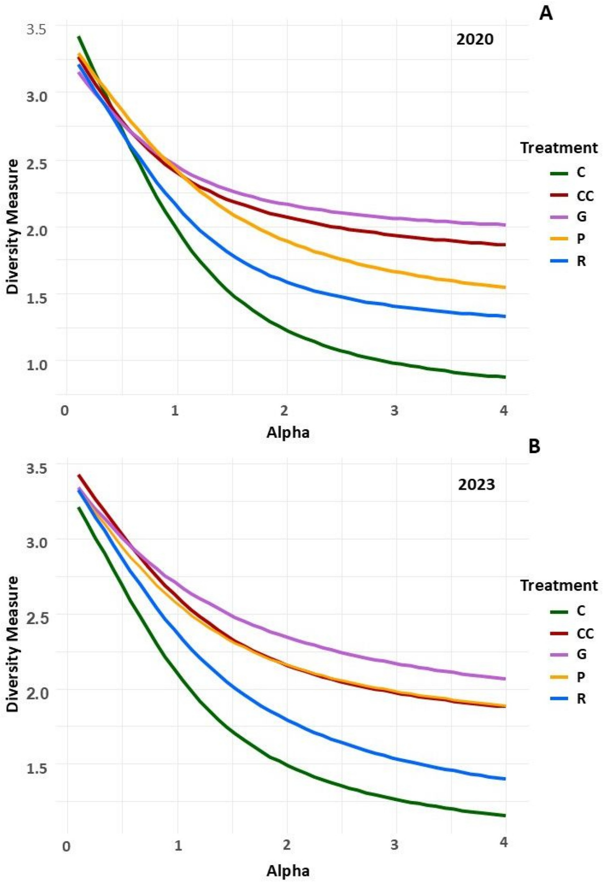

Fig. 5 Rényi diversity profiles of Collembola communities across five forest management treatments, based on samples collected in 2020 (A) and 2023 (B). Treatment abbreviations: C, control; P, preparation cutting; R, retention tree group; CC, clear-cutting; G, gap-cutting. The profiles show how the diversity index varies with the parameter α (ranging from 0.1 to 4), where higher curves reflect greater diversity. At α = 0, the index corresponds to species richness; at α = 1, it approximates Shannon diversity; and at α = 2, it reflects the logarithm of the reciprocal Simpson index.

and CC at low α values. In 2020, it declined more sharply beyond α = 1, indicating a less even community. In 2023, however, its profile closely resembled that of CC. The R treatment showed an intermediate pattern, beginning with moderate richness and gradually declining to maintain lower diversity than P at higher α values. Although R consistently supported higher diversity than C in the annual profiles, this was not true seasonally: in the seasonal analysis, autumn consistently exhibited the lowest diversity profiles (Supplementary Fig. S1).

4 Discussion

4.1 Treatment effects

Forest management treatments influenced Collembola densities across all ecomorphological groups, although the magnitude and consistency of these effects varied with group, season, and year. The experimental design also represents an increasing gradient of disturbance intensity, from undisturbed control stands through retention tree groups and preparation cutting to gap cutting and clear cutting. The RDA ordinations showed clear treatment-severity-related differences in community structure along this gradient. Control and retention tree group plots tended to cluster together, indicating similar assemblages, whereas clear-cutting and gap-cutting areas formed an opposing cluster, reflecting stronger disturbance effects. Preparation-cutting plots occupied an intermediate position between these two groups. These trends can be seen in diversity profiles as well.

4.1.1 No initial anthropogenic disturbance

Density values in the control plots were high across all ecomorphological groups, particularly among hemiedaphic species, likely due to the absence of disturbance and the presence of a well-developed litter layer. However, high density did not correspond to high diversity: although species richness was initially the greatest, control plots exhibited the lowest overall diversity across the entire α range five years post-treatment. Only the R plots, which experienced disturbance only in the surrounding matrix, showed similarly low values in autumn.

In the control treatment, diversity declined steadily at higher α values, indicating a strongly uneven community dominated by a few abundant taxa. While the epigeic cosmopolitan *L. cyaneus* occurred as an indicator species, most dominant taxa (*F. manolachei*, *M. macrochaeta*, *P. parvulus*) were eu- or hemiedaphic forest specialists typically associated with substrates rich in organic carbon or with high C/N ratios (Deharveng, 1996; Barrocas et al., 1998; Kováč et al., 2005). Such conditions are largely determined by leaf litter quantity and quality, which shape both resource supply and microhabitat structure, key drivers for Collembola communities (Kopeszki and Jandl, 1994; Osler et al., 2006; Pollierer and Scheu, 2017). In our study, the control plots contained the deepest humus and litter layers, particularly in spring, likely supporting the elevated densities of eu- and hemiedaphic species. The spring indicator *I. minor*, for example, is known to respond positively to rapidly decomposing litter (Kováč et al., 2005). This pattern was also observed for oribatid mites within the same experiment (Gergócs-Winkler et al., 2025), where leaf litter was the main factor shaping their communities. By contrast, epigeic species showed slightly lower densities in the control plots, especially in spring. Part of this may reflect their life cycles. Several epigeic taxa (e.g. *Tomocerus* spp.) overwinter as eggs, with adults such as *T. minutus* appearing only in summer. It also reflects the structurally simple understorey of the even-aged oak–hornbeam forest, which provides fewer microhabitats and less food for vegetation-associated species than the more heterogeneous conditions created by natural or anthropogenic disturbance events.

The strongly uneven community in the control plots suggests that environmental stability favoured competitively dominant species, reducing coexistence. This pattern aligns with the intermediate disturbance hypothesis (Connell, 1978), which predicts lower diversity under very low disturbance due to competitive exclusion compared to habitats with higher disturbance. In our experiment, even modest disturbance in the other treatments increased habitat heterogeneity and vegetation development, opening ecological space for a broader range of species. The magnitude of the responses, however, depended both on the severity of the initial disturbance and on the extent of vegetation regeneration that had occurred since then.

4.1.2 Low-level initial disturbance

The retention tree group treatment and preparation cutting represent the two low-intensity interventions in our study, and as we hypothesised, both produced community patterns broadly similar to the control plots. Collembola density and diversity remained close to undisturbed levels, reflecting the limited canopy opening and the maintenance of forest floor microclimates. These treatments supported slightly higher understorey vegetation than the control, which may have contributed to their elevated Collembola species richness. Rényi diversity profiles showed diversity comparable to, or marginally higher than, the control, particularly eight years after the intervention. The presence of forest-associated indicator species (e.g., *P. parvulus* in R; *L. curvicollis* and *T. minutus* in P), mostly litter-dwelling taxa (Tamura, 1967), further indicates that both treatments preserved largely forest-like habitat conditions. Although some contrary results exist (Chaudhary et al., 2016), species richness was expected to differ from the control. In our case, both R and P initially exhibited lower richness five years after disturbance, but as regeneration progressed, richness exceeded that of the control, consistent with earlier findings (Kudrin et al., 2023). R also supported the highest plant diversity (Aszalós et al., 2023), which likely enhanced Collembola richness through increased resource and microhabitat availability (Sabais et al., 2011; Zhang et al., 2022).

Despite their similarities, R and P differed in the magnitude and timing of faunal responses. R was the least disturbed treatment, yet five years after intervention, it still showed reduced densities of eu- and hemiedaphic Collembola. A comparable decline was observed in *Enchytraeidae* during the early phase of the experiment, attributed to locally drier soil conditions (Boros et al., 2019), and this mechanism likely explains the reduced densities in R. These differences diminished three years later, probably because the developing regeneration layer in the adjacent CC plots mitigated edge effects and allowed Collembola communities in R to stabilise.

By contrast, P generated a somewhat stronger ecological response due to relatively moderate canopy opening and enhanced herbaceous cover. Epigeic species, typically more mobile and disturbance-tolerant, responded rapidly, reaching their highest densities here, especially during the summer vegetation peak, reflecting improved shelter and food supply (Salamon et al., 2008). Euedaphic and hemiedaphic groups, which generally show delayed or weaker responses to disturbance (Chauvat et al., 2003), remained intermediate between the control and higher-disturbance treatments. Two species typical of moss- and litter-associated microhabitats, *A. pygmaeus* and *C. luteospina*, often associated with fungi (Bretfeld and Dunger, 1999; Thibaud et al., 2004), were characteristic of P in both years. *Deuteraphorura* sp., a shared indicator of CC and P, highlights the partial convergence of these treatments. Overall, P combined features of both forested and moderately disturbed conditions.

Both low-intensity interventions therefore retained forest-adapted Collembola communities, but P produced more pronounced increases in diversity and epigeic density. Epigeic species, especially larger taxa such as *Tomocerus* and *Entomobrya*, play important ecological roles by fragmenting litter and modulating microbial activity (Chahartaghi et al., 2005; Hasegawa et al., 2006). Their increased presence in P plots may enhance litter decomposition and accelerate nutrient cycling, with positive feedback on plant nutrient uptake (Faber and Verhoef, 1991; Partsch et al., 2006). Thus, through the combined effects of moderate canopy opening and biologically driven nutrient turnover, preparation cutting illustrates how low-level disturbance can simultaneously support soil faunal activity and vegetation development, aligning with predictions of the intermediate disturbance hypothesis.

4.1.3 High-level initial disturbance

Clear-cutting and gap-cutting were the two most intensive canopy-opening treatments in our study, although they differed markedly in disturbance severity. Despite this, they produced several shared ecological outcomes. In both treatments, Collembola communities reacted after five years to increased light, warmer microclimates, higher soil humidity, and enhanced herbaceous cover, environmental changes documented for these plots in a separate publication based on the same experiment (Kovács et al., 2020; Aszalós et al., 2023). By the eighth year, Collembola species richness exceeded that of the control plots, and both treatments supported communities with high evenness and elevated Rényi diversity profiles, indicative of greater habitat heterogeneity. Although disturbance can elevate diversity through the influx of generalist or non-forest species (Fedrowitz et al., 2014; Kirby, 2015; Tinya et al., 2019), neither CC nor G became dominated by disturbance-tolerant taxa. Instead, both maintained mixtures of forest species and generalists, likely because colonisation was constrained by the surrounding closed-forest matrix. These largely positive outcomes were unexpected, as CC is typically associated with negative or strongly reduced faunal responses (Bird et al., 2004; Kudrin et al., 2023), although neutral or positive effects have occasionally been reported (Huhta, 1976; Addison and Barber, 1997). Studies in deciduous forests have reported both increases (Kudrin et al., 2023) and reductions of up to 22% in richness (Chaudhary et al., 2016), highlighting the strong influence of site conditions, forest type, litter quality, and time since disturbance (Čuchta et al., 2019; Sławski and Sławska, 2019).

Despite these shared patterns in diversity, CC and G diverged in the magnitude and temporal progression of their responses. CC, as the most severe intervention, typically detrimental to forest soils (Keenan and Kimmins, 1993), produced unexpectedly high Collembola densities, contrasting with declines exceeding 50% reported elsewhere within a decade (Siira-Pietikäinen and Haimi, 2009). In our study, euedaphic and epigeic species increased, whereas hemiedaphic taxa declined, a pattern opposite to that reported from regenerating spruce stands (Farská et al., 2014; Sławski and Sławska, 2019) and partly contrary to our hypotheses. Seasonal conditions strongly modulated responses: elevated spring soil moisture temporarily boosted all ecological groups. *Sminthurinus aureus*, a disturbance-tolerant epigeic species, consistently characterised CC, yet overall epigeic densities remained similar to those in other treatments. Restricted dispersal into the isolated CC patches likely limited community turnover. As canopy closure progressed, the assemblage reflected both early-successional colonisers and the gradual return of forest-adapted species. In our oak–hornbeam system, CC plots also showed increased herbaceous plant richness before the regeneration processes of saplings (Aszalós et al., 2023), a trend reported in other temperate deciduous forests (Brunet et al., 1996; Kirby, 2015). This likely enhanced habitat complexity and litter heterogeneity, both important drivers of Collembola diversity (Saitoh et al., 2014; Zhang et al., 2025a). However, faunal responses diverged from plant patterns: although CC supported the highest number of plant indicator species (Aszalós et al., 2023), Collembola indicators were few.

Gap-cutting followed a different trajectory. Overall densities were lower, especially in spring, consistent with Zhang et al. (2025), who reported reduced Collembola density under gap conditions in regions with high precipitation, deep soils, and good water retention. In contrast, drier regions with shallower soils showed density increases following gap formation (Zhang et al., 2025b). By the eighth year, however, epigeic densities rose markedly, consistent with our hypotheses. This gradual increase coincided with persistent canopy openness and high plant richness (Aszalós et al., 2023), which were among the highest across treatments. Species composition in G resembled that reported by Zhang et al.(2025b) particularly the dominance of *Parisotoma notabilis*. While their study detected *Folsomia quadrioculata*, we identified the morphologically similar but more stress-tolerant *F. manolachei* (Potapov, 2001), indicating comparable ecological dynamics. Five years after the intervention, species richness in G had declined, but by the eighth year it matched or exceeded the control levels, consistent with earlier findings in temperate forests (Perry et al., 2018; Zhang et al., 2025b). Rényi profiles showed high diversity at larger α values, yet G lacked indicator species, suggesting variable occurrences and the absence of a dominant disturbance-tolerant taxon. In the eighth year, G supported richness comparable to the controls but with higher evenness than CC. This combination of high evenness, forest-leaning composition, and the absence of strong indicator taxa suggests that gap-cutting fosters a well-balanced assemblage of forest-adapted and disturbance-tolerant species, potentially enhancing beta diversity and contributing to landscape-scale ecosystem stability.

4.2 Recovery dynamics of collembolan communities

Several of our findings align with the intermediate disturbance hypothesis; however, under higher disturbance levels, the dominant driver appears to be post-disturbance regeneration of the vegetation. Our Collembola data, which provide finer taxonomic resolution than earlier mesofauna studies, corroborate previous work (Flórián et al., 2025) in showing that faunal regeneration was already underway five and especially eight years after the treatment. Densities and species richness in several treatments approached or exceeded control levels. Indicator species patterns further support this regeneration trajectory. *Mesaphorura macrochaeta*, initially characteristic of control plots, became associated with both CC and R by year eight, likely reflecting vegetation development and increasing canopy cover in CC. Although the K-strategist Oribatida responded more slowly to changes and exhibited only negative effects of high-disturbance treatments (Flórián et al., 2025; Gergócs-Winkler et al., 2025), the r-strategist Collembola, characterised by high regenerative capacity, showed earlier responses to the interventions. This further supports the view that Collembola are well-established indicators of early forest recovery (Casaril et al., 2024). Although our sampling did not capture the immediate post-disturbance decline, earlier studies have documented rapid rebounds following initial losses in deciduous and coniferous forests (Hasegawa et al., 2006; Lindberg and Bengtsson, 2006). Full faunal recovery after cutting treatments generally requires 10–30 years in coniferous forests (Siira-Pietikäinen and Haimi, 2009; Casaril et al., 2024), but our results suggest that key components of the Collembola community in deciduous forests begin to re-establish sooner.

Treatment effects were significant in both years but unexpectedly stronger in 2023, accompanied by reduced temporal variability. Soil variables contributed little to community differentiation, a result consistent with earlier observations (Laiho et al., 2001). Their inclusion in models remains justified, as soil properties are key determinants of soil fauna under different contexts (van Straalen and Verhoef, 1997; Peng et al., 2022). Although litter data were unavailable in the eighth year, reduced litter mass observed in CC and G during the fifth year suggests that later improvements in the microclimate and soil moisture may have compensated for early deficits. Vegetation cover and plant species richness were influential environmental predictors as well, indicating that regeneration dynamics of vegetation, rather than the initial disturbance itself, were the principal drivers shaping Collembola communities.

4.3 Limitations and evaluations of methodologies

Our study has several limitations that should be considered when interpreting the results. A central issue is whether a more than 80-year-old managed stand can serve as a reliable reference. In Hungary, the scarcity of pristine forests limits the availability of true baseline conditions. Even in comparatively intact systems such as the Białowieża Forest, differences between natural and managed stands persist for decades (Sławski and Sławska, 2019). Such long-lasting management legacies may explain why almost all treatments in our experiment exhibited increased diversity. A more structurally heterogeneous natural forest might have produced a different pattern. This also underlines that even-aged, monodominant stands, though nominally undisturbed, do not necessarily provide optimal conditions for Collembola or, by extension, for soil biota more broadly.

A further limitation is the absence of data from the immediate post-intervention period. Without a true baseline, short-term dynamics remain unresolved, and early declines, particularly in clear-cutting plots, cannot be evaluated. Our interpretation, therefore, relies partly on comparable studies (e.g., Boros et al., 2019). These suggest that while clear-cutting may have had strong initial negative effects, the regeneration phase may favour rapidly reproducing taxa such as Collembola, whereas other groups (e.g., Protura, Oribatida) recover more slowly (Flórián et al., 2025; Gergócs-Winkler et al., 2025). Retention tree groups within clear-cuttings can help conserve forest-adapted species, although the surrounding matrix imposes strong negative pressures. Similarly to R, gap-cutting also achieved favourable outcomes, supporting both forest species and balanced communities. Preparation cutting consistently enhanced Collembola richness and density across ecomorphological groups, although its positive effects may be transient, given that it typically precedes more intensive operations. Taken together, these patterns broadly reflect the disturbance gradient represented by the treatments. Lower-intensity interventions generally maintained Collembola communities closer to those of control plots, whereas stronger canopy disturbances were associated with more pronounced shifts in community structure, although recovery trajectories differed among treatments. Nevertheless, our findings indicate that gap-cuttings and irregular overstorey thinnings, key elements of continuous-cover forestry, can maintain Collembola community structure and diversity.

Methodological factors may also have influenced our results. The lack of pronounced differences among epigeic species is likely linked to the sampling technique: soil corers tend to underrepresent this group, which can be more effectively captured by pitfall traps. While we consider the overall community trends robust, future studies focusing on the rapid responses of epigeic Collembola should incorporate appropriate surface-active sampling methods. Finally, although seasonality did not significantly interact with treatment effects, the clearest differences occurred in spring and, to a lesser extent, summer, with few contrasts detected in autumn. These patterns emphasise the importance of seasonal coverage, particularly early in the vegetation period, when assessing faunal responses to forest management. Given the high time and energy demands associated with processing this faunal group, sampling in European deciduous forests should be prioritised in spring.

5 Conclusion

Our study demonstrates that Collembola communities respond to forest management, with detectable shifts in composition, diversity, and structure. Eight years after the interventions, most treatments, particularly retention tree groups and clear-cuttings, showed substantial signs of recovery, with densities and species richness reaching levels comparable to those of closed forests. These long-term trajectories confirm the value of Collembola as sensitive bioindicators of disturbance and regeneration in managed forests. Although we lacked immediate post-treatment data, the fine taxonomic resolution of our dataset revealed key temporal processes, including early community filtering followed by recolonisation. By the eighth year, convergence towards control conditions in both richness and abundance highlighted the recovery dynamics of Collembola even under extensive management. Forest management treatments were the dominant drivers of community composition, exceeding the influence of seasonal and environmental variability. Over time, vegetation structure emerged as a particularly important factor, emphasising the role of developing canopy and litter layers in promoting belowground biodiversity during succession. Overall, our findings indicate that silvicultural practices involving limited canopy opening, such as preparation cutting and gap-cutting, can maintain core characteristics of Collembola assemblages while slightly enhancing diversity and evenness. These results support broader adoption of close-to-nature (Larsen et al., 2022) and continuous-cover forestry (Pommerening and Murphy, 2004) as biodiversity-friendly alternatives to high-intensity rotational systems. We can also conclude that the regeneration potential of these assemblages is relatively high, and elements of retention forestry (Gustafsson et al., 2012) as retention tree groups, could effectively mitigate the negative effects of clear-cuttings. These findings contribute to a growing body of knowledge on soil fauna recovery dynamics and offer valuable insights for designing biodiversity-friendly forest practices or tools, even under rotation forestry that supports belowground ecosystem integrity.

Electronic supplementary material

Supplementary material is available in the online version of this article at https://doi.org/10.1007/s42832-026-0463-y and is accessible for authorized users.

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Data availability

Data will be made available on request.

Open Access

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