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RESEARCH

Drivers of belowground properties in fir-beech karst forests a decade after silvicultural treatment

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Abstract

Silvicultural treatments, such as thinning and clearcutting, significantly alter belowground forest processes, yet post-treatment forest ecology remains poorly understood, particularly within temperate mixed and broadleaved forests. Ten years after silvicultural treatments, we investigated fine root biomass (FRB), soil properties, microbial parameters (microbial biomass, mycelium production, potential decomposition) and vegetation cover (canopy, shrub, herb), in Dinaric fir-beech forests on high karst plateaus of Slovenia. We compared these parameters in 27 plots including control, thinning (50%), and clearcut sites. Tree FRB was significantly reduced in clearcuts (−80.5%) but not in thinned plots, where high local variability was found. Despite reduced tree FRB, total FRB (trees, shrubs and herbs) remained comparable across treatments, indicating compensatory growth of shrubs and herbs. Clearcutting shifted fine root community composition toward beech dominance and increased cover and productivity of herb layer. Arbuscular fungal biomass and decomposition potential were significantly higher in clearcuts, while mycelium production correlated positively with tree FRB and negatively with nutrient-rich conditions. Our findings show that thinning was related to higher biomass of tree fine roots and associated microorganisms, while clearcutting corresponded to dominance of shrubs and herbs, increased decomposition rates and showed moderate positive association with increased soil nutrient levels. A suite of factors associated with the absence or reduction of tree cover may be driving altered nutrient cycling under herb dominated vegetation. Results also suggest a potential role of bacteria in the decomposition processes, particularly in sites with elevated atmospheric N inputs. These results highlight the importance of selecting appropriate intensity of silvicultural treatment and incorporating belowground processes in forest management of Dinaric fir-beech forests.

Keywords Vegetation cover · Soil parameters · Fine root biomass · Microbial biomass · Mycelium production · Clearcut · Thinning

Introduction

Ecosystem functioning depends on trophic interactions between above- and belowground communities, biogeochemical cycling, and plant–soil feedbacks (van der Heijden et al. 2008, 2015; Nielsen et al. 2015; Bakker et al. 2019). Fine roots are an important sink for plant photosynthates, which are further channelled into the surrounding soil environment (McCormack et al. 2014). A large part of root-derived carbon (C) compounds is directly transported to mycorrhizal and other root-associated organisms (Högberg et al. 2001; Hawkins et al. 2023), while exudation and fine root necromass provide substrates for free-living soil fungi and bacteria (McCormack et al. 2014; Žifčáková et al. 2017). Through these continuous inputs of organic matter,

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microbial activity in forest soils is tightly coupled with plant productivity and supports a range of key ecosystem functions and processes, including decomposition, mineralisation, and nutrient cycling (Baldrian 2017).

The removal of trees due to natural disturbances or human interventions changes the quantity and quality of plant-C inputs into soil (Lindenmayer et al. 2000), nutrient availability, and climate (Covington 1981; Chen et al. 1995; Hassett and Zak 2005; Nave et al. 2010). Limited data indicate that the severity of impacts on soil properties from forest harvesting practices is greater for clear cuts compared to shelterwood systems (Roy et al. 2021). All practices generally affect soil microorganisms in the short term (Holden and Treseder 2013; Zhou et al. 2020; Roy et al. 2024), while changes over longer periods are less obvious due to the gradual recovery of most biological components (Marshall 2000).

Tree removal reduces net primary productivity (NPP) and thereby the rate of C allocation belowground, diminishing root inputs and exudation that sustain soil microbial and mycorrhizal communities (Holden and Treseder 2013). The resulting decline in belowground C inputs decreases the supply of fresh organic matter to soils and accelerates the turnover of existing soil organic matter (SOM), as decomposition becomes increasingly fuelled by more labile C fractions (Lacroix et al. 2016). Despite some variation, clear cutting typically reduces soil microbial biomass (on average by ~ − 19%; Holden and Treseder 2013), while the effects of selective cutting are more moderate (Holden and Treseder 2013). The removal of trees affects both bacteria and fungi (Hartmann et al. 2012; Holden and Treseder 2013), but fungi are affected to a greater extent (Kohout et al. 2018; Martinović et al. 2022). Forest harvesting particularly reduces the root-symbiotic fungi of trees that form ectomycorrhizal (EcM) associations (Kohout et al. 2018). In contrast, arbuscular mycorrhizal fungi (AMF) that associate with herbaceous plants (Brundrett and Tedersoo 2018) may benefit from the increase in the biomass of their hosts that increase in abundance after disturbance (Kermavnar et al. 2021). AMF can exude sugars (Hooker et al. 2007) and fuel microbial activity through the priming of SOM decomposition by soil saprotrophs (Paterson et al. 2016; Averill and Waring 2018). Conversely, EcM fungi may suppress SOM decomposition by competing with soil saprotrophs, a phenomenon known as the 'Gadgil effect' (Gadgil and Gadgil 1975; Fernandez and Kennedy 2016).

Mountainous silver fir–European beech forests, often containing a substantial proportion of Norway spruce (*Picea abies* (L.) Karst.), represent a significant part of the total forest cover in Central and Southeastern Europe (Klopcic and Boncina 2011). Dinaric silver fir–beech forests are among the most widespread forest types in Slovenia, covering more than 10% of the total forest area (Kutnar et al. 2015). They are characterised by diverse topography (karst dolines, ridges, rocky outcrops) and associated variation in soil conditions. A long tradition of sustainable forest management, systematic silvicultural planning, and, more recently, the development of close-to-nature management have ensured the relatively preserved vegetation composition and high species diversity of these forests in Slovenia (Kermavnar et al. 2019a, b). Slovenian legislation (Forest Act with amendments and supplements 1993–2025) generally prohibits clearcuts exceeding 0.5 ha. Clearcuts, when applied, are substantially smaller than those typically found in European temperate deciduous forests (3–10 ha) (Kovács et al. 2018). In this context, clearcutting to obtain small canopy gaps in the size of 0.4 ha was included in the experimental design as an intentional contrast to thinning and control stands, allowing the assessment of belowground patterns across a gradient of canopy removal intensity. Our study aimed to characterize the potential drivers of belowground properties across silvicultural treatments a decade after the silvicultural intervention in Dinaric silver fir–beech forests. This stage of stand development remains poorly understood in terms of forest ecology, particularly within temperate mixed and broadleaved forests.

We hypothesised that:

(1) Clearcutting reduces tree fine root biomass a decade after the silvicultural treatment. In contrast, we expect that thinning would not significantly change tree fine root biomass compared to controls, as the selective removal of trees reduces competition and existing trees can expand their roots into areas previously occupied by felled trees. We expect that total fine root biomass (trees, shrubs and herbs) would remain relatively comparable across all treatments. (2) Clearcut plots are more prone to shifts in the species composition of the fine root community compared to thinned plots. (3) Silvicultural treatment leads to changed soil properties; we expect that clearcutting reduces organic soil C and nitrogen (N) contents, thereby constraining belowground productivity expressed as fine root biomass and soil microbial biomass. Higher soil respiration rate is expected in plots with higher soil organic C (SOC) (i.e. in control plots), reflecting enhanced substrate availability and microbial activity. (4) Differences in aboveground vegetation properties and the corresponding fine root community are reflected in differences in the biomass of different groups of microorganisms. Higher biomass of AMF is expected in clearcut and thinned sites.

Methods

Description of the plots and the applied treatments

For our study, we selected 27 plots located in uneven-aged Dinaric fir–beech forests (ass. *Omphalodo-Fagetum*) on three high Karst plateaus: Kočevje, Snežnik, and Trnovo in Slovenia (Fig. 1, Table S1). In 2012, each plot, which was technically a karst doline (bowl-shaped depression, a sinkhole), was randomly assigned to one of three silvicultural treatments: control (no cutting of overstory trees), thinning (50% of the tree growing stock was cut, with the remaining trees left evenly distributed), and clearcut (100% of the tree growing stock was cut, with no mature trees left). The pre- and post-treatment growing stock is shown in Table S1. The treatment area measured 0.4 ha and was circular, with its centre at the bottom of the sinkhole. These sites were the subject of previous studies on various immediate effects of silvicultural interventions within the ManFor CBD 2010–2015 Life Environment Project LIFE09 ENV/IT/000078 (www.manfor.eu). Detailed information regarding the silvicultural experiment can be found in Kutnar et al. (2015), Eler et al. (2018), and Kermavnar et al. (2019a, b, 2020, 2023). A list of the sites and their respective treatments is presented in Table S1.

Climatic conditions, stand structure characteristics (tree species composition, stand age, understory development), and general topographic features (karst landscape) were similar across the study locations. The climate is moderately continental, with warm, dry summers and cold, wet winters. The position of Trnovo in the transition zone between the Mediterranean and the Julian Alps results in slightly higher yearly precipitation (1996.5 ± 347.3 mm) relative to Snežnik (1518.6 ± 241.2 mm) and Kočevje (1478.0 ± 248.8 mm), data are 1950–2018 averages

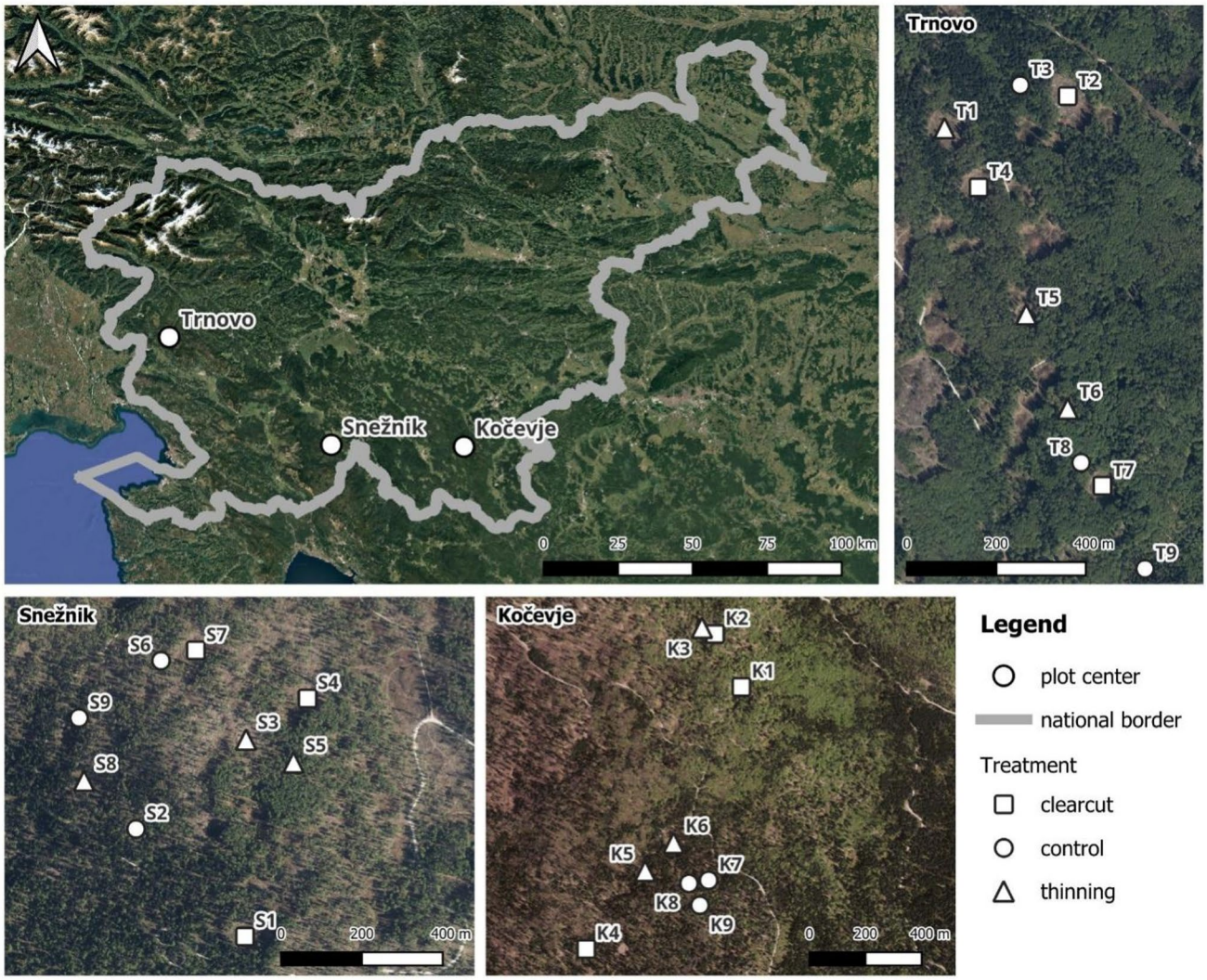

Fig. 1 Map of the plots in the karst high plateaus of Slovenia

obtained from Šercer et al. (under review). The prevailing soil types are Eutric Cambisols (calcareous brown forest soils), Leptosols (rendzinas), and Luvisols (IUSS Working Group WRB, 2015), all derived from limestone and dolomite parent materials. Eutric Cambisols typically occur at the bottom of karst sinkholes, while rendzinas are found on the slopes. Based on the pre-treatment soil analyses performed in 2011, soil conditions across the plots at all three locations were relatively comparable, with some notable differences among locations: the pH of mineral soil (0–10 cm) was highest at Kočevje (~ 5.3), while Snežnik and Trnovo had more acidic soils (~ 4.5), the C/N ratio in the mineral soil showed no major differences among locations, with slightly lower values observed at Trnovo. This suggests that nitrogen availability in the soil at Trnovo was higher already prior to the implemented experimental treatment. The amount of organic carbon in the organic soil layer at Trnovo was in the range ~ 15 t/ha, while at Snežnik and Kočevje it was < 10 t/ha. Carbon stocks in mineral soil were high (up to ~ 180 t/ha at Trnovo), and exhibited substantial variability (A. Marinšek, personal communication).

Before silvicultural treatment, stands were managed according to close-to-nature, sustainable, and multipurpose management principles (Kutnar et al. 2015), resulting in a multilayered structure with trees of varying diameters and ages. Forest regeneration in the investigated plots clearly reflected the different trajectories of stand development in these forests: in some plots, regeneration was rapid and abundant, while in others it was still almost completely absent even ten years after the treatment.

Evaluation of aboveground regeneration

Vegetation cover and regenerating tree species

Vegetation surveys were conducted on a 400 m^2 circular plots, each within a karst sinkhole. All vascular plant species present were recorded in different vertical vegetation layers: tree layer (trees and shrubs above 5 m, i.e. canopy cover), shrub layer (trees and shrubs < 5 m and > 0.5 m), and herb layer (trees and shrubs < 0.5 m and all herbaceous plants). The abundance of each species was estimated using the Barkman scale (Barkman et al. 1964). In addition, the cover of each vegetation layer (%) within a plot was estimated. The vegetation survey took place in June and July, at the peak of vegetation development. Vegetation surveys in the same plots were conducted in 2012 (shortly before tree cutting), 2014, 2018, and 2023 using the same sampling protocols. For data analysis, we used vegetation data from the last survey in 2023.

Vegetation production of the herb layer

Vegetation production of the herb layer was estimated in September 2023. Two 0.5 × 0.5 m wooden frames were placed on the ground approximately 3 m from the plot centre, covering a patch of ground vegetation typical for the respective plot. Herbs were cut at ground level with garden scissors, and leaves were collected from woody vegetation up to 0.5 m in height. The collected plant material was air-dried at 60 °C and weighed. The average dry mass was calculated for each plot and expressed in g/m^2.

Tree litter input

Tree litter input was monitored from 2021 to 2024 by installing one litter collector per plot. Litter collectors measured 0.65 m in diameter and were made of polyethylene mesh textile. Litter was removed from the collectors each year in late autumn after litterfall, placed in paper bags, dried at 60 °C, and weighed. Litter input was expressed in g/m^2.

Evaluation of belowground parameters

Soil physical–chemical parameters

Soil samples were collected in 2023 from five positions per plot—in the plot centre, and 2 m north, south, east, and west from the plot centre. Before sampling, leaf litter was removed and sampling was performed to 10 cm depth as all microbial parameters were studied in the top 10 cm of soil. Humus layer in all plots was thin and did not exceed 2 cm. Soil pH was measured in deionised water (1:10 w/v) after overnight incubation using a WTW Multilab 540 pH meter (Gemini BV, Apeldoorn, the Netherlands). Soil water content was determined by weighing fresh and freeze-dried soil and the difference expressed in % mass of dry soil. Organic C was determined by sulphochromic oxidation, and total N by a CHN Carlo Erba EA 1108 analyser (Carlo Erba, Milano, Italy). Available (water-extractable) phosphorus (P) was measured by shaking soil with deionised water (1:10) for 18 h, filtering through a 0.22 µm membrane, and quantifying spectrophotometrically using the malachite green method (Ohno and Zibilske 1991; Řezáčová et al. 2019). These analyses were conducted externally at the Institute of Botany of the Czech Academy of Sciences (Průhonice, Czech Republic).

Soil respiration

Soil respiration measurements were conducted within one week in May 2025 with the aim to ensure comparable weather conditions. Plots in Trnovo were measured on 13 May between 9:30 am and 2 pm, plots in Snežnik on 14 May between 9 am and 3 pm, and plots in Kočevje on 16 May between 9 am and 2:30 pm. Measurements were conducted using a LI-6400 with the 6400-09 soil chamber (LI-COR, Lincoln, NE, USA). Concurrently to soil CO_2 efflux, soil temperature was measured. In each plot, four measurement points were positioned 3 m from the centre, each aligned with one of the four cardinal directions using a compass. At each point, the soil chamber was inserted directly into the soil and set to run three cycles of soil efflux measurements. The first set of measurements was taken north of the centre, followed by east, south, and west, in that order. Soil temperatures at the time of soil respiration measurements did not differ significantly among treatments, however they were significantly lower in Kočevje than at the other two locations due to a cold spell. Soil respiration was analysed separately from other data, and soil temperature was included in the model.

Fine root biomass and necromass

Samples for evaluating standing fine root biomass (FRB) and necromass (FRN) were obtained by soil coring with a probe measuring 3 cm in diameter and 20 cm in length in June 2023. Soil cores were collected at eight sites per plot (two sites approximately 0.5 m apart, located 3.0–3.5 m north, south, east, and west from the plot centre). Soil cores were stored frozen at − 20 °C until analysis. Prior to processing, samples were thawed and washed through a 1 mm mesh sieve using tap water. Extracted roots were transferred to a water-filled tray and manually separated using tweezers. All root fragments longer than 5 mm were collected. Under a binocular microscope, roots were sorted into fractions. EcM tree species—European beech, Norway spruce, and silver fir—were identified based on morphological traits described by Mrak and Gričar (2016). Roots of shrubs and herbs symbiotic with AMF, including *Acer* sp. (present only in the herb layer), were grouped separately. Fine roots were defined as those with diameters less than 2 mm. Live and dead roots were distinguished by colour and tensile strength, with dead roots typically appearing as smaller fragments. Due to this fragmentation, necromass was likely underestimated; however, the data remain valid for relative comparisons across plots and treatments. Sorted roots were placed in Petri dishes and dried at 60 °C until reaching constant weight. After cooling in a desiccator, samples were weighed using an analytical balance (AS 82/220. X2 plus, Radwag, Poland). Root dry mass was expressed in g/m^2.

Indicators of fungal and bacterial biomass and fungal growth

To estimate soil microbial biomass, phospholipid fatty acids (PLFA) and neutral lipid fatty acids (NLFA) were extracted as described by Šnajdr et al. (2008) and Fernandez et al. (2022). Briefly, lipids were extracted from approximately 1 g of dry soil using a mixture of chloroform, methanol, and phosphate buffer (1:2:0.8), and separated using solid-phase extraction cartridges (HyperSep Silica SPE columns, 200 mg/3 mL, Thermo Fisher Scientific). The selected fractions underwent mild alkaline methanolysis, and the methyl esters of NLFA and PLFA were analysed by gas chromatography-mass spectrometry (GC-MS; 450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA). Fungal biomass in the polar PLFA fraction was quantified based on the content of 18:2ω6,9 (fungal PLFA), while bacterial biomass (total bacterial PLFA) was assessed by summing i14:0, i15:0, a15:0, 16:1ω5, 16:1ω7, 16:1ω9, 10Me-16:0, i16:0, i17:0, a17:0, cy17:0, 17:0, 10Me-17:0, 18:1ω7, 10Me-18:0, cy19:0 (Actinobacteria 10Me-16:0, 10Me-17:0, 10Me-18:0, Gram-positive i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 10Me-16:0, 10Me-17:0, 10Me-18:0, and Gram-negative 16:1ω7, 16:1ω9, 18:1ω7, cy17:0, cy19:0). Biomass of AMF was estimated using the concentration of 16:1ω5 in the NLFA fraction (Baath 2003; Frouz et al. 2016).

Fungal mycelium production was estimated as ergosterol content in sand-filled mycelium ingrowth mesh bags incubated in the soil. Mesh bags filled with sand were used to exclude most fungi other than EcM fungi (Wallander et al. 2001). The bags were made of 0.05 mm mesh Uhelon 100 T fabric, triangular in shape (13.5 cm per side), and contained 50 g silica sand (0.5–1.0 mm grain size). Bags were sterilised twice by gamma irradiation and buried in pairs at four microsites per plot, approximately 10 cm below the soil surface. After a 3-month incubation (June–September 2023), paired bags from each microsite were combined, yielding four samples per plot. Sand was immediately frozen, freeze-dried, and processed for fungal biomass determination. Ergosterol was extracted with 10% KOH in methanol and quantified by HPLC (Šnajdr et al. 2008).

Decomposition potential of soil microorganisms

The decomposition potential of soil microorganisms was assessed using filter paper as a cellulose substrate. Nylon mesh bags (Uhelon 100 T, 0.05 mm mesh; 10 × 13 cm) were filled with 3 g of oven-dried filter paper and buried

horizontally at a depth of 10 cm. Four bags were placed per plot, each approximately 5 m from the site centre to avoid interference with other experiments. After two months of incubation (June–August 2023), the bags were collected, freeze-dried, and stored over silica gel before weighing. Cellulose decomposition was expressed as the percentage of mass loss per day.

Statistics

Statistical analyses were performed in R (version 4.5.3; R Core Team 2026). To test the effect of treatment on response variables, we fitted linear mixed-effects models (LMMs) using the lme4 package (Bates et al. 2015). Treatment was included as a fixed effect, and study location (Kočevje, Snežnik, Trnovo) as a random intercept using the R syntax: lmer(y ~ treatment + (1|location)). Each response variable was first examined for distribution; where necessary logarithmic or logit transformations were applied to meet model assumptions (see Table S2). Within-site replicates were averaged prior to analysis to avoid pseudoreplication. Post-hoc pairwise comparisons among treatments were conducted using estimated marginal means obtained with the emmeans package (Lenth 2025), with *p*-values adjusted for multiple testing using the Tukey method. For each model we calculated Nakagawa's marginal R^2 (variance explained by fixed effects only) and conditional R^2 (variance explained by both fixed and random effects) using the performance package (Lüdecke et al. 2021). Then, depending on the model diagnostics for normality of residuals (Shapiro test) and variance of error terms (heteroscedasticity; Levene test), one-way ANOVA or non-parametric Kruskal–Wallis tests with Bonferroni correction were used to test potential difference between study locations, separately for each silvicultural treatment. In all tests, the threshold for statistical significance was taken at $\alpha = 0.05$.

Given the small overall sample size (n = 27) and the low number of levels of the random factor (only three locations), we performed a sensitivity analysis in which both treatment and location were treated as fixed effects in ordinary linear models (Gomes 2022), using the R syntax: lm(y ~ treatment + location). The results of the sensitivity analysis are presented in Table S2, which reports treatment effect estimates and p-values for both the fixed-location model (lm: y ~ treatment + location) and the random-location model (lmer: y ~ treatment + (1|location)) for each response variable. The direction and statistical significance of treatment effects were consistent across both modelling approaches for all key response variables, supporting the robustness of the conclusions drawn from the mixed-effects models. Assumptions of linear models were evaluated using conventional residual-versus-fitted and normal Q–Q plots. For the mixed-effects models, diagnostics were assessed using both conventional residual plots and simulated residuals generated with the DHARMa (Hartig 2024) and performance packages.

To summarise multivariate patterns in belowground responses, principal component analysis (PCA) was performed on the scaled belowground matrix. Treatment, location, vegetation variables, and soil variables were fitted passively onto the ordination using envfit function of the vegan package (Oksanen et al. 2024). Differences in the overall belowground response matrix were additionally tested by permutation analysis (adonis2, 999 permutations). Response variables were prioritised based on the strength of treatment effects in the main mixed-effects models and then examined further using restricted candidate predictor models. Priority was given to belowground response variables that showed the clearest treatment-related differences while also representing different components of belowground functioning. These included FRN of shrubs and herbs, tree FRB (beech, spruce and silver fir), AMF biomass, potential decomposition, FRB of shrubs and herbs and, more weakly, total FRB (trees, shrubs and herbs). For each prioritised response, a small set of a priori candidate predictor models was evaluated and ranked by AICc. These models were interpreted as associations only.

Results

Aboveground vegetation properties

Overall, canopy cover ranged from 0 to 100%. Significantly lower canopy cover was recorded in both thinning and clearcut plots (Fig. 2, Table 1). Shrub layer cover ranged from 2 to 82%, while herb layer cover ranged from 20 to 99%; both were significantly higher in thinning and clearcut plots compared to controls (Fig. 2, Table 1). Significantly lower shrub layer cover in thinning and clearcut plots was observed in Kočevje, while no significant differences between these two treatments were found in Snežnik and Trnovo. The highest herb layer cover was recorded in clearcut and thinning treatments in Trnovo, though the difference was not statistically significant. Herb layer cover in control plots was similar in Snežnik and Trnovo, but significantly lower in Kočevje compared to Snežnik (Fig. 2). Herb layer production (Fig. 2) was significantly lower in control plots compared to clearcuts, while thinning plots did not differ significantly from controls or clearcuts. No significant differences among locations were detected for herb layer production, likely due to high variability in thinning and clearcut treatments in Snežnik and Trnovo.

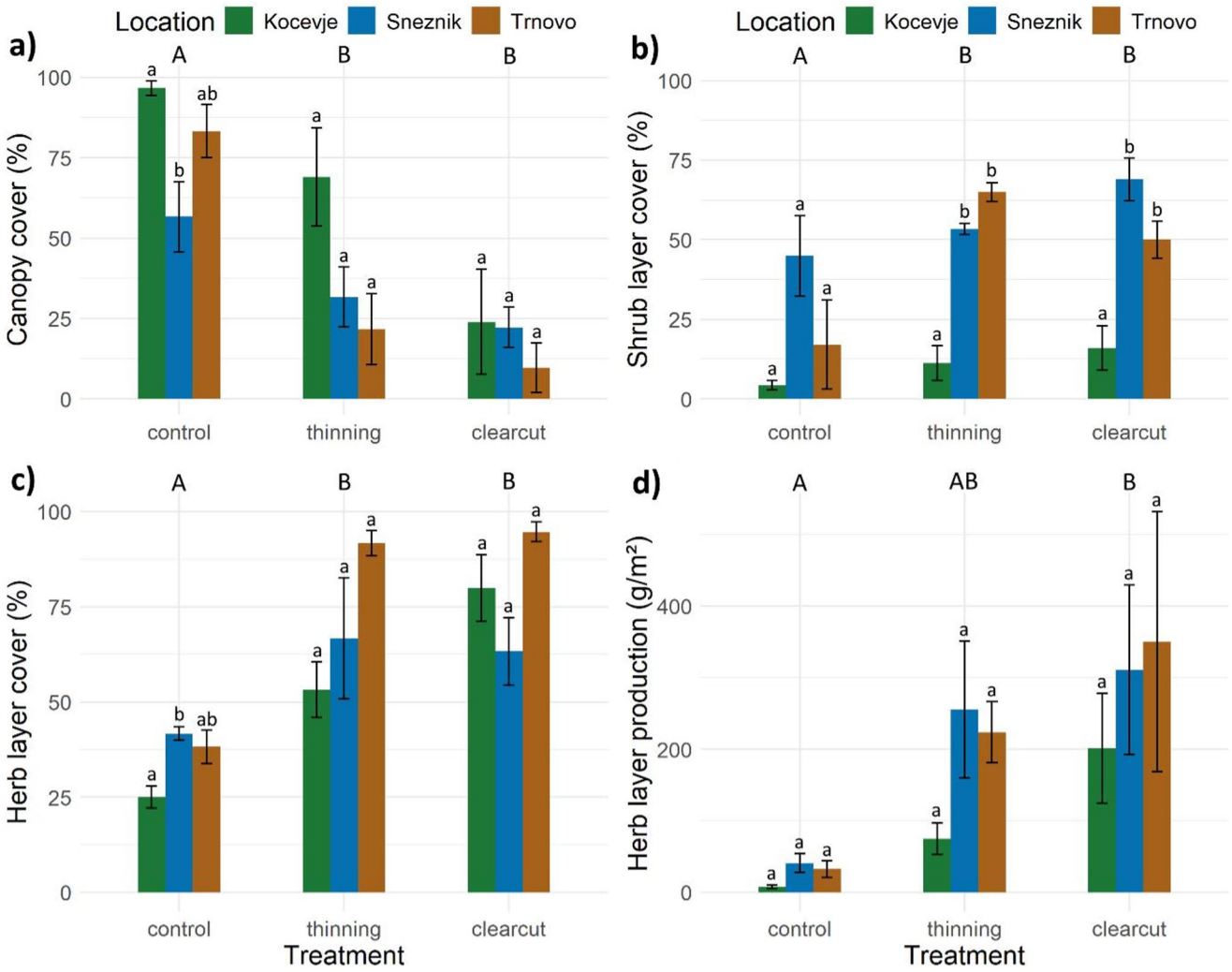

Fig. 2 **a** Canopy cover (%), **b** shrub layer cover (%), **c** herb layer cover and **d** herb layer aboveground production in relation to treatment and location, mean ± std. err. (N = 3). Capital letters above grouped bars denote differences among silvicultural treatments, tested with mixed-effects models. Lower-case letters above bars denote differences among study locations within each treatment, tested with ANOVA or Kruskal–Wallis test

Litter input in thinning (208 ± 36.5 g/m^2) and clearcut (151 ± 40.3 g/m^2) plots was significantly lower than in control plots (373 ± 27.6 g/m^2; Table 1). There were no significant differences in litter input among the locations.

Regeneration in the shrub layer consisted mainly of beech (Table S3, Fig. S1). Spruce and silver fir contributed minor percentages, up to 8.8% and 0.5%, respectively (Table S3). No significant differences in regeneration were observed among treatments and locations (Fig. S1). In the herb layer, regeneration percentages were much lower, reaching up to 8.8% for beech and up to 2% for both spruce and silver fir (Table S3).

Soil parameters

Treatment had no significant effect on soil physical–chemical parameters (Table 1, Fig. 3—pay attention to the legend, Fig. S3). Soil N, P, and organic C content were location-specific; soil N and P were significantly higher in Trnovo compared to Kočevje and Snežnik. SOC was higher in Trnovo than in Snežnik, with Trnovo and Kočevje showing similar levels (Fig. 3). As a result of increased N, soil C:N ratios were lower in Trnovo.

Treatment also showed no significant association with soil respiration (Tables 1 and S4). Plots in Kočevje had significantly lower soil respiration than both Snežnik ($p = 0.0005$) and Trnovo ($p = 0.0154$).

Table 1 Results of linear mixed-effects models for the parameters investigated in the study, where silvicultural treatment was considered as a fixed effect and location as a random effect

	Control	Thinning	Clearcut	R^2_c, R^2_m
Vegetation				
Canopy cover	87.2 [b] (56.7, 98.4)	38.0 [a] (10.3, 75.4)	12.2 [a] (1.5, 42.2)	0.592, 0.496
Shrub layer cover	14.0 [a] (-0.7, 75.0)	38.4 [b] (2.1, 92.5)	42.3 [b] (2.7, 93.7)	0.725, 0.159
Herb layer cover	34.5 [a] (9.7, 70.5)	75.5 [b] (40.3, 94.2)	84.6 [b] (54.0, 97.3)	0.678, 0.455
Herb layer production	20.2 [a] (6.2, 65.6)	142.4 [b] (43.7, 463.7)	216.5 [b] (66.5, 704.8)	0.734, 0.577
Beech in shrub layer	8.5 [a] (0.7, 31.6)	18.1 [a] (3.6, 50.5)	14.3 [a] (2.4, 43.8)	0.304, 0.057
Litter input	365.7 [b] (218.0, 613.4)	180.4 [ab] (107.6, 302.7)	101.4 [a] (60.4, 170.0)	0.356, 0.356
Fine root biomass				
Beech	96.9 [b] (34.3, 271.0)	44.5 [ab] (15.4, 125.4)	16.7 [a] (5.4, 48.1)	0.201, 0.201
Spruce	4.4 [a] (0.9, 14.6)	3.8 [a] (0.6, 12.9)	0.4 [a] (-0.5, 3.0)	0.165, 0.156
Fir	6.4 [a] (1.1, 24.6)	3.5 [a] (0.3, 14.6)	0.0 [a] (-0.7, 2.5)	0.200, 0.200
Total tree	181.4 [b] (72.3, 452.5)	78.6 [ab] (31.0, 196.9)	16.8 [a] (6.2, 43.3)	0.375, 0.375
Shrubs and herbs	36.5 [a] (14.5, 91.7)	97.4 [ab] (38.7, 244.7)	106.8 [b] (42.5, 268.5)	0.361, 0.218
Total	242.2 [a] (95.9, 611.6)	229.8 [a] (91.0, 580.2)	161.7 [a] (64.1, 408.4)	0.589, 0.093
Fine root necromass				
Beech	13.1 [a] (3.3, 52.3)	7.2 [a] (1.8, 28.9)	13.2 [a] (3.3, 52.7)	0.143, 0.032
Spruce	2.4 [a] (0.5, 6.5)	1.2 [a] (-0.01, 3.8)	0.2 [a] (-0.5, 1.6)	0.255, 0.179
Fir	3.0 (0.5, 9.7)	2.1 (0.2, 7.2)	0.0 (-0.6, 1.7)	0.166, 0.166
Total tree	31.9 [a] (7.5, 136.4)	14.7 [a] (3.4, 62.6)	15.1 [a] (3.5, 64.3)	0.289, 0.069
Shrubs and herbs	2.9 [a] (0.4, 21.0)	6.7 [a] (0.9, 49.4)	18.7 [b] (2.5, 137.5)	0.665, 0.283
Total	37.3 [a] (7.1, 197.1)	29.0 [a] (5.5, 153.2)	42.1 [a] (8.0, 222.3)	0.565, 0.024
Soil properties				
pH	6.2 [a] (5.7, 6.7)	6.2 [a] (5.7, 6.7)	6.2 [a] (5.8, 6.7)	0.359, 0.005
Organic C	6.3 [a] (3.5, 11.5)	7.4 [a] (4.1, 13.5)	5.8 [a] (3.2, 10.6)	0.452, 0.054
Total N	0.4 [a] (0.2, 0.9)	0.4 [a] (0.2, 1.0)	0.3 [a] (0.1, 0.8)	0.743, 0.040
C/N ratio	16.5 [a] (13.6, 20.1)	17.7 [a] (14.5, 21.5)	17.2 [a] (14.2, 21.0)	0.238, 0.021
P	7.4×10^{-4} [a] (5.3×10^{-4}, 10.3×10^{-4})	7.6×10^{-4} [a] (5.4×10^{-4}, 10.6×10^{-4})	8.0×10^{-4} [a] (5.7×10^{-4}, 11.1×10^{-4})	0.552, 0.024
Soil water content	0.3 [a] (0.3, 0.4)	0.3 [a] (0.3, 0.4)	0.3 [a] (0.3, 0.4)	0.089, 0.030
Soil respiration	5.2 [a] (2.2, 12.2)	5.5 [a] (2.4, 12.9)	4.3 [a] (1.8, 10.0)	0.661, 0.051
Fungal and bacterial biomass and activity				

Table 1 (continued)

	Control	Thinning	Clearcut	R^2_c, R^2_m
Total microbial biomass	20.6[a] (15.5, 27.4)	21.4[a] (16.1, 28.6)	21.3[a] (16.0, 28.4)	0.179, 0.004
Fungal PLFA	0.7[a] (0.4, 1.2)	0.8[a] (0.5, 1.3)	0.7[a] (0.5, 1.2)	0.007, 0.007
Bacterial PLFA	14.1[a] (9.5, 20.9)	14.4[a] (9.7, 21.4)	14.2[a] (9.6, 21.1)	0.308, 0.001
Fungi/bacteria	0.1[a] (0.0, 0.1)	0.1[a] (0.0, 0.1)	0.1[a] (0.0, 0.1)	0.304, 0.005
AMF (NLFA)	2.2[a] (1.3, 3.8)	5.6[b] (3.3, 9.5)	7.2[b] (4.2, 12.3)	0.324, 0.324
Mycelium production	0.1[a] (0.0, 0.2)	0.1[a] (0.0, 0.2)	0.1[a] (0.0, 0.2)	0.392, 0.012
Potential decomposition	0.3[a] (0.2, 0.6)	0.6[ab] (0.3, 1.2)	0.7[b] (0.4, 1.3)	0.348, 0.231

Reported are the predicted values, i.e. estimated marginal means (with 95% confidence intervals in parentheses) for each treatment category. Means labelled with the same letter are not significantly different at alpha = 0.05. R^2_m denotes variance explained by the fixed effects, while R^2_c denotes variance explained by the entire model, i.e. fixed and random effects

Fine root biomass and necromass

In the control plots of Kočevje, Snežnik and Trnovo, 69.0–91.4% of total FRB (trees, shrubs and herbs) consisted of tree roots. In thinning plots, this percentage ranged from 21.0 to 75.9%, while in clearcut plots, tree FRB (beech, spruce and silver fir) accounted for 15.9–38.5% of total FRB (Fig. 4). The lowest tree FRB after silvicultural treatment was observed in Trnovo (Fig. 4).

Beech was the dominant contributor to tree FRB in all treatments. Comparison of treatments showed that spruce and silver fir were absent or their share was negligible in the FRB of clearcuts, while they were present in the control and thinning treatments (Fig. 4).

Mean FRB values for spruce (25.69 ± 16.29 g/m^2) and silver fir (37.76 ± 19.11 g/m^2) in control plots were much lower compared to beech (146.15 ± 38.79 g/m^2). When FRB of each investigated tree species was analysed separately, no significant differences among silvicultural treatments were observed, likely related to high within-treatment variability (Table S5, Table 1). When the FRB of all three species were combined, mean total tree FRB in the thinning treatment was by −37.5% lower than in the control; however, values among individual thinning plots ranged from exceeding those of controls to substantially lower values (Table S5) and this difference was not significant. On the other hand, a significant reduction in total tree FRB (by −80.5%) in clearcut plots compared to controls was detected (Table 1).

FRB of shrubs and herbs was significantly higher in clearcut plots (141.4 ± 34.1 g/m^{-2}) compared to controls (53.0 ± 16.6 g/m^2) (Table 1, Fig. 5). No significant differences among the locations were observed (Fig. 5). No significant differences in total FRB (trees, shrubs, and herbs combined) among control (262.6 ± 34.0 g/m^2), thinned (265.7 ± 48.4 g/m^2) and clearcut (182.4 ± 30.6 g/m^2) plots were detected (Table S5, Table 1, Fig. 5). Similarly, no significant differences among treatments were observed for total FRN (control: 47.33 ± 10.78 g/m^2, thinning: 46.46 ± 16.91 g/m^2, clearcut: 61.53 ± 16.18 g/m^2; Table S5, Table 1). FRN of shrubs and herbs was significantly higher (Table 1) in clearcut plots (30.74 ± 10.25 g/m^2) compared to control plots (6.33 ± 3.57 g/m^2), with values for thinning plots intermediate (10.28 ± 3.53 g/m^2).

Fungal and bacterial biomass and activity

The abundance of AMF (based on the NLFA content) and potential decomposition rates responded significantly to silvicultural treatment in the model (Tables 1 and S6, Fig. 6). Significantly higher AMF biomass and potential decomposition rates were detected in clearcut plots compared to controls, while values for thinning plots were between control and clearcut treatments (Fig. 6). In addition to the treatment, potential decomposition rates were also significantly associated with location. Significantly higher potential decomposition rates were observed in Trnovo thinning plots compared to thinning plots in other two locations. In contrast, total microbial biomass, bacterial biomass, and mycelium production were significantly associated only with location. Significantly higher values of total microbial and bacterial biomass were detected for Trnovo clearcuts relative to clearcuts in other two locations. Snežnik was characterised by significantly higher mycelium production in clearcut treatment relative to Trnovo clearcuts (Fig. 6). Fungal biomass (PLFA) and the fungi to bacteria ratio were not associated with treatment or location.

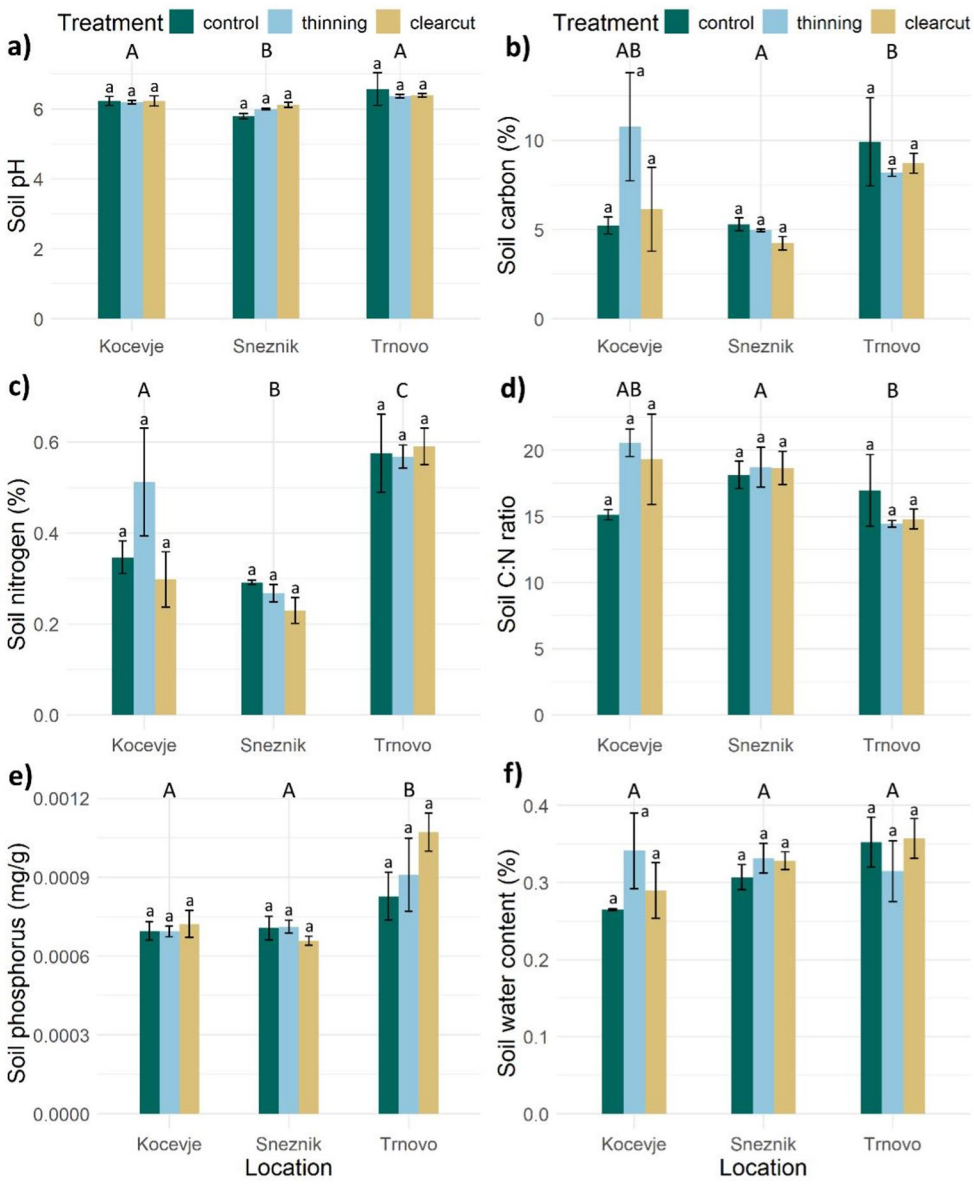

Fig. 3 Soil parameters in the investigated plots in relation to location and silvicultural treatment. As location was the only significant parameter for soil parameters, results are grouped primarily according to locations here to accentuate this finding. To distinguish from other Figures where results are grouped primarily according to silvicultural treatments, colours used in this Figure are intentionally different. Capital letters above grouped bars denote differences among locations, tested with mixed-effects models. Lower-case letters above bars denote differences among silvicultural treatments within each location, tested with ANOVA or Kruskal–Wallis test

Patterns in belowground properties

To visualise covariation among belowground response variables, we performed a PCA on the scaled matrix of belowground variables with treatment, location, aboveground vegetation, and soil variables fitted passively onto the ordination (Fig. 7). PCA shows clear shift in ecosystem structure. Plots with higher tree cover, litter input, and a higher proportion of tree FRB were positioned toward the positive side of PC1, whereas plots with higher herb-layer cover, herb-layer production, and higher soil nutrient variables (pH, P, organic C, and total N) were positioned toward the negative side of PC1. Shrub-layer cover was aligned mainly with negative values of PC2. The multivariate belowground response matrix varied significantly in the additive treatment + location model (adonis2: $R^2 = 0.374$, $F = 3.28$, $P = 0.001$).

To complement the ordination, we further examined the belowground response variables that showed the clearest treatment-related patterns in the main mixed-effects models (Table S7). The restricted candidate-model analysis did not support a single explanation for belowground variation. Instead, different belowground properties were associated with different components of canopy structure, understory development, fine-root composition, decomposition, and litter input.

For tree FRB (beech, spruce and silver fir), the candidate model was restricted to tree cover, litter input, and herb-layer cover. The model including tree cover alone had the lowest AICc (85.79), although a model additionally including litter

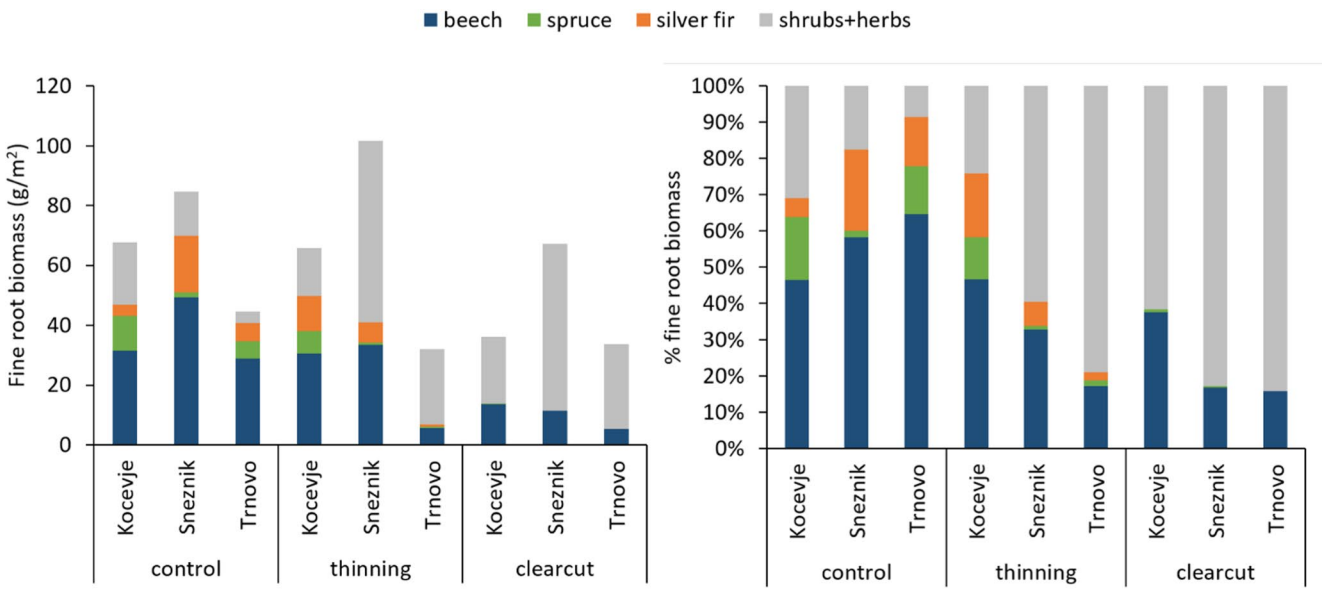

Fig. 4 Mean fine root biomass (g/m.^{2}) of beech, spruce, silver fir and shrubs + herbs in three locations (Kočevje, Snežnik, Trnovo) of Dinaric fir-beech forests grouped by silvicultural treatment (left panel) and share of the fine root biomass of these types of roots in relation to the total fine root biomass (right panel)

input was also competitive (ΔAICc = 0.55). Tree FRB was therefore associated mainly with canopy cover, which contributes litter input to the plots.

For FRB of shrubs and herbs, the candidate model was restricted to herb-layer production, herb-layer cover and soil P. The model including herb-layer production had the lowest AICc (62.97), whereas the next-best model was 2.80 AICc units higher. This suggests that FRB of shrubs and herbs was associated more closely with herb layer productivity than with herb-layer cover alone or with soil P.

For total FRB (trees, shrubs and herbs), the model including tree cover alone had the lowest AICc (29.05), but the model additionally including herb-layer cover and litter input was also competitive (ΔAICc = 1.47). Because total FRB is a composite response integrating opposite changes in tree and fine roots FRB of shrubs and herbs, it was interpreted more cautiously than the component fractions.

For FRN of shrubs and herbs the candidate model set was restricted to FRB of shrubs and herbs, herb-layer cover, and potential decomposition. The best model (AICc 60.14) included FRB of shrubs and herbs and potential decomposition, whereas the next-best model was 2.59 AICc units higher. This suggests that FRN of shrubs and herbs was positively associated with the understory FRB and with decomposition potential.

For AMF biomass, the candidate model set for this response was restricted to herb-layer cover, FRB of shrubs and herbs and soil P. The model including herb-layer cover and FRB of shrubs and herbs had the lowest AICc (43.61), whereas the next-best model was more than two AICc units higher. This suggests that AMF biomass was more closely associated with understory development and the fine-root fraction of shrubs and herbs than with soil P alone.

For potential decomposition, the candidate model set for this response was restricted to AMF biomass, litter input, and total N. The model including AMF biomass and litter input had the lowest AICc (−0.51), but an AMF-only model and a model including AMF biomass, litter input, and total N were also competitive (ΔAICc < 2). Potential decomposition was therefore not explained unambiguously by a single predictor, although the best-supported models consistently included AMF biomass and/or litter-related terms.

Discussion

Effect of silvicultural treatments on aboveground vegetation, fine root biomass, soil properties and microbial biomass

The aboveground vegetation was the biotic variable that responded most strongly to silvicultural treatment. After ten years, even the thinning treatments did not have canopy cover levels comparable to that of the controls. This was reflected in higher shrub and herb cover in thinning and clearcut plots, as well as higher herb layer production relative to control plots. In some of the clearcut plots, the canopy cover was not totally absent which could be attributed to the retention of naturally regenerating beech trees of variable age structure in shrub layer within the canopy gaps during harvesting. Consequently, improved post-treatment light availability accelerated the growth of these regenerating

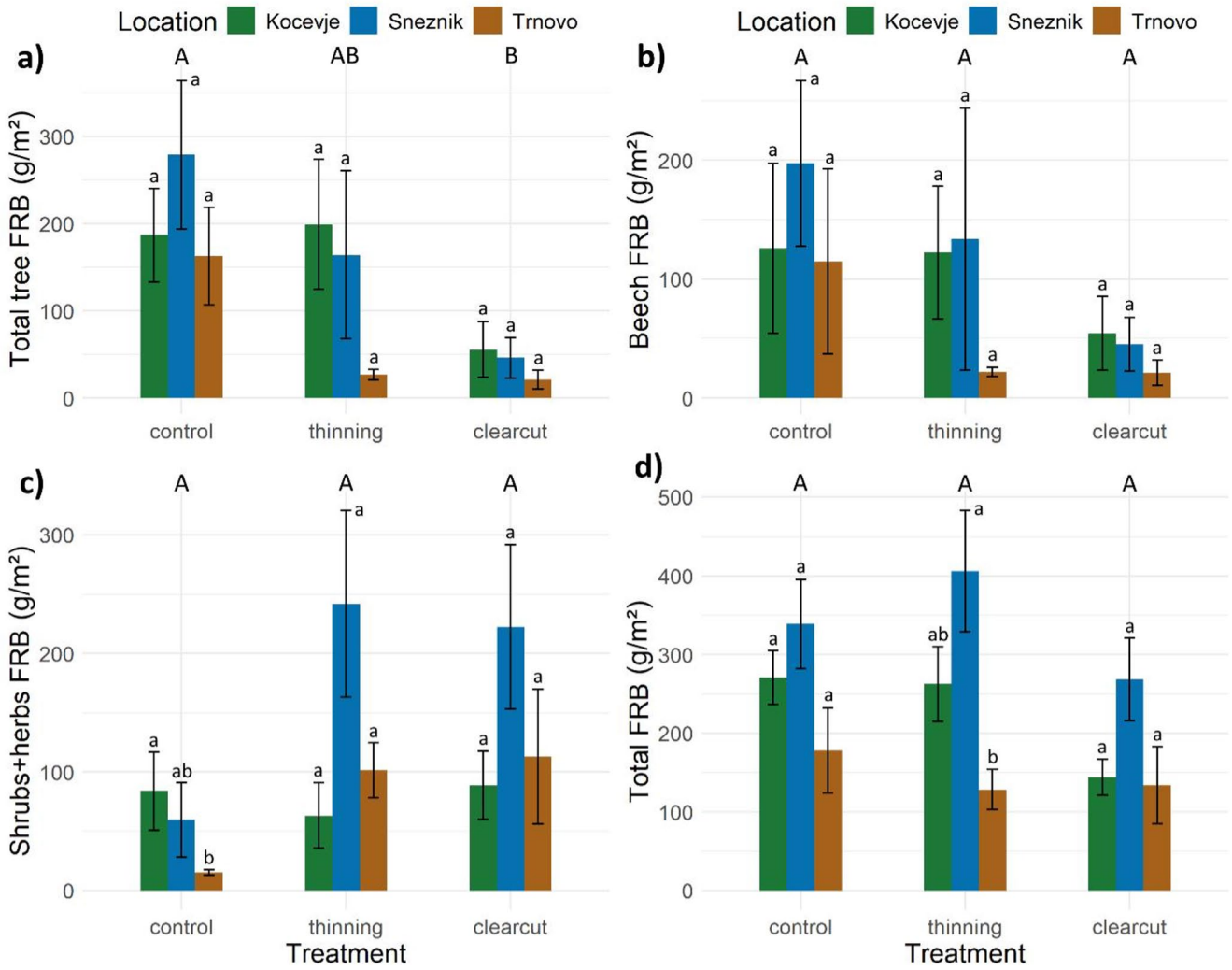

Fig. 5 Fine root biomass of **a** total trees, **b** beech, **c** shrubs and herbs and **d** all plant species, in relation to treatment and location, mean ± std. err. (N = 3). Capital letters above grouped bars denote differences among silvicultural treatments, tested with mixed-effects models. Lower-case letters above bars denote differences among study locations within each treatment, tested with ANOVA or Kruskal–Wallis test

beech trees, and in a decade, some of them already reached the crown layer. The tree regeneration consisted mainly of beech. Although canopy cover was significantly lower in thinning plots, the difference in tree FRB (beech, spruce and silver fir) was not statistically significant (by −37.5% lower relative to controls). The high variability observed suggests that the effect may be ecologically relevant at a local scale. In contrast, clearcut plots showed much stronger, significant reduction of total tree FRB by −80.5% compared to control values.

There is very limited knowledge about post-treatment effects of silvicultural treatments on tree fine root pool in temperate forests. Three years after thinning in 20–30-year-old stands of oriental beech in Turkey, light thinning had no significant effect on FRB of oriental beech, but heavy thinning significantly reduced beech FRB by −7% (Tufekcioglu et al. 2005). In contrast, different levels of thinning in Czech beech forest resulted in significantly reduced tree FRB in the top ten centimetres of soil even after 24 years (Konôpka et al. 2020). A global meta-analysis indicates that thinning in temperate forests generally reduces FRB in early stages (on average by −13.8%), with later (> 10 years) increases in FRB occurring in some heavily thinned stands (Qin et al. 2024), which are likely due to vigorous regeneration of understory plants, as well as accelerated growth of retention trees (Qin et al. 2024). Although fine roots of EcM tree species and arbuscular (AM) shrub and herb species have distinct properties (Zhao et al. 2023), this remains unspecified in many studies. In our experiment, the total FRB (trees, shrubs, and herbs) was statistically comparable across all treatments, but in clearcut plots tree FRB was mainly substituted by FRB of AM shrubs and herbs. In temperate forests, roots of AM species decompose significantly faster than those of EcM species due to their lower

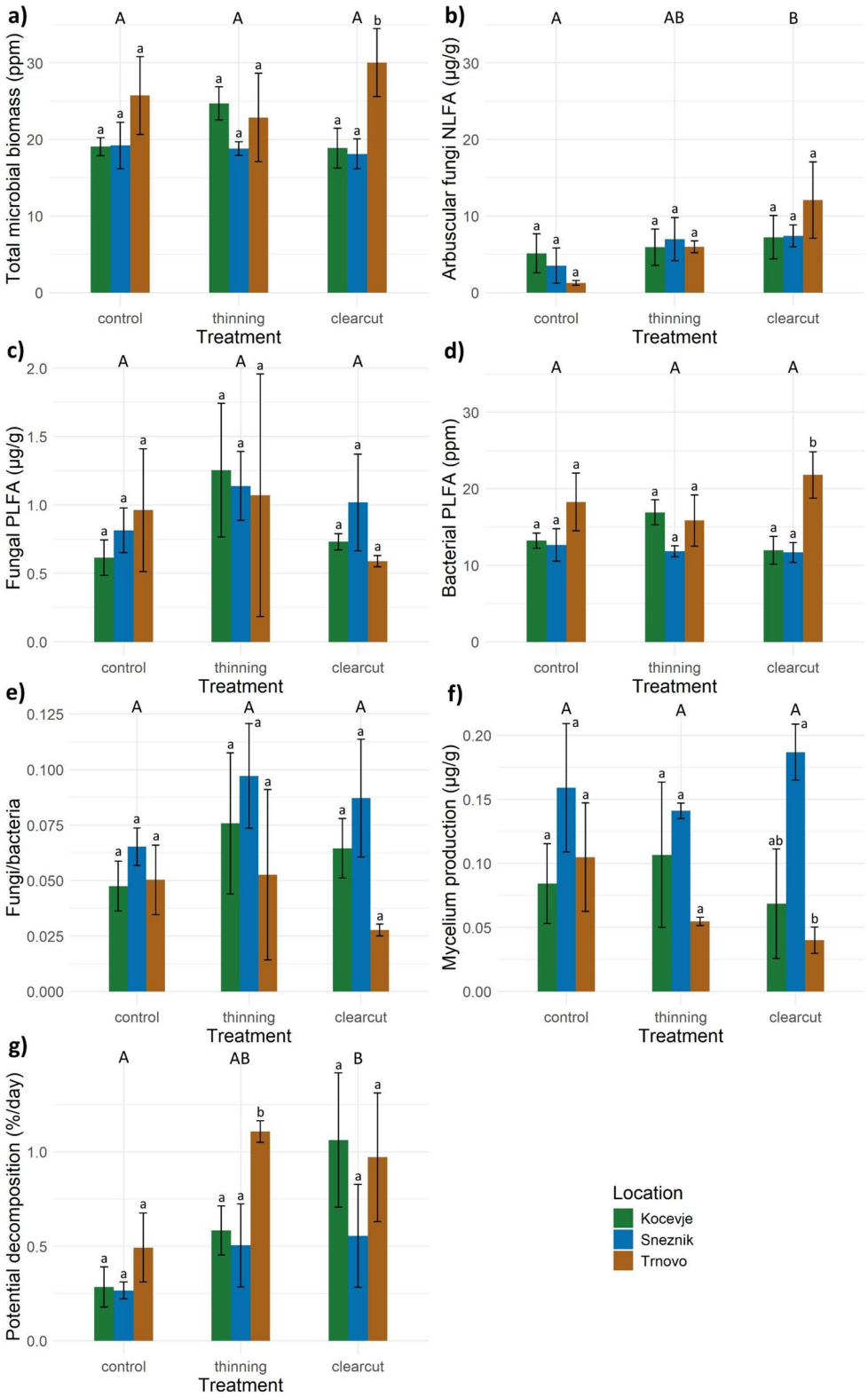

Fig. 6 Parameters of microbial biomass and activity in relation to silvicultural treatment and location, mean ± std. err. (N = 3). Capital letters above grouped bars denote differences among treatments, tested with mixed-effects models. Lower-case letters above bars denote differences among study locations within each treatment, tested with ANOVA or Kruskal–Wallis test

lignin content, which may affect carbon and nutrient cycling (Zhao et al. 2023). Increased organic matter input into soil is fueling microbial growth, which may result in a higher ratio of microbial-derived compounds with lower C: N ratio in soils under AM plants (Zhao et al. 2023). These results statistically support our first hypothesis: tree FRB was significantly lower in clearcut plots relative to controls, did not differ between thinned and control plots, and total FRB

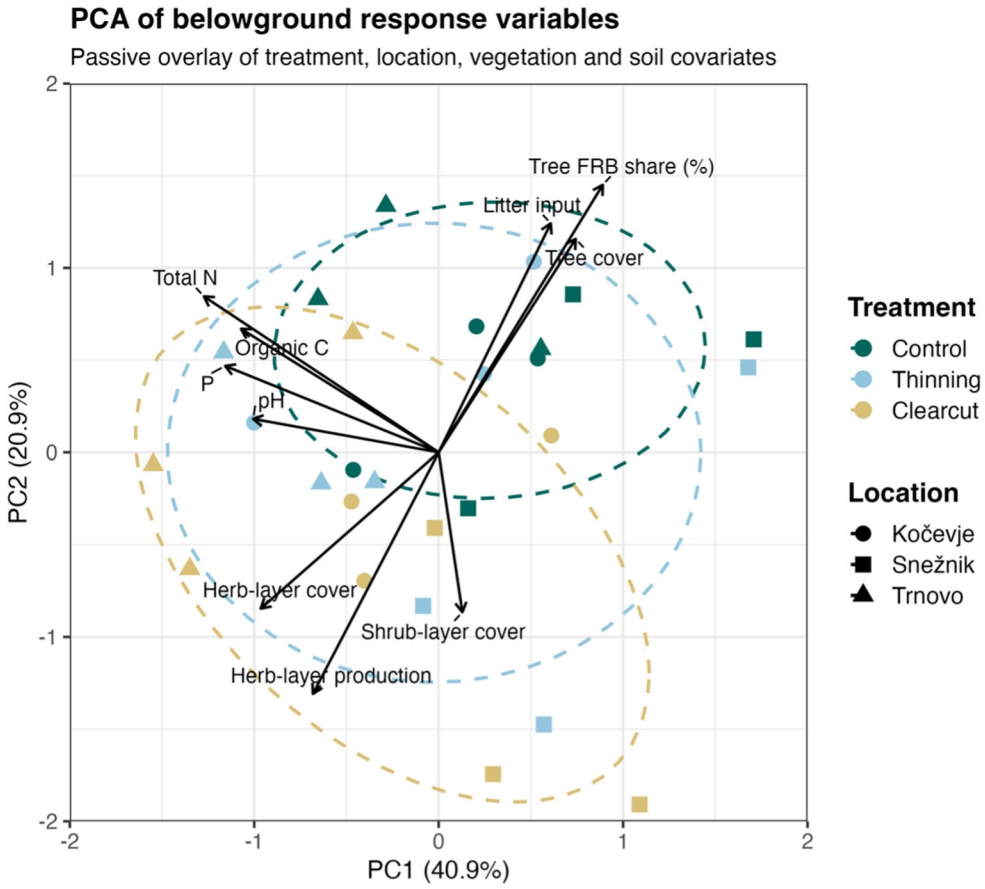

Fig. 7 Principal component analysis (PCA) of the scaled belowground response matrix with passive overlay of treatment, location, vegetation, and soil variables. The first two axes explained 61.8% of the total variation (PC1 = 40.9%, PC2 = 20.9%). Symbols represent plots; treatment is indicated by colour and dashed ellipses, and location by symbol shape. Arrows indicate significant fitted vectors (envfit, $P < 0.05$) for vegetation and soil covariates

(trees, shrubs and herbs) was comparable across treatments. High among-plot variability and limited replication may have reduced the statistical power of our study, resulting in limited ability to detect statistically significant differences in some comparisons, despite effect sizes that may be ecologically relevant at local scales.

The species composition of tree FRB was influenced by silvicultural treatments. In clearcuts, tree fine roots were almost exclusively from beech, with small admixture of spruce. In contrast, thinning plots had a fine root community comparable to control plots, probably due to the presence of adult silver fir and spruce trees, as regeneration of these species was minimal, thus confirming our second hypothesis. Silver fir and spruce regeneration is strongly affected by ungulate browsing (Diaci 2002; Vettori et al. 2024). The relatively small difference between control and clearcut plots in the FRB of spruce and silver fir could be attributed to the low and gradually decreasing representation of both species in the tree layer of control plots (see Fig. S2), which resulted from natural disturbances such as windthrow and dieback of trees in some control plots. Natural intermediate severity events at the stand scale are an important part of the disturbance regime in these forests (Nagel et al. 2017). Consequently, the controls represent a realistic low-intensity managed system subject to background disturbance, rather than unchanged baseline condition.

After ten years of natural regeneration, no significant effect of clearcutting or forest thinning on selected soil physical–chemical properties or soil respiration was observed, rejecting our third hypothesis. The absence of significant effects on soil properties may be explained by the fact that the plots are located in karst sinkholes, where nutrients are delivered during precipitation events from the surrounding area. However, some caution is needed here. A study conducted on the same plots, comparing pre- (2011) and post- (2014) treatment conditions, detected a significant decrease in total N content of organic soil in thinning and clearcut plots (Hukić et al. 2021). Moreover, when analysing SOC stocks separately for organic and mineral soil it was found that SOC stocks decreased in organic soil but increased in the 0–10 cm mineral soil following harvesting, likely reflecting reduced litter inputs, enhanced decomposition and leaching from organic into mineral soil (Hukić et al. 2021). As our study did not separate organic and mineral soil in the top 10 cm and did not calculate SOC stocks, we might have missed the opposite changes in soil physical–chemical properties in these layers. A global metadata study showed that the removal of litter results in decreased SOC concentrations, SOC stocks and soil nutrients (Feng et al.

2022) which we could not detect despite obvious reductions in litter inputs. On the other hand, root-derived carbon has been shown to contribute disproportionately to SOC formation compared to aboveground litter, as it is more efficiently stabilised in soil and more likely to contribute to mineral-associated organic matter (Rasse et al. 2005; Cotrufo et al. 2013). The comparable total FRB (trees, shrubs and herbs) observed a decade after silvicultural treatment indicates that belowground C inputs may have recovered to some extent, potentially reducing the relative importance of decreased aboveground litter inputs. However, differences in fine root turnover of EcM trees and AM shrubs and herbs, exudation rates, and mycorrhizal associations functioning likely result in differences in C input pathways and stabilisation as well as nutrient cycling differences (Phillips et al. 2013).

Higher soil N content in the Trnovo location is of transboundary air pollution origin (Pintar et al. 2025). N input may induce mineralisation of P from SOM by soil microorganisms (Arenberg and Arai 2021) which would explain the correlation between N and P soil levels (Fig. S3). Interestingly, SOC was not depleted in Trnovo despite increased potential decomposition rates there, particularly in thinning plots. This suggests that either fresh organic matter input is high (although our current data do not support this), decomposition residues bind to mineral particles, forming stable mineral-associated organic matter (Cotrufo et al. 2013), or pre-existing SOC is already present as stable organo-mineral complexes and is thus protected from decomposition (Cotrufo and Lavallee 2022).

Soil respiration in our study was measured only once, in spring, and did not show any significant treatment effect, but should be repeated or extended to provide insight into soil CO_2 efflux throughout the year. Given the strong seasonal variability of soil respiration, primarily driven by temperature under non-limiting moisture conditions (Janssens et al. 2003), a single measurement may not adequately capture treatment effects and should be interpreted with caution. Generally, soil respiration decreases after clearcutting but returns to the level of a mature stand within a few years to a decade (Peng et al. 2008).

Among all measured microbial parameters, only the biomass of AMF and potential decomposition rate were significantly associated with silvicultural treatment; both parameters were significantly higher in clearcut plots compared to controls. As clearcutting typically promotes the growth of herbs and shrubs (Zenner et al. 2006; Heinrichs and Schmidt 2009), the higher biomass of AMF in clearcut plots is an evident consequence, as many shrubs and majority of herbs are mycorrhizal with AMF (Soudzilovskaia et al. 2020). Accelerated decomposition rates in clearcuts compared to controls could be at least partly associated with changed microclimatic conditions (Šercer et al. under review). Moreover, some studies suggest that AMF fungi may contribute to accelerated decomposition processes (Hodge et al. 2001; Kong et al. 2018).

However, the indirect effect of silvicultural treatments on soil microbial parameters was evident through their association with fine root parameters (Fig. S3), supporting our fourth hypothesis. Fine roots, as central channels of energy delivery into the soil and further into the soil food web, strongly shape belowground communities and their functioning (Prescott and Grayston 2023). We have shown a positive association between tree FRB and mycelium production in mesh bags, and between FRB of shrubs and herbs and AMF biomass (see previous section). Mesh bags are primarily used as indicators of mycelium production by EcM fungi (Wallander et al. 2001), which is consistent with our results, as all three dominant tree species are EcM.

Patterns in belowground properties

Soil nutrients were inversely related to canopy cover and moderately positively associated with the herb layer, pointing to a linkage between nutrient patterns and vegetation structure, although these relationships were not clearly attributable to treatment effects alone, as indicated with PCA. The increased light availability in clearcut and thinned plots was a factor likely promoting herb-layer development (Landuyt et al. 2019). The positive association between shrub layer productivity and FRB of shrubs and herbs, is reflecting a connection between potential resource acquisition and biomass allocation (Wang et al. 2025), while higher FRB of shrubs and herbs also contributes to higher FRN of this functional group. Positive association of FRN of shrubs and herbs with potential decomposition likely reflects greater inputs of labile belowground litter in the form of FRN (Zhao et al. 2023), higher fine root turnover of herbaceous vegetation (Solly et al. 2014; Wang et al. 2019), and changed site microclimate (Solly et al. 2014, Šercer et al. under review) that could stimulate microbial activity and decomposition processes. Moreover, the observed increase in decomposition under these circumstances could also result from shifts in different microbial groups due to the absence of tree roots. The reduction in mycorrhizal fungi associated with tree fine roots (Fig. S3) may have released decomposers from competitive suppression by physical exclusion (Gadgil and Gadgil 1975), but increased nutrient levels (shown by association between decomposition and N in a competitive AIC model, as well as by association between nutrients and herb cover in PCA) could also alleviate nutrient limitation of decomposers (Gadgil and Gadgil 1975), thereby accelerating decomposition. Bacteria and fungi compete for C and energy resources in soil, with fungi being better competitors for plant residues compared to bacteria because

they produce nearly all exoenzymes required to decompose such materials (Wang and Kuzyakov 2024). As bacteria are more N demanding than fungi, strong competition is expected to decrease in sites richer in N, with a lower C/N ratio (Wang and Kuzyakov 2024). This was supported in our data by lower fungi-to-bacteria ratio in sites richer in N. Bacterial biomass was positively correlated with potential decomposition rates (Fig. S3), supporting the presumption of released competition. This finding is also supported by the evidence that bacteria typically dominate SOM transformation processes in systems characterised by AMF associations (Cotrufo and Lavallee 2022). Collectively, these processes may help explain the observed effects of the herb layer on soil nutrient concentrations reported by Xiong et al. (2024).

Conclusion

In summary, our results indicated that ten years after silvicultural treatment tree FRB was higher in stands subjected to thinning compared to clearcuts. In thinned stands, fine root species composition also more closely resembled that of the control communities. Under reduced canopy cover, increased light availability likely promoted herb layer cover, which was associated with increased FRB of AM shrubs and herbs, enhanced FRN inputs from this functional group, higher biomass of AMF fungi, and higher decomposition rates. Increased decomposition rates in this context could be linked to changed microclimatic conditions at the site, release of competition due to absence of ectomycorrhizal fungi associated with tree roots, input of easy decomposable organic matter from herb layer and possible contribution of AMF to the decomposition processes. Positive association between elevated soil nutrient levels and bacterial biomass indicated greater involvement of bacteria into decomposition processes under herb cover, which may be particularly relevant at sites with higher atmospheric N inputs. These patterns may reflect distinct biotic interactions influencing organic matter breakdown under reduced or absent canopy cover. Based on this, forest management planning should consider belowground processes in their management plans to enable sufficient forest regeneration and maintain forest soil functions. The predominance of beech in forest regeneration of Dinaric fir-beech forests indicates potential biodiversity loss of soil (micro)organisms associated with silver fir, which is threatened by grazing and increased temperature caused by canopy openings and climatic change. To preserve the existing forest composition and, consequently, soil functions, close-to-nature forest management principles should be followed.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-026-01939-w.

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Data availability The dataset generated and analyzed during the current study is publicly available in the DiRROS repository under the https://doi.org/10.20315/Data.0011.

Declarations

Conflicts of interest The authors declare no competing interests.

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