



Original article

Leaf litter quantity shapes oribatid mite assemblages five years following forestry interventions in a European deciduous forest

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ABSTRACT

Continuous cover forestry is widely regarded as a more ecologically sustainable alternative to traditional rotation-based systems in Europe. However, the short- and long-term impacts of different forestry interventions on soil biota remain poorly understood. We investigated the effects of four forest management treatments on soil-dwelling oribatid mites in a European oak–hornbeam forest, five years post-intervention. Assemblages in clear-cut, gap-cut, preparation-cut, and retention tree group plots were compared with controls. Soil fauna were sampled seasonally; climatic conditions were continuously monitored, and vegetation and soil properties measured annually. Mites were identified to species level, and both taxonomic and trait-based community metrics were analysed to assess ecological responses to the treatments. Microclimatic and soil variables did not differ significantly among treatments, but leaf litter quantity was highest in the control, preparation-cutting, and retention tree group plots. Oribatid mite density and species richness were lowest in clear-cutting and gap-cutting plots, highest in the control, and intermediate in the preparation-cutting and retention tree group plots. The most abundant species, mainly from the family Oppiidae, had reduced densities in the more intensively disturbed treatments, contributing to higher evenness in those plots. Less disturbed habitats were dominated by omnivorous, predatory, and scavenger species, with higher proportions of parthenogenetic individuals. In contrast, sexual and predominantly detritivorous species were more prevalent in the clear-cutting and gap-cutting plots. Furthermore, seasonal variation in species composition was more pronounced in these disturbed plots, whereas species composition remained more stable and homogeneous in the control plots. In conclusion, higher amount of leaf litter in less disturbed plots supported the dominance of parthenogenetic and omnivorous species. Oribatid mites proved to be sensitive indicators of long-term ecological effects, highlighting the lasting impact of forestry interventions in oak–hornbeam forests, even five years after disturbance.

1. Introduction

Even-aged rotation forestry systems, including clear-cutting and shelterwood-cutting methods [1], remain the most widely practised approaches to forest management in Europe [2]. However, these systems significantly reduce structural complexity by creating even-aged stands and often alter the natural tree species composition within forests. These changes often result in a decline in biodiversity, which has cascading effects on the entire ecosystem - from the soil to the canopy [3]. Consequently, ecological sustainability has gained increasing importance as a primary objective in forest management, striving to

preserve biodiversity, ecosystem functions, and ecological integrity while still allowing for timber production [4–6]. In contrast, continuous cover forestry, which includes tree selection and group selection systems [1], is more consistent with sustainability goals than rotation-based systems. Continuous cover forestry more closely replicates the natural disturbance regimes typical of temperate forests, thereby enhancing ecological resilience [6]. It preserves a continuous forest canopy and maintains structurally complex, uneven-aged stands through small-scale, low-intensity interventions such as upper canopy thinning and gap-cutting [7,8].

Forest management can significantly influence soil conditions and

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the communities of soil-dwelling organisms [9,10]. Silvicultural interventions may alter the chemical, physical, and biological properties of soils [11–13]. In the absence of living tree canopies and roots, the input of organic matter and other essential food resources declines [14]. These changes negatively affect the abundance and diversity of bacteria and fungi in the soil [15–17]. As soil-dwelling microarthropods are closely linked to soil structure and microbial communities, they are sensitive to such changes and serve as effective indicators of shifts in soil ecosystem condition [18,19]. Management recommendations should be guided by effective indicator groups that reflect the impacts of treatments, thereby supporting evidence-based decisions for ecologically sustainable forestry [20]. Although soil-dwelling organisms are intimately connected to forest ecosystems, strongly reflect soil ecological processes, and represent a substantial component of biodiversity, they remain underrepresented as indicators in forest management research [21].

Oribatid mites are typically the most abundant and diverse group of microarthropods in forest ecosystems (e.g. Refs. [10,22,23]). They play an important role in organic matter decomposition and nutrient cycling, primarily feeding on dead plant material and decomposing fungi and bacteria [24]. In addition to their ecological roles, oribatid communities exhibit several distinctive characteristics. They occupy all trophic levels within the soil food web [25,26], comprise a substantial proportion of parthenogenetic species [27], and demonstrate a diverse array of life-history strategies, including both long-lived, slow-reproducing species and shorter-lived, fast-reproducing species [28]. Due to this ecological and functional diversity, oribatid mites exhibit a range of responses to environmental disturbances, making them a highly effective indicator group for assessing changes in soil ecosystems [29,30].

We have substantial information on the responses of soil oribatid mite communities to silvicultural interventions; however, most of this knowledge originates from coniferous forests in Europe and North America [31–34]. These studies generally report negative impacts of forest management on the abundance, diversity, and community composition of oribatid mites. The magnitude and direction of these effects can vary depending on the intensity of management [19,35], regional environmental conditions [36], and the time elapsed since intervention [37]. In contrast, relatively few studies have examined the effects of forest management on oribatid mite communities in deciduous forests, and these are predominantly from North America [13,22]. This represents a significant knowledge gap, particularly considering that broadleaved forests account for approximately 37 % of Europe's total forest cover [38]. Yet, research on the impacts of forest management on oribatid mites in European deciduous forests remains very limited (but see Ref. [36]).

Temperate deciduous and coniferous forests differ markedly in several ecological aspects, and these differences are reflected in the composition of soil oribatid mite communities [39–42]. A key difference between these forest types is resource dynamics: deciduous forests have pulsed leaf litter input, while coniferous forests offer continuous but lower-quality organic material [43]. This variation in resource availability and quality is particularly relevant for oribatid mites, which are highly sensitive to changes in their food base [44]. Both litter quality and quantity have been shown to strongly influence oribatid mite communities in deciduous [45–47] and coniferous forests [48]. In addition to the limited research on managed deciduous forests, the seasonal dynamics of oribatid mite communities and how these patterns interact with silvicultural interventions remain poorly understood (but see Refs. [49–51]). This temporal aspect may be especially important in managed deciduous forests, where seasonal changes in litter input can modulate the impact of forest operations. In contrast, seasonal effects of cutting treatments appear to be less pronounced in managed coniferous forests [19,31]. However, studies in mixed forests have demonstrated that forestry management can influence oribatid mite communities differently across seasons [34,52]. Therefore, it is timely to investigate how forestry practices affect oribatid mites in relation to litter input in

deciduous forests. Specifically, investigating the effects of silvicultural interventions in deciduous forests, while explicitly considering seasonal variation, may yield valuable insights into the mechanisms driving soil biodiversity responses.

As species-level responses of oribatid mite communities to forestry interventions have shown considerable variability [13,23,34], trait-based approaches may offer a more consistent and informative framework for assessing their reactions to forest management [53]. There is growing evidence that functional traits such as feeding guild composition [31,54] and rate of reproductive modes [35,55] are influenced by forest disturbances. Therefore, incorporating these trait-based metrics alongside traditional species-based analyses can provide deeper insights into the ecological impacts of silvicultural interventions on soil-dwelling oribatid mites.

Our study was part of a silvicultural experiment in an oak-hornbeam forest [56]. In the experiment, treatments commonly used in European forestry were applied according to two management systems (rotation forestry and continuous cover forestry). Clear-cutting and preparation-cutting (partial-cutting) are representative treatments of the rotation forestry [1]. Clear-cutting is the most characteristic intervention within this system, typically followed by artificial regeneration through seeding or planting. In contrast, under the shelterwood system, the mature stand is removed gradually over two or three interventions during a regeneration period, usually spanning 5–20 years. Regeneration in this case relies on natural seedling recruitment from the existing stand. The first step in the shelterwood regeneration sequence is a preparation cutting, which removes a portion (10–40 %) of the mature trees to facilitate regeneration. Both clear-cutting and shelterwood cutting are forms of rotation forestry aimed at maintaining even-aged stand structures. As a standard mitigation measure within rotation forestry, a small group of retention trees was also left standing within clear-cut areas [57]. Gap-cutting (creation of cutting areas smaller than 0.1 ha) is a widely used approach for regeneration in continuous cover forestry [7]. The effect of these treatments were compared with the mature stage of an 85 year-old sessile oak (*Quercus petraea* (Matt.) Liebl) and hornbeam (*Carpinus betulus*, L.) dominated stand as untreated control plots, which was managed by the traditional shelterwood system in the past. The treatments were conducted five years before our samplings. We investigated the effects of these treatment types on soil-dwelling oribatid mite communities. Our hypotheses were as follows:

- (1) oribatid mite density and diversity will remain significantly reduced in all cutting treatments compared to control plots, even five years after silvicultural intervention in oak-hornbeam forests, as has been repeatedly demonstrated in coniferous forest systems. In addition, these reductions will lead to shifts in species composition among treatments.
- (2) Differences in oribatid mite communities among treatments will be reflected in variations in the composition of functional traits, indicating shifts in environmental conditions;

and (3) the effects of forestry treatments on oribatid mite communities and their associated traits will vary seasonally, due to the seasonal dynamics of leaf litter and resource availability in deciduous forests.

2. Material and methods

2.1. Study site and silvicultural treatments

The study site is located in northern Hungary, within the Pilis Mountains (47°40'N, 18°54'E), at an elevation of 380–450 m above sea level. The mean annual temperature ranges from 9.0 to 9.5 °C, while annual precipitation averages between 600 and 650 mm [58]. The predominant soil type is luvisol, with some areas characterised by rendzic leptosol (FAO 2009; [59]). The study was carried out in a

managed, even-aged (85-year-old) sessile oak–hornbeam forest. In the experimental stand, the upper canopy is dominated by sessile oak (*Quercus petraea*), while hornbeam (*Carpinus betulus*) is the most abundant species in the secondary canopy. The shrub layer is sparse and mainly consists of hornbeam, manna ash (*Fraxinus ornus* L.), and dogwood (*Cornus sanguinea* L.). In the understorey, hairy sedge (*Carex pilosa* Scop.) and wood melic (*Melica uniflora* L.) are the dominant herbaceous species. Further details on the study site are provided in Kovács et al. [56].

During the winter of 2014–2015, six blocks were selected following a randomised complete block design. Within each block, five treatments, including a control (C), were established (Fig. 1). The treatments were as follows:

C (control): The stand retained its original characteristics.

CC (Clear-cutting): A circular clear-cut area of 0.5 ha (80 m in diameter) was created within the stand. All trees with a diameter at breast height (DBH) > 5 cm and/or height > 2 m were felled and removed from the plot.

G (Gap-cutting): A circular gap of 300 m² (20 m in diameter) was created within the closed canopy by felling and removing the trees. The gap size was based on documented natural gap areas in deciduous forests [60].

P (Preparation-cutting or Partial-cutting): This treatment was applied to circular plots of 0.5 ha. Approximately 30 % of the basal area of the dominant oak trees and the subdominant hornbeam layer was selectively removed.

R (Retention): A 300 m² circular group of trees was retained within the area subjected to the clear-cut (CC) treatment to mimic structural retention.

In total, 30 plots were established (5 treatments × 6 blocks) under the complete block design. Further details of the experimental design are provided in Kovács et al. [56].

2.2. Understorey, soil and microclimate variables

Vegetation surveys were conducted in each plot using a 2 × 2 m

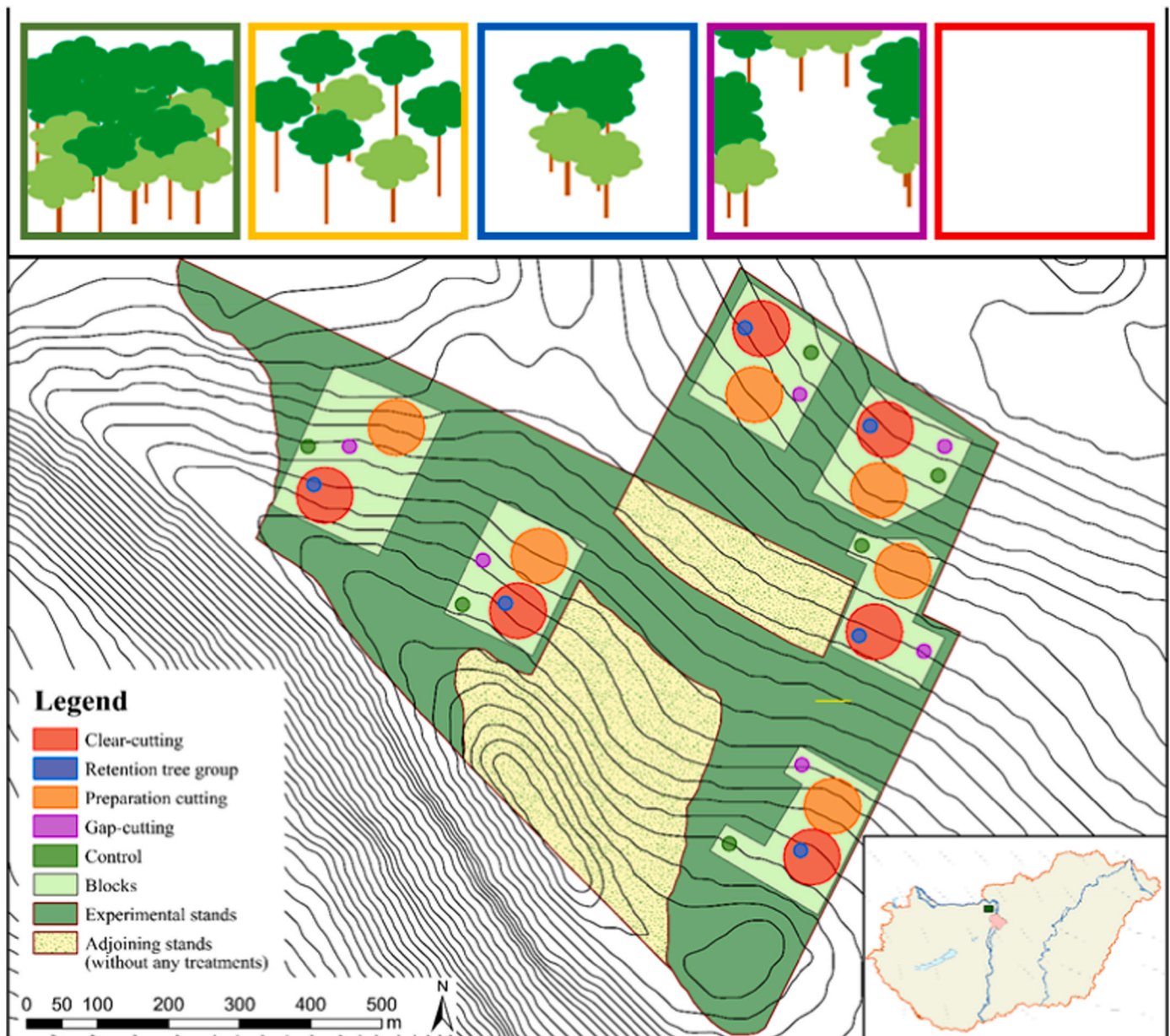


Fig. 1. Experimental design of the Pilis Forestry Systems Experiment in Pilis Mountain based on Fig. 1(b) in Ref. [56].

quadrat. Surveys took place in April (to capture early spring species) and again in June 2020. Within each quadrat, the cover of all herbaceous species and woody species shorter than 50 cm was visually estimated. Total vegetation cover was calculated as the sum of the individual species' cover values, and species richness was defined as the total number of species recorded per quadrat. The density of saplings—defined as woody individuals taller than 50 cm with a diameter at breast height (DBH) of less than 5 cm—was also recorded within each quadrat. Litter samples were collected in May 2020 from four 30 × 30 cm sub-quadrats located near the vegetation quadrat in each plot. Litter mass (g m^{-2}) was determined by weighing the oven-dried samples.

In each plot, four soil samples were collected in May 2020 from a depth of 0–20 cm, adjacent to the litter quadrats. Samples were air-dried and sieved to <2 mm. Soil pH was measured potentiometrically using the supernatant of a suspension prepared from 10 g of soil and 25 cm^3 of distilled water, following Hungarian Standards [61]. For the analysis of total carbon and nitrogen content, the four subsamples per plot were further sieved to <0.5 mm and combined into a single composite sample. Total carbon content was determined colorimetrically after oxidation with potassium dichromate (MSZ 21470–52:1983), while total nitrogen content was measured using the Kjeldahl method [62]. These soil variables were measured once during the study period.

Microclimatic variables were measured in the centre of each plot in April, June, and October 2020. These included soil temperature (Tsoil; °C), relative air humidity (RH, %), measured at 130 cm above ground level, and soil water content (SWC, $\text{m}^3 \text{m}^{-3}$) in the upper 20 cm of the soil. Different equipment was used for measurements in April compared to those in June and October. In April, soil temperature was recorded using 'S-TMB-M0020 12-Bit' sensors (Onset Computer Corporation, Bourne, MA, USA) placed 2 cm below the soil surface. Relative humidity was measured with combined temperature/humidity (T/RH) sensors from the same manufacturer, installed in passively ventilated radiation shields to prevent direct solar exposure. Soil water content was measured using 'S-SMD-M0050' soil moisture sensors (Onset Computer Corporation). All sensors were connected to 4-channel 'HOBO H021-0020' data loggers (Onset Computer Corporation), mounted on wooden poles. In June and October, Tsoil and SWC were measured using TOMST TMS-4 integrated sensors and loggers [63]. Relative humidity was recorded with MCC USB-502 combined temperature and humidity loggers (Measurement Computing Corp., Norton, MA, USA). Measurements were continuous in each month, with data recorded at 15-min intervals. For each plot, the mean values of each variable were calculated from the daily means over the 14 days preceding soil organism sampling. To account for differences between sensor types and to isolate treatment effects, relative differences between treated and control plots were calculated within each block. Control values were set to zero, and all treatment values were expressed relative to this baseline. These relative values were used in subsequent analyses.

2.3. Samplings and preparation of soil mites

Five years after the interventions, soil samples were collected from each plot during three seasons in 2020: 2 April, 10 June, and 20 October. Sampling was conducted using a cylindrical metal soil corer (8 cm diameter, 8 cm depth; volume 400 cm^3). To minimise edge effects, sampling points were located near the centre of each plot. All samples were taken within an area of approximately 1 km^2 , ensuring consistent environmental conditions across treatments. The close spatial arrangement of plots facilitated a focused assessment of treatment impacts, while the block design provided replication to account for spatial variability. Samples were collected from the 0–16 cm soil depth by taking two consecutive 8 cm depth cores, which were subsequently pooled. In total, 90 samples were obtained, corresponding to three sampling dates, six blocks, and five treatments ($3 \times 6 \times 5 = 90$). Samples were transported to the laboratory on the day of collection and extracted using a Berlese-Tullgren funnel in 70 % ethyl alcohol over a seven-day period.

Oribatida specimens were separated from other soil fauna and debris, then counted. The specimens were cleared using lactic acid and examined under a light microscope (Nikon Eclipse Ts2R). Adult individuals were identified to species level following taxonomic keys [64–68]. Due to taxonomic uncertainty and constraints in expertise with this genus, specimens of *Suctobelbella* were identified only to genus level. During taxonomic identification, the sex of individuals was determined whenever possible, and the number of eggs in gravid females was recorded.

Density values and derived variables for oribatid mite groups refer to soil samples from the 0–16 cm depth layer. Total density and juvenile density were considered separately. The derived variables included the following. Proportion of juveniles, calculated as the ratio of juvenile individuals to total Oribatida density per sample. Species richness (S), defined as the number of oribatid species per sample. Pielou's evenness (J), calculated from Shannon diversity (H) using the formula: $J = H/\ln(S)$ [69]. Reproductive mode and feeding guild classifications were assigned based on literature sources (Table A1). The relative abundance of parthenogenetic species was determined by dividing the total abundance of parthenogenetic species (Table A1) by the total number of adult oribatid mites per sample.

To characterise the feeding guild structure of oribatid mite communities, a community-weighted mean (CWM) was calculated based on an ordinal feeding guild system comprising four categories [25,31]:

- Omnivores (#1): primarily feeding on fungi and/or living or dead animals;
- Secondary decomposers (#2): mainly feeding on fungi, with partial consumption of plant material;
- Primary decomposers (#3): predominantly consuming plant parts and litter;
- Lichen and algae feeders (#4).

This calculation was applied only to the 24 most abundant species (92 % of the total), as it is a weighted mean and accurate trophic guild information is not available for all species. For each sample, the proportion of gravid females was calculated based on the total number of adult oribatid mites within a selected group of 20 species for which eggs were observed during the study. Species with no detected eggs were excluded from this analysis (see Table A1).

2.4. Statistical analyses

All statistical analyses were conducted using the R statistical environment [70]. Understorey vegetation, soil, and litter variables were compared among treatments (five levels of the treatment factor), primarily using generalised least squares (gls) models [function gls ()] incorporating a variance structure (varIdent) to account for heteroscedasticity across treatment and month (package nlme [71]). The most appropriate model type was selected based on likelihood ratio tests using the anova () function, and model assumptions were assessed via diagnostic plots. Pairwise contrasts between treatments were calculated from predicted marginal means using the lsmeans () function in the lsmeans package [72]. For vegetation species richness, a generalised linear model with a Poisson distribution was fitted using the glm () function in the stats package [70]. Microclimatic variables (Tsoil, RH, SWC) were analysed using gls models that included treatment, season (three levels: April, June, and October), and their interaction, comparing relative values across these factors.

Derived variables of oribatid mite assemblages were compared across treatments and seasons. Due to the varying nature of the data, different modelling approaches were employed. Densities (log-transformed), Shannon diversity, species richness, evenness and feeding guild data were analysed using generalised least squares (gls) models incorporating variance structures for the factors treatment and season. Proportion data were analysed using generalised linear mixed models with

a quasi-binomial distribution, including block as a random effect (function `glmmPQL()` in the MASS package) [73]. Following the initial modelling, relationships between annual environmental variables and total annual Oribatida density (calculated as the sum of seasonal densities) were examined using either linear models (`lm`) or Spearman's rank correlation tests (`cor.test`), depending on whether the assumptions for parametric analysis were met. Only statistically significant results from this analysis are reported.

The 24 most abundant oribatid mite species accounted for 92 % of the total oribatid mite abundance. Redundancy analysis (RDA) was performed on these species to explore the main patterns in community composition. Due to the limited number of replicates ($N = 6$), the RDA results are interpreted descriptively rather than inferentially. Species density data were Hellinger-transformed prior to analysis. The RDA incorporated categorical factors (treatment, season, and block) alongside relative microclimatic variables, including soil temperature (Tsoil), relative humidity (RH), and soil water content (SWC). Significant explanatory variables were selected manually based on permutational analysis of variance. Analyses were conducted using the `rda()` function from the `vegan` package in R [74]. To further elucidate the patterns of the most abundant species, their log-transformed abundances were analysed separately using generalised least squares (`gls`) models.

3. Results

3.1. Understorey, soil and microclimate variables

Herbaceous vegetation cover and sapling density were lowest in the control plots compared to the other management types (Table 1). Plant species richness was highest in the retention tree group and preparation-cutting plots, and lowest in the control plots. In contrast, litter weight was greatest in the control and retention tree group plots, and lowest in the clear-cutting plots. Sapling density was highest in the preparation- and gap-cutting plots, while the clear-cutting plots exhibited a very high standard deviation. Soil carbon and nitrogen content, as well as pH, did not differ significantly among treatments. The greatest deviation in soil temperature relative to the control occurred in the retention tree group plots in April. In all other treatments and seasons, no significant differences in relative soil temperature were detected. Relative humidity was significantly lower only in the clear-cutting plots, compared to the

control, in October. Soil water content did not differ significantly from the control in any of the treatments.

3.2. Oribatid mites

In total, 18,310 oribatid mites individuals were collected, including 4226 immature individuals. We identified 116 species. Mean population densities (individuals $m^{-2} \pm SD$) in the control plots were 96,636 ($\pm 39,300$) in spring, 74,601 ($\pm 16,497$) in summer, and 44,884 ($\pm 31,891$) in autumn (Fig. 2). Corresponding species richness per sample (mean $\pm SD$) in the control plots was 27 (± 5), 25 (± 4), and 17 (± 4) in spring, summer, and autumn, respectively. A total of 69 species were recorded in each of the clear-cutting, gap-cutting, and retention tree group plots, whereas 77 species were found in both the control and preparation-cutting plots.

Oribatid mite density was highest in the control plots, lowest in the clear-cutting and gap-cutting treatments, and intermediate in the preparation-cutting and retention tree-group plots. However, in October, density in the gap-cutting plots was comparable to that in the control (Fig. 2A–Table A2). Species richness displayed a pattern similar to that of total density, with the highest values in the control plots, the lowest in the clear-cutting and gap-cutting plots, and intermediate values in the preparation-cutting and retention tree group treatments. However, these differences were statistically significant only in June (Fig. 2B). Shannon diversity generally did not differ significantly among treatments. A significant difference was observed only in June, when diversity was lower in the clear-cutting plots compared to the control (Fig. 2C). This is likely related to evenness, which was higher in the clear-cutting and gap-cutting plots in June (Fig. 2D). The linear model revealed a significant positive relationship between total Oribatida density and litter mass (Fig. 3.). In contrast, total density was negatively correlated with vegetation cover (Spearman's $\rho = -0.54$, $p = 0.002$).

Juvenile densities followed a similar pattern to total densities, with the highest values observed in the control plots and the lowest in the clear-cutting plots. Intermediate densities occurred not only in the preparation and retention plots but also in the gap-cutting plots (Fig. 4A). The proportion of juveniles was similar across all treatments in June and October, but was reduced in spring in both the control and clear-cutting plots (Fig. A1). The proportion of gravid females was similar across all treatments in April and June. By autumn, it had

Table 1

Absolute and relative background variables (mean $\pm$ SD) for the five treatment types. Relative values for microclimate data are expressed relative to the control plots. The choice of statistical model depended on the data distribution: `gls` refers to generalised least squares models with variance structure for the treatment factor, and `glm` denotes generalised linear models with a Poisson distribution. F- and p-values are presented for each model. Within each variable, different lowercase letters indicate significant differences between treatments. Abbreviations: C, control; CC, clear-cutting; G, gap-cutting; P, preparation-cutting; R, retention tree group. Sample size: $N = 6$.

	C	CC	G	P	R	model (factor)	F	p
vegetation cover (%)	41.6 $\pm$ 13.9 ^a	133.4 $\pm$ 43.5 ^b	122.0 $\pm$ 17.6 ^b	130.3 $\pm$ 9.1 ^b	93.9 $\pm$ 28.6 ^b	gls (treatment)	44.88	<0.0001
plant species richness (n plot ⁻¹)	6.7 $\pm$ 2.8 ^a	10.3 $\pm$ 5.6 ^{ab}	10.5 $\pm$ 3.9 ^{ab}	12 $\pm$ 4.1 ^b	15.5 $\pm$ 5.9 ^b	glm (treatment)	Chi ² = 22.64	<0.0001
Litter weight (g m ⁻²)	618.8 $\pm$ 126.6 ^c	49.3 $\pm$ 59.1 ^a	272.6 $\pm$ 91.3 ^b	385.3 $\pm$ 137.6 ^{bc}	565.2 $\pm$ 76.7 ^c	gls (treatment)	55.04	<0.0001
Sapling density (ind m ⁻²)	0.5 $\pm$ 1.2 ^a	12.5 $\pm$ 9.1 ^{ab}	21.7 $\pm$ 12.9 ^b	8.7 $\pm$ 4.3 ^b	3.2 $\pm$ 1.9 ^{ab}	gls (treatment)	11.9	<0.0001
pH	4.4 $\pm$ 0.2	4.6 $\pm$ 0.2	4.6 $\pm$ 0.2	4.4 $\pm$ 0.2	4.6 $\pm$ 0.3	gls (treatment)	1.74	0.172
Carbon content (m/m%)	4.0 $\pm$ 0.4	3.9 $\pm$ 0.4	3.8 $\pm$ 0.9	3.9 $\pm$ 0.3	4.0 $\pm$ 1.3	gls (treatment)	0.22	0.922
Nitrogen content (m/m%)	0.2 $\pm$ 0.0	0.2 $\pm$ 0.0	0.2 $\pm$ 0.0	0.2 $\pm$ 0.0	0.2 $\pm$ 0.1	gls (treatment)	0.14	0.968
T soil (°C)						gls		
April	0	-0.64 $\pm$ 0.49 ^a	-0.12 $\pm$ 0.19 ^a	-0.10 $\pm$ 0.22 ^a	0.52 $\pm$ 0.22 ^b	(treatment)	11.25	<0.0001
June	0	0.01 $\pm$ 0.65 ^a	0.06 $\pm$ 0.53 ^a	0.35 $\pm$ 0.43 ^a	0.21 $\pm$ 0.30 ^a	(month)	1.7	0.192
October	0	0.06 $\pm$ 1.32 ^a	-0.01 $\pm$ 0.31 ^a	0.23 $\pm$ 0.24 ^a	0.29 $\pm$ 0.72 ^a	(interaction)	2.48	0.033
Relative humidity (%)						gls		
April	0	0.81 $\pm$ 0.79 ^a	0.34 $\pm$ 1.36 ^a	-0.35 $\pm$ 1.27 ^a	-0.26 $\pm$ 0.71 ^a	(treatment)	10.71	<0.0001
June	0	-0.89 $\pm$ 2.52 ^a	-0.10 $\pm$ 1.75 ^a	0.41 $\pm$ 0.86 ^a	-0.97 $\pm$ 1.46 ^a	(month)	0.47	0.63
October	0	3.09 $\pm$ 1.44 ^b	0.50 $\pm$ 1.38 ^a	0.74 $\pm$ 2.73 ^{ab}	-0.83 $\pm$ 0.58 ^a	(interaction)	3.23	0.008
SWC (m ³ m ⁻³)						gls		
April	0	0.10 $\pm$ 0.17	0.02 $\pm$ 0.04	0.02 $\pm$ 0.03	0.01 $\pm$ 0.01	(treatment)	1.33	0.275
June	0	0.00 $\pm$ 0.13	0.06 $\pm$ 0.11	-0.04 $\pm$ 0.07	-0.01 $\pm$ 0.07	(month)	1.39	0.256
October	0	0.09 $\pm$ 0.12	0.07 $\pm$ 0.10	-0.04 $\pm$ 0.07	0.02 $\pm$ 0.05	(interaction)	1.4	0.231

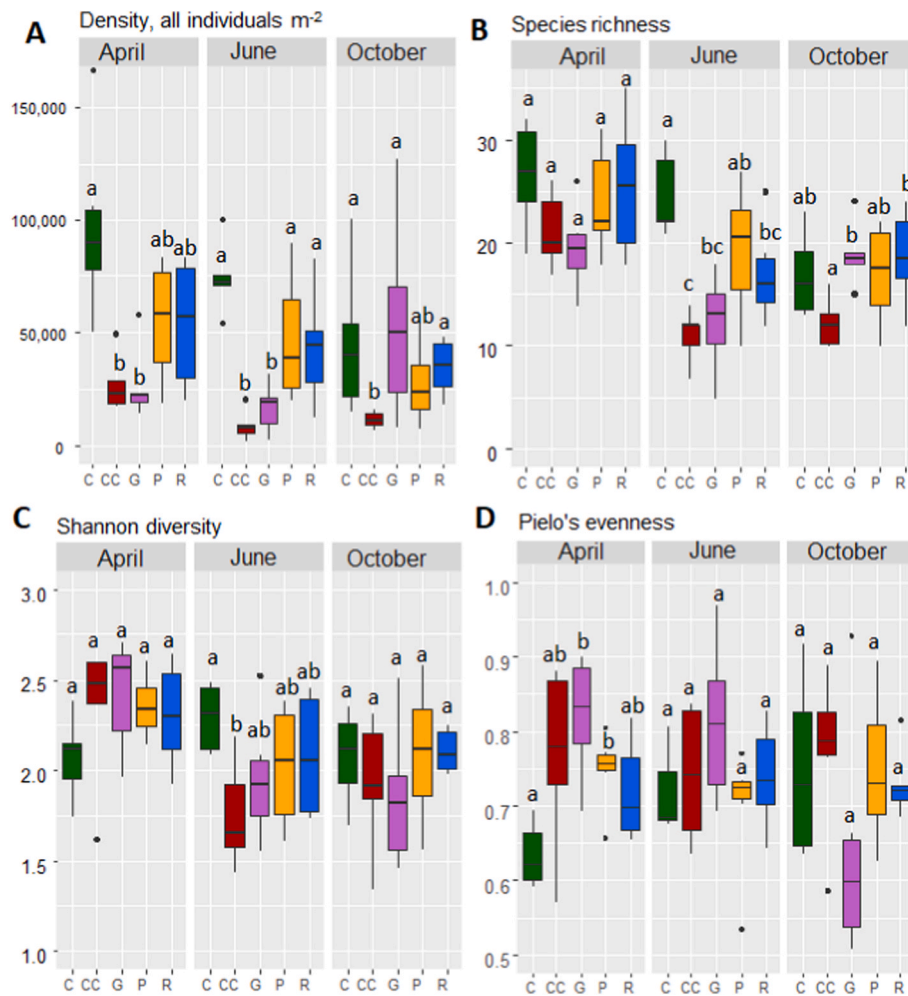


Fig. 2. Boxplots of derived variables of oribatid mite assemblages: (A) Total density (individuals m⁻²), (B) Species richness (per sample), (C) Shannon diversity, and (D) Pielou's evenness. Different lowercase letters denote significant differences between treatments within each month. Abbreviations: C, control; CC, clear-cutting; G, gap-cutting; P, preparation-cutting; R, retention tree group.

declined in all plots; however, the proportion remained higher in the clear-cutting plots compared to the other treatments (Fig. 4B). The proportion of parthenogenetic species followed a similar pattern to that of density and species richness: highest in the control plots, lowest in the clear-cutting treatment, and intermediate in the other treatments (Fig. 4C). This difference was statistically significant only in spring. Community-weighted mean (CWM) values of feeding guilds were highest in the clear-cutting and gap-cutting plots in April. In contrast, in the other treatments, CWM values were close to 1, suggesting dominance by feeding guild #1 (predators, scavengers, and omnivores). By June and October, feeding guild composition had become similar across all treatments (Fig. 4D).

The final constrained ordination model (RDA), based on the 24 most abundant oribatid species, included only significant explanatory variables: treatment, month, and block. The model revealed that oribatid mite community composition was similar within the control, retention tree group, and preparation-cutting plots, with no clear seasonal separation (Fig. 5). In contrast, the assemblages in the clear-cutting and gap-cutting plots differed markedly from those in the other treatments and exhibited stronger seasonal variation, particularly with spring (April) samples clearly separated from those collected in June and October.

The four most abundant species (*Oppiella (Rhinoppia) obsoleta*, Paoli; *Dissorhina ornata*, Oudemans; *Oppiella nova*, Oudemans and *Micropiia minus*, Paoli) contributed substantially to the observed patterns across treatments and seasons. *R. obsoleta* reached its highest abundances in

April and June within the control plots, but in October it became particularly abundant in the gap-cutting plots (Fig. A2). *D. ornata* occurred in high numbers during spring across almost all treatments, with its peak abundance also observed in the control plots. The parthenogenetic species *M. minus* and *O. nova* were consistently most abundant in the control plots throughout all seasons, while their abundances were lowest in the clear-cutting and gap-cutting plots (Fig. A2).

4. Discussion

4.1. Oribatida density, species richness and composition

This study is the first to examine the effects of multiple forest management interventions on soil-dwelling oribatid mites in a European deciduous forest. In line with our first hypothesis, five years after the forestry treatments were applied, oribatid mite densities were significantly lower in both the clear-cut and gap-cut plots compared to the untreated control plots. This pattern is consistent with previous research reporting declines in oribatid mite populations following clear-cutting in coniferous forests, as well as in North American oak-hickory forests several years post-harvest (e.g. Refs. [18,34,37,51,75]).

Differences in oribatid mite density can be attributed to several environmental conditions that persist following forest management interventions. In the present study, microclimatic variables did not differ markedly among treatments, suggesting that measured microclimatic

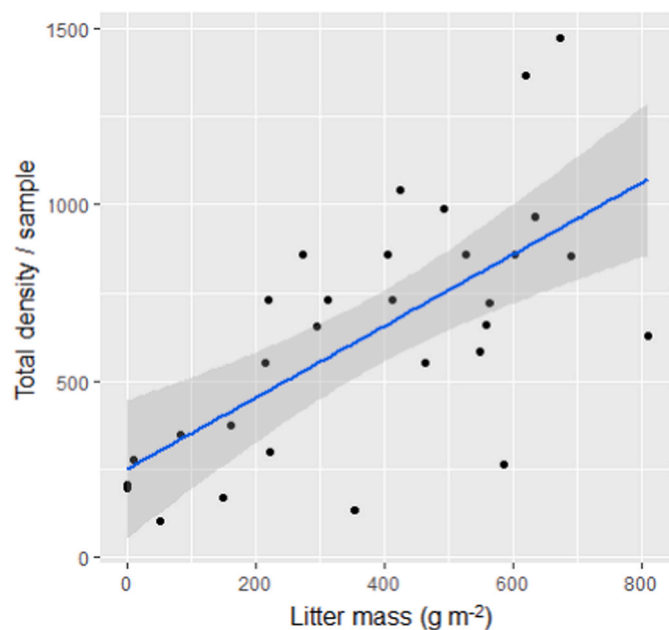


Fig. 3. Linear model describing the relationship between total annual density of Oribatida and annual litter mass. Model: $\text{Density} = 248.7 + 1.02 \times \text{Litter mass}$ ($F = 22.17$, $p < 0.0001$).

conditions played a less significant role five years after the intervention. However, previous studies have shown that microclimatic extremes in temperature and moisture between control and disturbed habitats can be more influential in the initial years following intervention, particularly when vegetation cover is sparse [22,52]. In contrast, the most pronounced differences observed between treatments in this study were in vegetation cover and leaf litter quantity. We found that lower litter mass in disturbed habitats was associated with reduced Oribatida density. Both clear-cutting and gap-cutting likely led to decreased annual litter input, reduced availability of organic material, diminished root biomass, and lower microbial activity at the experimental sites [23,76] all of which may have negatively impacted oribatid mite communities [10,51].

Several studies have reported reductions in the species richness and diversity of oribatid mites following clear-cutting interventions [19,32,50,77]. In contrast, our findings did not support the first hypothesis with respect to total species richness, which remained relatively stable across all treatments, ranging from 69 to 77 species. Similar patterns have been observed in other studies, where species richness persisted despite disturbances [18,23,31,49].

In line with our first hypothesis, species composition differed among the forest management treatments, primarily due to variations in the densities of dominant oribatid mite species. Species belonging to the family Oppiidae, including *Oppiella nova*, *Microppia minus*, *Rhinoppia obsoleta*, and *Dissorhina ornata*, were the most prevalent taxa in our study. Members of this family are typically dominant in coniferous forests (e.g. Refs. [23,31,51,52,78]), but can also be abundant in

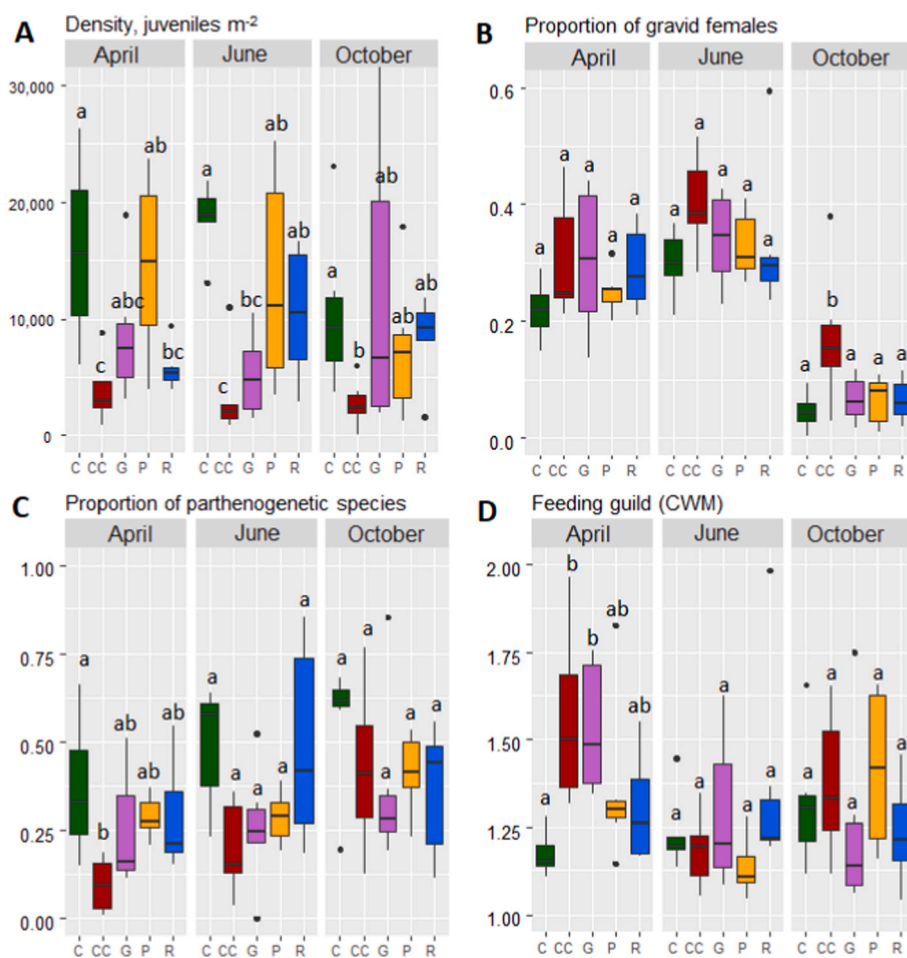


Fig. 4. Boxplots of functional traits of oribatid mite assemblages: (A) Density of juveniles (individuals m^{-2}), (B) Proportion of gravid females, (C) Proportion of parthenogenetic species, and (D) Community-weighted mean (CWM) of feeding guilds. Different lowercase letters denote significant differences between treatments within each month. Abbreviations: C, control; CC, clear-cutting; G, gap-cutting; P, preparation-cutting; R, retention tree group.

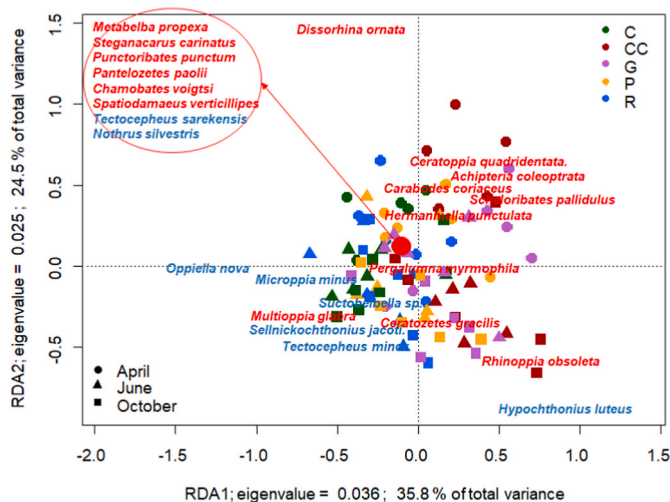


Fig. 5. Redundancy analysis (RDA) of the 24 most dominant oribatid species, representing 92 % of the total community, based on significant explanatory variables: month ($F = 4.33$, $p = 0.001$), treatment ($F = 2.82$, $p = 0.001$), and block ($F = 2.18$, $p = 0.001$; not visualised in the plot). The total explained variance (R^2) was 0.183. Species names located near the centre of the ordination space are shown in the top left corner of the plot. Treatments are indicated by colour, and sampling months are distinguished by different plotting symbols. Abbreviations: C = control, CC = clear-cutting, G = gap-cutting, P = preparation-cutting, R = retention tree group. Species in red are sexual, and those in blue are parthenogenetic. (RDA scaling = 1).

oak-dominated ecosystems [79–81]. In our study, *Oppiella nova* and *Microppia minus* were most abundant in the control plots and, to a lesser extent, in the preparation-cutting and retention tree group plots. *Oppiella nova* is often highly abundant in deciduous forests [19,49,51, 52] and generally exhibits sensitivity to various forms of disturbance [18,31,82]. While *Microppia minus* is also a common dominant species in forested habitats [83–85], it is frequently recorded in disturbed and open environments [86,87]. In our study, *Microppia minus* showed increased abundance in the clear-cutting and gap-cutting plots during autumn, suggesting a greater tolerance to habitat disturbance compared to *Oppiella nova*. The other two dominant species, *Dissorhina ornata* and *Rhinoppia obsoleta*, are also characteristic of oak forests [79,88] and contributed substantially to the differences in species composition between the control plots and the clear-cutting and gap-cutting treatments. However, these patterns also exhibited seasonal variation (see Section 4.3).

4.2. Functional traits

In accordance with our second hypothesis, differences among forestry treatments were detectable based on the reproductive mode of oribatid mites. Oribatida is a distinctive suborder of microarthropods, with approximately 10 % of species reproducing via parthenogenesis [27]. Sexual and parthenogenetic reproduction represent alternative adaptive strategies, and the proportion of parthenogenetic species within a community may reflect the assemblage's ability to cope with environmental disturbance [77]. In our study, the relative abundance of parthenogenetic species was highest in control plots and lowest in clear-cut plots, particularly in April and June. Interestingly, the observed increase in the relative proportion of sexual species in clear-cutting treatments was due to a reduction in the abundance of parthenogenetic species. This indicates that parthenogenetic species are more sensitive to disturbance, likely due to their reduced competitive ability under resource-limited conditions [44]. Sexual species may have a competitive advantage over parthenogenetic species when food resources, such as fungi and nematodes associated with leaf litter, are

scarce. In contrast, when food availability is high, as in undisturbed forests with abundant leaf litter, competition is reduced, enabling parthenogenetic species to persist and reproduce successfully [44,89]. In disturbed habitats (e.g. clear-cut and gap-cut plots), the reduction in leaf litter and associated food resources likely increases competition and limits the success of parthenogenetic species. Notably, the two most abundant sexual species, *Dissorhina ornata* and *Rhinoppia obsoleta*, were also highly abundant in the control plots but parthenogenetic species were also able to coexist with them and maintain high population densities under such favourable conditions.

Oribatid mites are generally considered K-selected organisms, characterised by low fecundity and long life cycles [90]. However, some species, particularly those within the family Oppiidae, exhibit higher fecundity than is typical for the group. For example, *Oppiella nova* and *Oppia denticulata* reach maturity in just 23 and 27 days, respectively [28]. In addition, certain Oppiidae species can produce exceptionally high numbers of eggs such as *Dissorhina ornata*, *Oppia subpectinata*, and *Oppiella nova* [91]. The influence of forest management on oribatid mite fecundity has not been widely studied. Wehner et al. [77] found no significant differences in the proportion of gravid females across various land-use types. Similarly, our study revealed that forestry treatments did not affect the proportion of gravid females, which remained consistent across all treatments. However, the proportion of juveniles also remained stable across treatments and seasons, consistent with findings by Lósková et al. [51]. This stability supports the interpretation that fecundity was not significantly influenced by forestry management practices.

In line with our second hypothesis, differences in feeding guild composition were observed among the forest management treatments. Most species within the dominant family Oppiidae are classified as fungivores, predators, or scavengers. The dominance of this feeding guild in oribatid mite assemblages from control and moderately disturbed habitats may be attributed to the greater amount of leaf litter in these plots. Increased organic matter supports higher fungal biomass and activity [92], as well as greater densities of soil-dwelling nematodes [93], which serve as potential prey for predatory and scavenging oribatid mites. In contrast, clear-cut plots were characterised by a higher relative abundance of species belonging to primary and secondary decomposer feeding guilds, such as *Ceratoppia quadridentata*, Haller, *Achipteria coleoptrata*, L. and *Scheloribates pallidulus*, C. L. Koch which primarily consume dead plant material and associated microbiota. This pattern is consistent with the findings of Farska et al. [31], who reported that oribatid mite assemblages in intensively managed forests were dominated by detritivorous and detrito-fungivorous species. However, it is important to note that species from these feeding guilds also occurred in similar absolute abundances in control plots. The observed differences in feeding guild composition were mainly due to the higher abundance of omnivorous Oppiidae species in the control and less disturbed plots. Therefore, the negative effects of forest management can be seen primarily in the decline of omnivorous species in disturbed habitats.

4.3. Seasonal changes

Seasonality in oribatid mite populations is often underrepresented in forest management research, as some studies rely on a single annual sampling event (e.g. Ref. [36]), or aggregate data across multiple sampling periods (e.g. Refs. [22,33,81,94]). However, seasonal fluctuations in oribatid mite density within deciduous forests have been associated with broader macroclimatic conditions, such as temperature and precipitation patterns [88,95,96]. In the present study, several community-level attributes exhibited clear seasonal trends, thereby supporting our third hypothesis.

Species richness was initially high across all treatments in April but declined over time, with reductions observed earlier in disturbed plots and later in the control plot, equalising by October. While the control plots maintained higher overall densities, species richness remained

comparable to that of the disturbed plots. This pattern led to higher species evenness in the clear-cutting and gap-cutting plots, particularly in April and June. These differences appear to be largely driven by reduced dominance of certain species, particularly those belonging to the family Oppiidae (e.g. *R. obsoleta*, *M. minus*, *D. ornata*, *O. nova*), in the disturbed plots. *R. obsoleta* and *D. ornata* reached peak abundance in spring, followed by a gradual decline throughout the year. The seasonal patterns and the higher abundances of these species in control and moderately disturbed plots, compared to clear-cut and gap-cut plots, may be attributed to differences in leaf litter quantity and, consequently, to species-specific functional traits related to habitat preference and resource utilisation. The findings of this study align with those of several previous investigations [13,52,97], which observed that following disturbance, the species pool of oribatid mites does not change substantially. Most species persist in disturbed habitats; however, shifts occur in their relative abundances. In our case, certain species decreased in abundance, indicating that the community changes were primarily quantitative rather than qualitative [23,52].

The most striking seasonal change occurred in the proportion of gravid females, although this was independent of forestry interventions. A seasonal decline in this proportion was observed in October in nearly all treatments. This seasonal trend contrasts with Luxton [91], who reported continuous egg-laying throughout the year, suggesting little seasonality in oribatid reproduction in Danish beech forests. To our knowledge, seasonal variation in oribatid mite fecundity has not been extensively investigated. The observed decline in gravid females in October may be related to a seasonal reduction in food availability. By this time, most of the previous year's leaf litter had decomposed, while new litter was only beginning to accumulate, potentially reducing resource availability for reproduction. It is unclear whether this pattern persists across years; however, we observed peak oribatid abundances in April, suggesting that fecundity likely increases over winter to produce high spring populations. This interpretation is supported by earlier observations from Reeves [98], who found that populations of dominant species such as *Oppia subpectinata* and *Oppiella nova* were lowest at the start of spring but increased significantly by April. This implies that reproductive activity may be highest in early spring.

5. Conclusions

This study provides the first evidence of long-term impacts of multiple forest management treatments on oribatid mite communities in a European deciduous oak-hornbeam forest. Five years after intervention, intensive treatments, particularly clear-cutting and gap-cutting, led to reduced oribatid densities and altered species composition, although overall species richness remained stable. Community changes were primarily quantitative, driven by shifts in dominant species, especially within the family Oppiidae. Functional trait analyses revealed that parthenogenetic species were more sensitive to disturbance, likely due to reduced food availability linked to lower leaf litter mass. Seasonal patterns further highlighted shifts in species dominance and reproductive activity, with notable declines in gravid females by autumn, possibly due to resource limitation.

Our results confirm that oribatid mites are sensitive and reliable bioindicators of forest disturbance, even years after intervention. Retention tree groups appear to mitigate negative effects, supporting their value in sustainable forest management. However, due to the limited spatial scale of this study, broader investigations across multiple forest types and environmental gradients are needed to fully understand the mechanisms shaping oribatid communities in response to management in deciduous forests. Incorporating a wider set of microbial variables will be crucial for guiding ecologically informed forestry practices.

CRedit authorship contribution statement

Veronika Gergőcs-Winkler: Writing – review & editing, Writing –

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

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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Appendix A. Supplementary data

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