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SHORT COMMUNICATION

Variations in soil compositions and fungal communities are linked to tree composition and understory management

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Abstract

The increasing prevalence of abandoned secondary forests, resulting from human land use and forest management, often cause the dominance of specific plant species. In the Rokko mountain range (Hyogo Prefecture, Japan), *Pieris japonica* and dwarf bamboo form a dense understory, hindering the establishment of other plant species. This study investigated how diverse tree compositions and the selective removal of dominant understory plants affect soil environmental conditions (litter and humus contents and soil nutrient levels) as well as fungal community dynamics in these forests. Plots dominated by trees associated with ericoid mycorrhizal (ErM), arbuscular mycorrhizal (AM), and both ectomycorrhizal (ECM) and AM (ECM–AM) fungi had higher proportions of corresponding mycorrhizal fungi. *Pieris* removal led to enhanced humus accumulation and organic matter content and a shift toward pathotroph–symbiotic fungal dominance. Conversely, dwarf bamboo removal resulted in a minor increase in soil pH and a shift toward pathotrophic fungal communities. The effects of *Pieris* removal were also observed in plots following removal of both species. Understory management significantly alters soil biogeochemistry and fungal community composition and function. This study underscores the importance of maintaining tree diversity and implementing appropriate understory management strategies to conserve local fungal communities and landscape elements in secondary forests.

Keywords Fungal functionality · *Pieris japonica* · Dwarf bamboo · Rokko mountains · Symbiotroph

Introduction

Effective secondary forest management is necessary to sustain local biodiversity. Human–mediated environments maintain vegetation at various successional stages, supporting a diverse species, including endangered flora and fauna (Buckley 2020). The ecological importance of human–influenced forests has been recognized since the Satoyama Initiative's approval. However, socioeconomic shifts have resulted in numerous unmanaged secondary forests (Takeuchi 2010; Nakajima & Ishida 2014). Specifically, understory dominance by certain plant species impedes the establishment of other tree species, impacting soil physicochemical properties, light availability, and soil microbial communities (Mallik 2003; Royo & Carson 2006; Hirayama et al. 2011; Hédl et al. 2010; Nakajima et al. 2018). Although studies on coppice forests have explored land–use change, forest structure, and plant species diversity (Fukamachi et al. 2001; Nakajima & Ishida 2014; Müllerová et al. 2015), research on soil ecosystems, particularly fungal communities, remains limited. Nonetheless, such studies offer crucial insights for developing informed secondary forest management strategies.

The Rokko mountain ranges, located near Kobe city, Hyogo Prefecture, Western Japan, are characterized by extensive secondary forests undergoing noticeable vegetational shifts (Uchida et al. 2006; Kamiya 2014). Disease–induced dieback of canopy trees, *Pinus* and *Quercus*, in the forests surrounding Mount Rokko has facilitated the proliferation of *Pieris japonica* (Thunb.) D.Don ex G.Don and dwarf bamboo in the forest understory (Yoshioka et al. 2024). Seedling recruitment of diverse plant species has

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been infrequent, raising concerns that local landscape elements, composed of various plant and tree species, may be lost due to these dominant understory plants (Kamiya 2014). To reverse this successional trend, understory removal trials have been initiated by both official and private sectors (Oka & Doma 2016). These trials have reported increased light penetration postcutting and observed seedling establishment of other plant species (Oka & Doma 2016). However, quantitative data and robust evidence regarding the effects of understory removal on soil environmental conditions and fungal communities remain lacking. Hence, comprehensive analyses of the impacts of understory management on soil ecosystems are essential to develop effective forest management policies for local authorities and municipalities.

Vegetation and soil microbial communities have strong reciprocal interactions. Canopy tree composition and topography modulate soil environments and microbial communities (e.g., Urbanová et al. 2015), yet the effects of understorey vegetation are unexplored. Research on *P. japonica* dominance in broadleaved forests demonstrates its mutualistic relationships with ericoid mycorrhizal (ErM) and arbuscular mycorrhizal (AM) fungi (Fujiyoshi et al. 1999). Understory dominance by *P. japonica* alters microbial communities, with reduced ectomycorrhizal (ECM) fungi and increased saprotrophic fungi (Tokumoto & Katayama 2024). Moreover, increased humus accumulation due to *Pieris* dominance hinders plant establishment (Tokumoto & Katayama 2024; in press), necessitating intense management. Dwarf bamboo, including *Sasa senanensis* (Franch. & Sav.) Rehder (AM−associated), impacts soil nutrient cycles and forest regeneration (Itô & Hino 2007; Fukuchi et al. 2011; Fukuzawa et al. 2015). *Sasa kurilensis* (Rupr.) Makino & Shibata dominance alters microbial communities, favoring Pezizaceae (Ascomycota) mycorrhizae (Kong et al. 2017). Removing these dominant understory species can considerable change soil nutrient availability and fungal community composition.

This study aimed to elucidate understory environments and soil microbial communities across varying tree compositions and management regimes. We first compared soil and fungal parameters among plots with different tree compositions, correlating microbial community variations with environmental factors. We hypothesized that the proportions of trees with three mycorrhizal types (ECM, AM, and ErM−associated) alter fungal diversities, communities, and functionalities. Second, we compared parameters across different understory conditions created by management. We hypothesized that differences in understory vegetation, specifically removal of *Pieris* and dwarf bamboo, are associated with distinct soil fungal community compositions and related soil parameters. Then, we discussed the linkages between varying tree compositions, management regimes, and forest soil ecosystems in secondary forests.

Materials and methods

Study site description

This study was conducted within the Kobe Golf Club, Rokko mountain range (32°45'N, 135°14'E, 818 m a.s.l.), southeastern Hyogo Prefecture, Japan. The site experiences an annual mean precipitation of 1,871 mm and a mean annual temperature of 10.1°C (Uchida et al. 2006). The area is characterized by a secondary forest, *Pinus densiflora* Siebold & Zucc., *Pinus thunbergii* Parl. (Pinaceae), and *Quercus serrata* Murray (Fagaceae) dominating its upper canopy (Kamiya 2014). The understory features diverse evergreen and deciduous shrubs, including *Rhododendron* spp. (Ericaceae), *Pieris japonica* (Thunb.) D.Don ex G.Don (Ericaceae), *Clethra barbinervis* Siebold & Zucc. (Clethraceae), *Deutzia crenata* Siebold & Zucc. (Hydrangeaceae), *Ilex crenata* Thunb. (Aquifoliaceae), *Sasa nipponica* (Makino) Makino & Shibata and *Pleioblastus chino* var. *viridis* (Makino) Sad.Suzuki (Poaceae) (Kamiya 2014; Kishimoto & Azuma unpublished data). Canopy tree wilt disease has caused understory dominance by *P. japonica* and dwarf bamboos, resulting in reduced light and limited sapling/seedling recruitment. Understory removal trials conducted in nearby areas, aimed at restoring natural succession, have confirmed seedling establishment in cleared areas (Oka & Doma 2016).

Four vegetation plots (A1, A2, A3, and B) were established in April 2020 to quantify forest structural attributes (Kishimoto & Azuma unpublished data; Table S1). Plots A1, A2, and B encompassed 300 m^2 (15 m × 20 m), whereas A3 comprised 151 m^2. All trees exceeding 1.3 m (breast height) were identified and their diameters were measured at the breast height (DBH) in 2020. In August 2021, within plot A3, three experimental sub−units were delineated to evaluate the effects of *Pieris* and *Pleioblastus* manipulation: A3−PierisCut (37.5 m^2, 3.75 × 10 m); *Pieris* excision), A3−BothCut (40.0 m^2, 4 × 10 m); combined excision), and A3−DBCut (36.0 m^2, 6 × 6 m); *Pleioblastus* excision) (Table S1). A3−Control (37.5 m^2, 3.75 × 10 m)) served as the untreated control. All excised biomass was removed from the plots and continuous removal of dwarf bamboo was conducted in 2022. The light environment, specifically canopy openness, was measured in August 2022 in each plot. Hemispherical photographs were taken above the understory and at the soil surface in the central areas of each plot using RICOH THETA (SC; Ricoh Company, Ltd., Tokyo, Japan). Canopy openness was analyzed using Gap Light

Analyzer (ver.2.0; Simon Fraser University, BC, Canada). Subsequent comparative analyses among the primary plots (A1, A2, B, A3−Control) and among the A3 experimental sub−units (A3−Control, A3−PierisCut, A3−BothCut, A3−DBCut) were conducted.

Soil property measurements

To assess soil property variations across plots and treatments, 19 physicochemical parameters were measured at four points in every plot in September 2023 (Table S2, Appendix 1). Sampling points were spaced approximately 7–10 m apart. O horizon mass of the litter and humus layers was determined using a 20 × 20−cm frame. The litter was air−dried and sieved through a 4−mm mesh. Particles >4 mm were classified as litter and those <4 mm as humus. Both fractions were oven−dried at 72°C for 72 h and weighed to 0.1 g. Leaf litter was categorized as *Pieris*, *Pleioblastus*, or other tree species and weighed separately (in g m^{-2}). Soil hardness was measured four times per plot using a Yamanaka Soil Hardness Meter (Fujiwara Scientific, Tokyo, Japan), and averaged. Soil properties below the O horizon were quantified using 100−cm^3 syringe samples, which were oven−dried at 108°C for 72 h. Bulk density and water content were calculated from pre− and postdrying weights. Root content (g 100 cm^{-3}) was separated and weighed (±0.01 mg). Additional soil samples were collected for chemical and microbial analyses. Chemical samples were sieved (2−mm mesh), and soil carbon and nitrogen percentages, along with the C/N ratio, were measured using an N, C, H analyzer with an oxygen circulating combustion system (Sumigraph NC−220F; Sumika Chemical Analysis Service, Osaka, Japan), following the manufacturer's protocols. Soil pH (H_2O) was determined using a 1:2.5 (w/w) soil−to−deionized water extraction method and measured with a soil pH tester (HI−981030; Hanna Instruments, Woonsocket, RI, USA). Electrical conductivity (EC) was measured using a 1:5 (w/w) soil−to−deionized water extraction method with a conductivity tester (HI−98331; Hanna Instruments). Soil organic matter (SOM; g g^{-1}) was determined using the loss−on−ignition method. To accommodate many samples, disposable aluminum foil tubes were used instead of standard porcelain crucibles for drying and combustion. Approximately 1000 mg of air−dried, 2−mm sieved soil was weighed into each tube and dried at 105°C for 24 h to determine the dry mass. Then, the tubes were placed in a muffle furnace (FUW210PB; Advantec Corporation, Tokyo, Japan) and heated to 550°C for 12 h. After cooling in a desiccator, the mass was measured to calculate the loss−on−ignition, which was then converted to g g^{-1} based on the initial dry mass. A simplified soil nutrient analyzer (EW−THA1J; Air Water Biodesign Inc., Osaka, Japan) was used to measure NO_3, NH_4, P, K, Ca, and Mg, in accordance with the manufacturer's protocols. The P and K values were below the detection limit; thus, were excluded from analyses.

Soil fungal community analysis

Soil samples for fungal community analysis were stored at −20°C until processing. DNA was extracted using a NucleoSpin Soil kit (Macherey−Nagel GmbH & Co. KG, Düren, Germany) per the manufacturer's instructions. Fungal ITS1 regions were amplified using the primers ITS1−F_KYO1 and ITS2_KYO2 (Toju et al. 2012) with the KOD−FX Neo enzyme (Toyobo Co., Ltd., Osaka, Japan). Libraries were sequenced on an Illumina MiSeq System (300−bp paired−end reads; MiSeq Reagent Kit v3; Illumina, Inc., San Diego, CA, USA) at Bioengineering Lab. Co., Ltd. (Kanagawa, Japan). In total, 1,879,771 paired reads were obtained (mean, 67,135; range, 47,552–78,465) (Table S3). Sequence quality was assessed using the FASTX−Toolkit (v0.0.14), and reads below Q20 or <130 bp were discarded using the sickle tool (v1.33). Paired reads were merged using FLASH (v1.2.11). Chimeras and noise were removed using QIIME2 (v2023.7) dada2, and amplicon sequence variants (ASVs) were exported with read counts. In total, 1,375,063 reads remained (mean, 49,109; range, 24,419–61,280) (Table S3). Fungal phylogeny was estimated using the QIIME2 feature−classifier with UNITE (v9.0, 97% threshold), and function was predicted using FUNGuild (Nguyen et al. 2016).

Plot census data calculation

For fungal community data analyses, we used tree census data from Kishimoto & Azuma (unpublished data). Tree census data were summarized as species abundance (trees ha^{-1}) and basal areas (BA, cm^2 ha^{-1}) based on DBH. For the PierisCut and BothCut plots, we did not conduct a separate plot census after *Pieris* removal rather simply excluded the data of the removed *Pieris* individuals from the original 2020 data before to the analysis. The mycorrhizal types were identified using the FungalRoot database (Soudzilovskaia et al. 2020, 2022). Species names were queried, and registered mycorrhizal types were extracted. In case of absent species, the genus or a related genus within the subfamily was queried (Table S4). The mycorrhizal types were categorized into four groups: AM−associated trees; trees associated with both ECM and AM (ECM−AM trees), *P. japonica* (ErM−Pieris), and other ErM−associated Ericaceae (ErM−Others). Relative abundances (%) were calculated to determine the dominant mycorrhizal types in each plot. Given the variation in plot areas and the presence of large BA trees, relative

BA scores could bias plot representation (Table S1). The acquired relative abundances were used for subsequent statistical analyses.

Statistical analysis

To evaluate environmental differences among plots, a linear mixed model (LMM) was constructed for each variable. Measured environmental variables served as response variables. For among−plot analyses, "plot" was the fixed effect, and "sampling point" was the random effect. For among−treatment analyses within plot A3, fixed effects included *Pieris* treatment (cut/remained), dwarf bamboo treatment (cut/remained), and their interaction, while "sampling point" was the random effect. Type II ANOVA was used to test the significance of the fixed effect. Significant variables ($p < 0.05$) were subjected to Tukey's multiple comparison test ($p < 0.05$). Principal component analysis (PCA) of normalized environmental variables was performed to characterize plots and treatments.

Fungal community read counts were rarefied to the minimum sample depth (24,419 reads; Table S3, Figure S1). Four alpha diversity indices (ASV richness, Shannon, Simpson, inverse Simpson) were calculated using rarefied data. Alpha diversity indices and relative abundances of fungal taxonomic/functional groups were compared among plots and A3 treatments using previously described LMMs.

To assess fungal community compositional differences among plots and A3 treatments, Bray–Curtis similarity indices were calculated using rarefied read counts. We plotted the samples based on the index using nonmetric multidimensional scaling (NMDS). Permutational multivariate analysis of variance (PERMANOVA) was conducted using 20,000 permutations, using explanatory variables from the LMM analyses. The effects of 19 soil physicochemical properties, canopy openness (%), and relative abundances of AM, ECM, ErM−Pieris, and ErM−Others mycorrhizal types on fungal communities were tested using the envfit function of the R package vegan (Oksanen et al. 2024). Spearman's correlation coefficient tests of all paired environmental variables used in envfit were performed to assess correlation relationships. All statistical analyses were performed with R v4.3.3 (R Core Team 2024) using the car (Fox & Weisberg 2019), emmeans (Lenth 2024), and lme4 (Bates et al. 2015) packages.

Results

Inter−plot forest environmental differences

Significant differences were observed among plots for most measured variables, excluding *Pieris* leaf litter, root weight, volumetric water content, and soil Ca and Mg contents (Table S2). Plot A2 exhibited the highest total litter and humus weight, whereas plot B had the highest dwarf bamboo leaf litter weight. Plot A3−Control showed the highest soil hardness and bulk density. SOM and soil N were highest in A2, with A3−Control displaying lower values. Plot B had the highest NO_3 levels. PCA revealed distinct plot distributions: A2 (right), B (bottom left), A3−Control (upper right), and A1 (center) (Fig. 1a). Environmental variable vectors in the PCA confirmed these plot characteristics (Table S5).

Plot census data (Table S1) revealed that A1 was dominated by ErM−Others (70.2%). A2 exhibited a high percentage of ECM−AM trees (21.3%), including *P. densiflora* and ErM−Pieris (47.8%), whereas A3−Control was characterized by AM trees (63.6%), including understory shrubs like *I. crenata* and *Symplocos coreana* (H.Lév.) Ohwi. The mycorrhizal composition of plot B was intermediate, resembling A3−Control. Species richness was higher in A1 and A2, despite the smaller plot size of A3−Control. Canopy openness was lower in plot B (10.41%) and A3−Control (10.56%) compared with A1 (13.68%) and A2 (12.19%).

Inter−plot variation in soil fungal communities and functions

Inter−plot analyses of fungal community alpha diversity revealed significant differences, excluding ASV richness (Table 1). A3−Control exhibited higher diversity than other plots, particularly A2. Seventeen phyla were identified (Fig. 2a, Table S6), with Ascomycota, Basidiomycota, and Mortierellomycota being the most prevalent. Relative abundances of eight phyla differed significantly among the plots. Ascomycota was more abundant in B and A3−Control (average 43.9%), whereas Basidiomycota was more abundant in A1 and A2 (average 47.8%). Fungal functional groups, defined by trophic modes and guilds, varied significantly among the plots (Fig. 2b, Table S7, S8). A2 exhibited higher relative abundances of symbiotrophs. A1 was characterized by elevated saprotroph–symbiotroph and symbiotroph abundances. A3−Control had the highest saprotroph abundance. Among 92 guilds, symbiotrophic guilds showed plot−specific patterns. A3−Control had higher AM fungal abundance ($p < 0.001$, Fig. 3a, Table S8). A2 had higher ECM, and A1 had higher ErM. Endophytes were more abundant in A1 and A2 ($p < 0.05$). Plot B had higher frequencies of pathotroph/saprotrophic multifunctional guilds

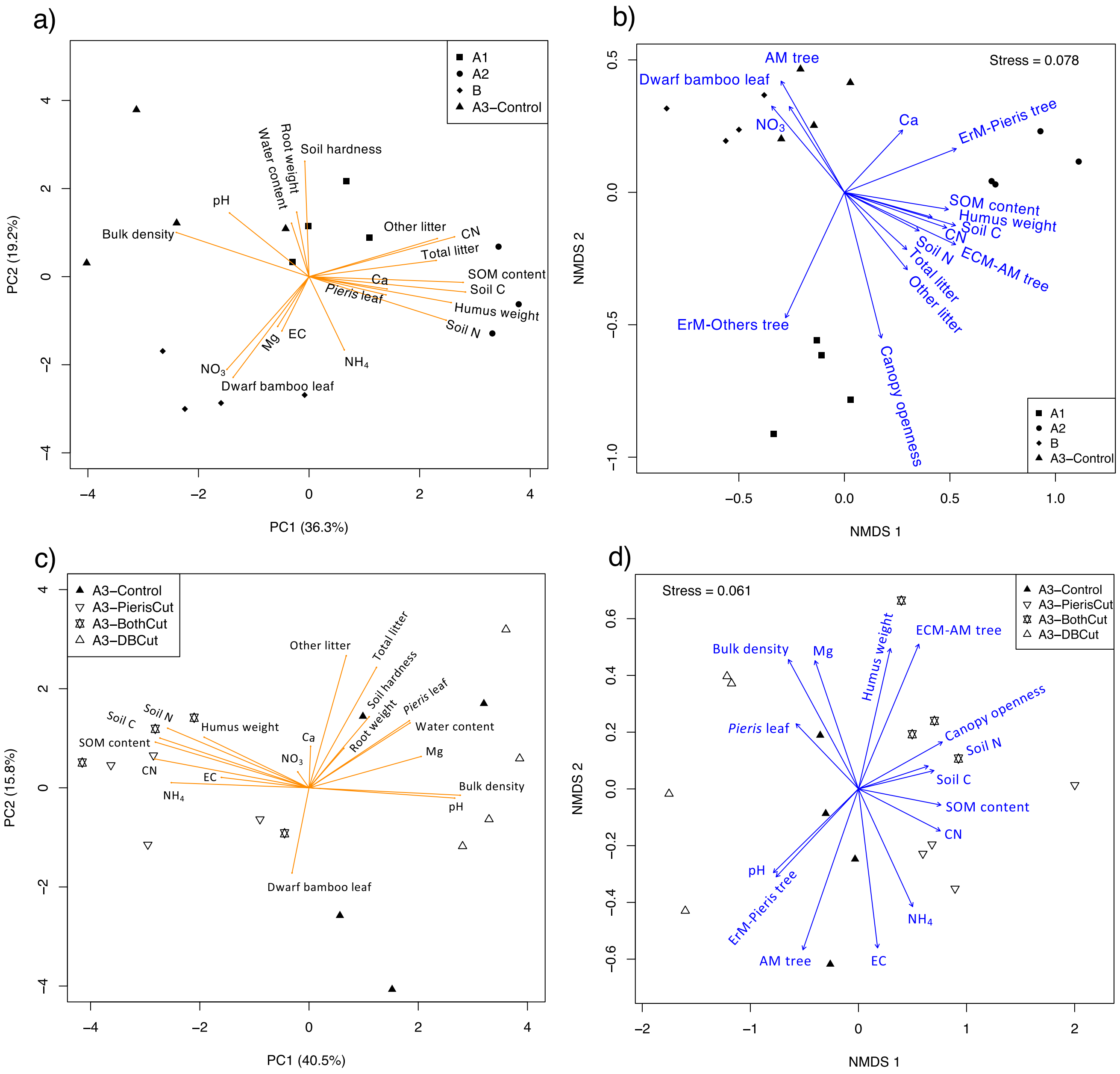

Fig. 1. Principal component analysis (PCA) of environmental variables and nonmetrical multidimension scaling (NMDS) of fungal communities (Bray–Curtis dissimilarity). **a** PCA and **b** NMDS: among−plot analyses. **c** PCA and **d** NMDS: A3 treatment analyses. NMDS overlays show significant environmental vectors (envfit, $p < 0.05$, Table S4)

(endophyte−plant pathogen, endophyte−epiphyte−fungal parasite−insect parasite, dung saprotroph) ($p < 0.01$).

Fungal NMDS and PERMANOVA indicated significant community differences among plots ($F_{3,12} = 3.1125$, $p = 0.001$). Plot samples exhibited distinct distributions (Fig. 1b); A1 (bottom left), A2 (right), B and A3−Control (top left). Fourteen environmental variables significantly influenced fungal communities ($p < 0.05$, (Table 2). Canopy openness had the highest R^2 (0.958), opposing the NMDS2 axis, reflecting the direction of A1. ErM−Pieris tree percentages ($R^2 = 0.867$) aligned with A2. AM tree ($R^2 = 0.766$), NO_3 ($R^2 = 0.645$), and dwarf bamboo leaf ($R^2 = 0.498$) aligned with B and A3−Control. NO_3 and dwarf bamboo leaf were significantly correlated ($p < 0.001$, Table S9).

Environmental variation among A3 understory treatments

Treatment-induced differences in measured variables within A3 plots were analyzed (Table S2). Cutting significantly affected *Pieris* and dwarf bamboo leaf litter. *Pieris* leaf litter in A3-PierisCut was lower than that in others, whereas

Table 1. Fungal alpha diversity: linear mixed model results across plots and A3 treatments.

Plot	A1	A2	B	A3−Control	P−values among plots
ASV richness	714.5 ± 122.8	705.0 ± 85.8	801.5 ± 76.4	632.8 ± 206.9A	0.358
Shannon	4.66 ± 0.35ab	4.27 ± 0.35b	4.87 ± 0.32ab	5.16 ± 0.16aA	< 0.001***
Simpson	0.970 ± 0.011ab	0.934 ± 0.024b	0.961 ± 0.025ab	0.984 ± 0.004a	0.001***
Inverse Simpson	37.45 ± 13.84ab	16.92 ± 6.37b	36.73 ± 24.85ab	63.31 ± 13.18aA	< 0.001***

Plot	A3−PierisCut	A3−BothCut	A3−DBCut	P−values among treatments		
				Pieris cutting	Dwarf bamboo cutting	Interaction
ASV richness	743.3 ± 158.5 A	722.3 ± 99.3A	931.0 ± 182.2A	0.537	0.082	0.045*
Shannon	4.52 ± 0.74 A	4.49 ± 0.52A	5.24 ± 0.53A	0.008**	0.927	0.833
Simpson	0.954 ± 0.041	0.953 ± 0.045	0.968 ± 0.026	0.172	0.613	0.680
Inverse Simpson	33.30 ± 18.25A	32.97 ± 17.37A	59.71 ± 49.40A	0.046*	0.891	0.909

Scores denote mean and standard deviation (SD).

Red and bold text indicates significant differences ($p < 0.05$).

p−value notation: [blank] > 0.05, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Differences among plots (lowercase letters) and treatments (uppercase letters) are indicated by unique letters ($p < 0.05$, Tukey's test).

dwarf bamboo litter did not differ statistically based on Tukey's test. Humus weight and soil C content were higher in A3-BothCut. Significant interaction effects were observed for pH ($p < 0.05$), with A3-DBCut exhibiting the highest pH. PCA of the treatments revealed that A3-PierisCut and A3-BothCut clustered on the left, whereas A3-Control and A3-DBCut clustered on the right (Fig. 1c). Treatment effects were delineated along PC1, whereas within-treatment variation was evident along PC2. Organic matter variables (SOM, soil C, humus) aligned with PC1 minus values of A3-PierisCut and A3-BothCut. *Pieris* leaf weight and bulk density aligned with PC1 plus values of A3-Control and A3-DBCut. Total, dwarf bamboo, and other leaf litter weights were associated with the PC2 axis (Table S5).

Plot census data (Table S1) revealed tree compositional differences. A3-DBCut had the highest percentage of AM trees (80.8%), followed by A3-Control (63.6%), whereas A3-BothCut (14.3%) had the lowest. ECM-AM tree percentages were higher in A3-BothCut (57.1%) and A3-PierisCut (50.0%). ErM-Others tree percentages were highest in A3-BothCut (28.6%), followed by A3-Control (22.7%). Canopy openness was higher in A3-PierisCut (20.82%) and A3-BothCut (18.49%) than in others, and soil surface openness (0.1 m) was highest in A3-BothCut (16.23%) compared with 3.48%–5.61% in others.

Variation in soil fungal communities and functions among understory treatments

Treatment effects on alpha diversity were observed, influenced by *Pieris* treatment or interaction terms, excluding the Simpson index (Table 1). Shannon and inverse Simpson indices were affected by *Pieris* cutting. A3-PierisCut and A3-BothCut had potentially lower scores than A3-Control and A3-DBCut, though Tukey's test showed no significant differences. Sixteen phyla were identified in the fungal community (Fig. 2a, Table S6). Ascomycota and Basidiomycota constituted >60% of reads, followed by Mortierellomycota (9.3%), Rozellomycota (1.6%), Chytridiomycota (0.8%), Glomeromycota (0.7%), and Mucoromycota (0.5%). Nine phyla constituted <0.5% of reads. Of the seven phyla, Basidiomycota, Mortierellomycota, Glomeromycota, and Mucoromycota were significantly affected by the *Pieris* cutting (Table S6). In contrast, Rozellomycota was significantly affected by the dwarf bamboo cutting and the interaction effect, whereas Chytridiomycota was significantly influenced by all three effects (Table S6). Two trophic modes (pathotroph, pathotroph–symbiotroph) were significantly affected by treatment (Fig. 2b, Table S7). Specifically, the pathotrophs was significantly influenced by *Pieris* cutting, dwarf bamboo cutting, and the interaction effect, and A3-DBCut exhibited a higher pathotroph abundance as compared to other treatments. The pathotroph–symbiotroph was significantly affected only by *Pieris* cutting, and tended to be higher in the A3-PierisCut and A3-BothCut, where *Pieris* were removed. Ninety-five guilds differed significantly (Table S8). *Pieris* cutting significantly affected symbiotic guilds (AM, ECM, ErM; $p < 0.01$). AM abundance was lower in A3-BothCut (Fig. 3b). ErM abundance was higher in A3-PierisCut and A3-BothCut, but ECM abundance did not differ significantly (Tukey's test). Plant pathogen guilds (pathotrophic) differed significantly by dwarf bamboo cutting ($p < 0.001$), with A3-DBCut exhibiting higher abundance. Similar trends were observed for litter and leaf saprotrophs (Table S8).

Fungal NMDS and PERMANOVA indicated significant treatment effects (*Pieris* cutting: $F_{1,12} = 3.7525$, $p = 0.001$; dwarf bamboo cutting: $F_{1,12} = 1.9141$, $p = 0.011$) and interaction effects ($F_{1,12} = 1.8762$, $p = 0.017$). Distinct sample distributions were observed (Fig. 1d) among A3-PierisCut (bottom right), A3-BothCut (top right), A3-DBCut (left), and A3-Control (middle). Fifteen environmental variables

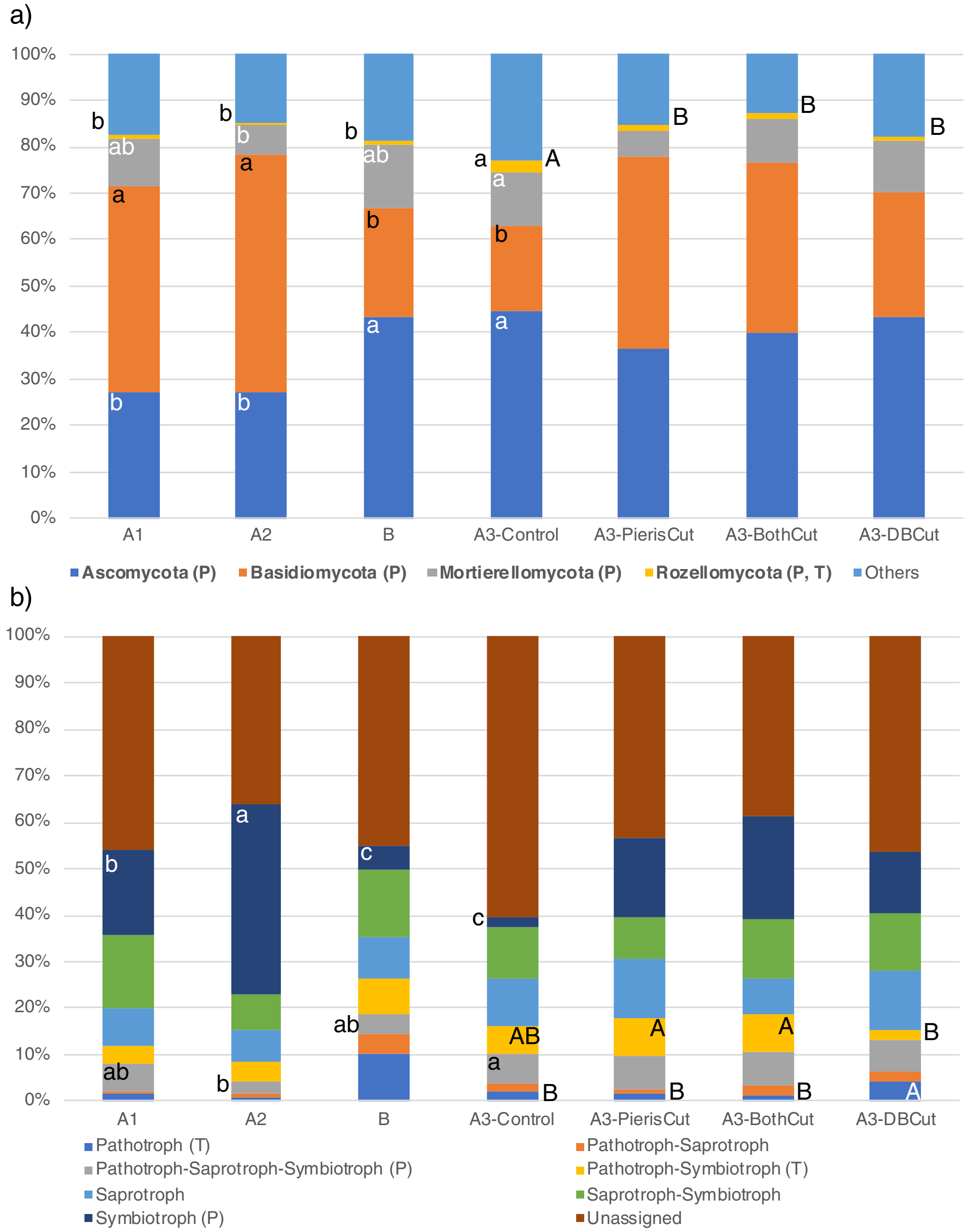

Fig. 2. Relative abundances of major fungal phyla **a** and trophic modes **b** at the plot level. Phyla with relative abundances <1% are summed in Others. The bold letters in the parentheses after the phylum names and trophic modes indicate significant differences detected by Tukey's test ($p < 0.05$) after linear mixed model analysis. This figure presents two separate analyses to show among plot and among A3 treatments: P indicates significant differences among the four plots (A1, A2, A3−Control, and A3−BothCut), reflecting the influence of site conditions, whereas T indicates significant differences among the A3 treatments (A3−Control, A3−DBCut, A3−PierisCut, and A3−BothCut), reflecting the effects of experimental manipulations. Significant differences among plots are further indicated by unique lowercase letters, and those among treatments are indicated by unique uppercase letters. Detailed results are presented in Tables S6 and S7.

significantly affected fungal communities ($p < 0.05$, Table 2). Soil pH ($R^2 = 0.843$) and ErM-Pieris tree percentage ($R^2 = 0.807$) aligned with A3-DBCut/A3-Control. Canopy openness ($R^2 = 0.751$) opposed these variables, aligning with A3-BothCut. Soil C/N ($R^2 = 0.709$) and SOM ($R^2 = 0.697$) aligned along NMDS1, relating to A3-PierisCut.

Discussion

Landscape-scale variation in understory environments and fungal communities

Soil environments and fungal communities varied among the four proximate plots. Consistent with our first hypothesis, inter-plot analyses revealed links between fungal communities and tree compositions. A1, dominated by Ericaceae trees (Table S1), had higher ErM fungal proportions (Fig. 3a). A2, with high ECM-AM and *Pieris* tree percentages and elevated soil C/N (Table S2), had higher symbiotrophic fungal proportions, particularly ECM (Fig. 3a). B and A3-Control were dominated by AM trees (Table S1);

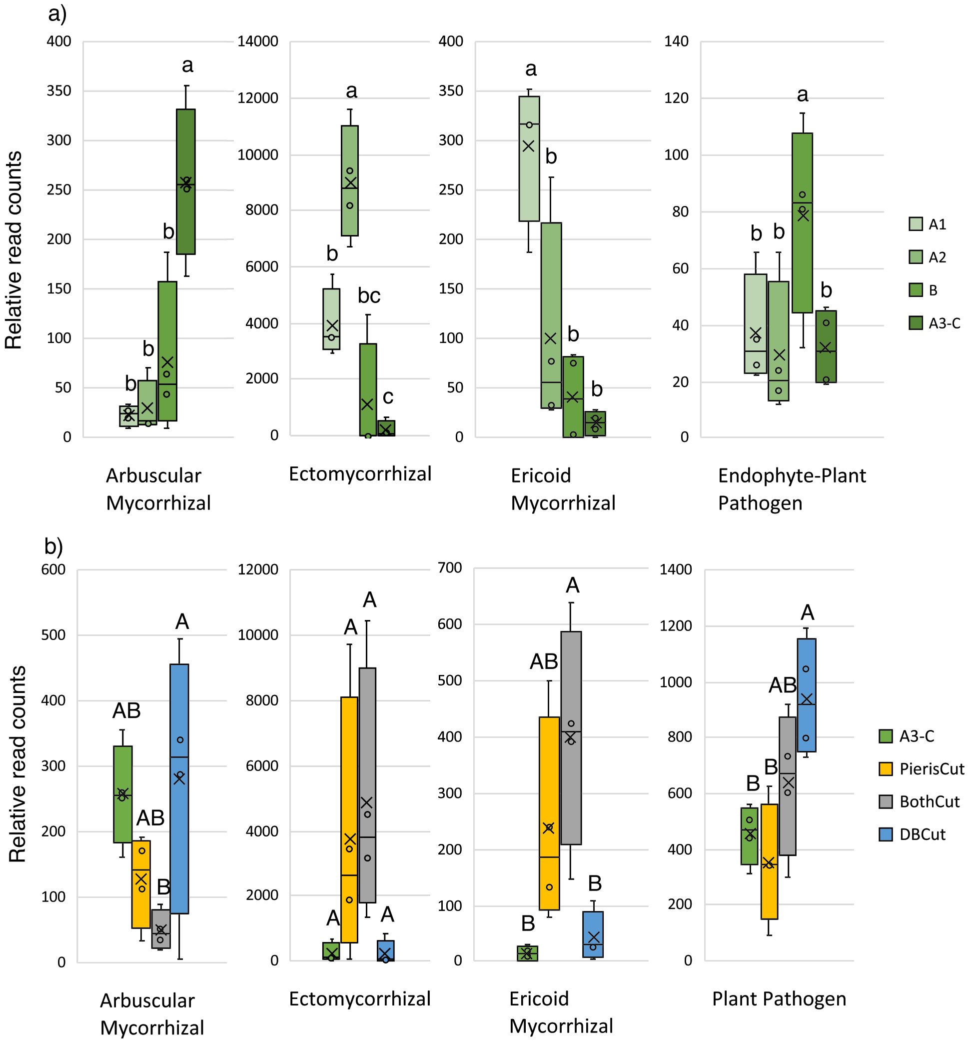

Fig. 3. Box plots showing relative abundances of major fungal guilds. **a** Among–plot comparisons. **b** A3 treatment comparisons. Letters above the box plots indicate significant differences (Tukey's multiple comparisons, $p < 0.05$). In the box plots, the black horizontal line represents the median, the box indicates the interquartile range from the 25th to the 75th percentile, and the whiskers extend to the minimum and maximum values, excluding outliers. The open circle (○) shows the individual data points (inner points). The cross mark (×) represents the mean. Detailed guild–level results are presented in Table S8.

however, B had high dwarf bamboo litter and A3-Control had a high bulk density (Table S2). NMDS analysis revealed a clear separation of fungal communities, primarily driven by differences in tree composition and soil environmental variables (Fig. 1b). The fungal communities in plots dominated by ECM-AM trees and ErM-Pieris (A2) were distinct from those in plots dominated by AM trees (B and A3-Control) and ErM-Others (A1). This suggests that *Pieris* and ECM-AM tree may foster comparable fungal communities, despite different mycorrhizal associations, and AM tree and ErM-Others indicated a unique influence on the composition of each soil fungal community. These tree compositional linkages, particularly those between AM/ECM trees and symbiotic fungal proportions, are consistent with previous reports (Urbanová et al. 2015; Rożek et al. 2023). Furthermore, environmental factors such as soil pH and SOM were strongly associated with clustering of the plots, highlighting roles as key drivers of fungal community variation. This linkage can be further discussed in the context of the mycorrhizal-associated nutrient economy (Phillips et al. 2013). For instance, the plots with a higher proportion of ECM-AM trees, particularly those with high SOM contents, may exhibit enhanced decomposition of organic matter by ECM fungi to acquire nitrogen, as described by Phillips et al. (2013). This relationship between ECM-tree abundance and SOM content suggests a direct coupling between aboveground tree composition and belowground biogeochemical processes, which shapes the fungal community in the soil. In plots dominated by AM trees, NMDS indicated similar fungal communities in B and A3-Control (Fig. 1b); however, B had higher pathotrophic multifunctional guilds [e.g., endophyte-plant pathogen (Fig. 3a), endophyte-epiphyte-fungal parasite-insect parasite (pathotroph–symbiotroph), and algal parasite-bryophyte parasite-fungal parasite-undefined saprotroph (pathotroph–saprotroph)], and A3-Control higher AM fungi (Fig. 3a, Table S8). Although the overall tree composition was similar among the plots, the dominance of dwarf bamboo was confirmed in the understory of plot B (Kishimoto & Azuma unpublished) and likely created a unique microenvironment that influences dwarf

Table 2. Environmental variable effects on fungal community (NMDS envfit analysis)

Variables	Among plots				Among treatments			
	NMDS2	R^2	NMDS1	P−values	NMDS1	NMDS2	R^2	P−values
Soil hardness	−0.699	0.050	0.715	0.713	−0.360	−0.933	0.149	0.355
Total litter weight (g/m^2)	−0.590	0.384	0.807	0.035*	−0.528	0.849	0.100	0.508
Pieris leaf litter weight (g/m^2)	0.543	0.257	0.840	0.141	−0.932	0.361	0.460	0.011*
Dwarf bamboo leaf litter weight (g/m^2)	0.779	0.498	−0.627	0.013*	0.512	−0.859	0.092	0.536
Other litter weight (g/m^2)	−0.700	0.500	0.714	0.009**	−0.202	0.979	0.042	0.757
Humus weight (g/m^2)	−0.221	0.522	0.975	0.011*	0.506	0.863	0.398	0.043*
Root weight (g/100cc)	−0.980	0.058	0.197	0.721	−0.901	−0.434	0.008	0.955
Volumetric water content (g/100cc)	0.995	0.127	0.099	0.422	−0.931	0.366	0.299	0.102
Soil bulk density (g/cc)	0.251	0.356	−0.968	0.057	−0.820	0.572	0.748	< 0.001***
pH (H_2O)	−0.715	0.224	−0.700	0.192	−0.933	−0.360	0.843	< 0.001***
EC	0.952	0.291	−0.308	0.103	0.303	−0.953	0.410	0.032*
NO_3 (mg/100g)	0.687	0.645	−0.727	0.002**	0.018	−1.000	0.100	0.521
NH_4 (mg/100g)	−0.983	0.031	−0.182	0.819	0.776	−0.631	0.504	0.012*
Ca (mg/100g)	0.649	0.377	0.761	0.040*	−0.338	0.941	0.017	0.894
Mg (mg/100g)	−0.026	0.014	−1.000	0.936	−0.672	0.740	0.434	0.023*
Soil C (%)	−0.267	0.727	0.964	< 0.001***	0.995	0.102	0.587	0.003**
Soil N (%)	−0.380	0.420	0.925	0.029*	0.991	0.134	0.505	0.012*
Soil C/N	−0.232	0.840	0.973	< 0.001***	0.983	−0.181	0.709	< 0.001***
SOM content	−0.130	0.709	0.992	0.001***	0.998	−0.066	0.697	0.001***
Canopy openness	−0.953	0.958	0.304	< 0.001***	0.976	0.218	0.751	< 0.001***
% AM trees (Individual No)	0.814	0.766	−0.581	< 0.001***	−0.664	−0.748	0.701	0.001***
% ECM−AM trees (Individual no)	−0.351	0.910	0.936	< 0.001***	0.733	0.680	0.684	0.001**
% ErM−Pieris trees (Individual no)	0.297	0.886	0.955	< 0.001***	−0.922	−0.387	0.807	< 0.001***
% ErM−Other trees (Individual no)	−0.862	0.867	−0.507	< 0.001***	0.635	0.773	0.253	0.150

Red and bold text indicates significant differences ($p < 0.05$).

p-value notation: [blank] > 0.05, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

bamboo leaf litter decomposition and resource availability. This finding is partially consistent with previous research showing that significant changes in understory vegetation, such as land-use conversion to bamboo forests, can alter the fungal nutritional type from saprotroph to a more complex combination of pathotroph–saprotroph–symbiotroph (Jian et al. 2025). Dominant tree species likely influenced fungal diversity indices, which were lowest in A2 (excluding ASV richness, Table 1). ECM trees and increased litter are known to promote ECM fungal proportions (Zhu et al. 2022; Geng et al. 2023). Hence, the tree composition and the environment of A2 likely induced high ECM fungal proportions, potentially biasing community compositions and reducing the diversity indices (Table 1). Conversely, A3-Control, which had higher AM fungal/tree proportions, exhibited higher diversity indices (Tables 1, S1, Fig. 3a). This observation is in line with the tendency of AM-dominated ecosystems to support greater fungal diversity (Geng et al. 2023). This highlights how the type of mycorrhizal association of dominant tree species can play a significant role in shaping the diversity and composition of the soil fungal community.

Species-specific effects of Ericaceae on ErM fungal communities were evident in A1 and A2. A1, dominated by ErM-Others (e.g., *Rhododendron* spp., Table S1), exhibited the highest ErM relative abundance, surpassing A2 (dominated by *Pieris*) (Fig. 3a, Table S8). Ericaceae plants are known for mutualistic ErM associations and adaptation to nutrient-poor environments (Schwery et al. 2015; Tabata et al. 2017). However, Ericaceae effects on soil fungal communities are species-specific, as the genera *Vaccinium* and *Calluna* enhance ErM proportions (Sietiö et al. 2018), whereas *Pieris* has no effect (Tokumoto & Katayama 2024), and *Rhododendron* removal reduces these effects (Osburn et al. 2021). Our ErM abundance results support previous studies, indicating species-specific Ericaceae feedback on soil fungal communities.

Despite their proximity, these four plots exhibit diverse forest structures in the Rokko mountains. Our findings, demonstrating environmental effects on fungal communities, underscore the importance of maintaining this structural diversity for fungal community preservation.

Understory differences and relationships with understory environments and fungal communities

Our study conducted a comparative analysis of understory environments and soil fungal communities across four understory treatments. In partial consistency with the second hypothesis, *Pieris* cutting was associated with significant differences in environmental variables and fungal communities. A3-PierisCut and A3-BothCut shared similar environments (high nutrients, Table S2) and fungal communities (high pathotroph–symbiotroph, high ECM/ErM, Fig. 3b, Table S7). A3-Control and A3-DBCut exhibited similar environments (high soil hardness, pH, *Pieris* litter, Table S2) and fungal communities (high pathotroph/AM fungi, Fig. 3b, Table S8). Notably, plant pathotrophic guilds were abundant in A3-DBCut (Fig. 3b, Tables S7, S8). NMDS analyses among treatments in A3 suggest that differences in the proportion of fungal guilds were driven by tree composition and environmental parameters (Fig. 1d), suggesting that understory removal could be associated with changes to soil fungal diversity and its functionality.

The plots with *Pieris* removal had higher abundances of pathotrophic–symbiotic fungi (Table S7), as well as ECM and ErM fungal guilds (Table S8). This finding aligns with the observation from the removal of another Ericaceae species, *Rhododendron maximum* L., which showed a decrease of ErM and increase of AM/wood saprotrophs (Osburn et al. 2018; 2021). These examples suggest that changes to the host plant community can be linked to shifts in fungal symbiotic relationships. In our plots, the observed abundances of pathotrophic–symbiotic fungi may be a reflection of the altered understory conditions resulting from *Pieris* removal. Contrary to the findings of Osburn et al. (2018; 2021), higher abundances of ErM were confirmed in this study (Table S8). One of the most plausible explanations for the higher abundances of ErM in plots after *Pieris* cutting was their ability to persist and thrive in the absence of a host plant, as another study (Bergero et al. 2003) demonstrated that the persistence of ErM without hosts is due to free-living and saprotrophic growth. ErM proportions were higher in A3-PierisCut (average relative abundance: 237.75) and A3-BothCut (400.75) than A3-Control (14.75) and A3-DBCut (43) (Fig. 3b, Table S8). Precutting *Pieris* densities were 213.3/ha (BA: 8,010.6 cm^2/ha) in A3-PierisCut and 425.0/ha (BA: 23,306.4 cm^2/ha) in A3-BothCut (Kishimoto & Azuma et al. unpublished data), significantly exceeding A3-Control (53.3/ha and 2,451.5 cm^2/ha of BA) and A3-DBCut (83.3/ha and 2,183.8 cm^2/ha of BA). These results show positive relationships between *Pieris* abundances and ErM proportions, suggesting ErM persistence in soils. Although another previous study reported that *Pieris* dominance was not significantly correlated with the proportion of ErM (Tokumoto & Katayama 2024). Considering previous studies as well as other existing ErM trees around the plots, such as the *Rhododendron* spp., *Vaccinium smallii* L., the effects of *Pieris* cutting were unclear. Regarding the higher abundances of ECM fungi in the *Pieris* cutting plots, Tokumoto & Katayama (2024) indicated that *Pieris* dominance reduces symbiotic fungal proportions, particularly ECM. Therefore, *Pieris* cutting would be expected to positively affect ECM. Indeed, A3-PierisCut and A3-BothCut had higher ECM proportions, which is consistent with this expectation (Fig. 3b). However, it should also be noted that the initial higher abundances of ECM-AM trees in the A3-PierisCut and A3-BothCut plots, as compared to other treatments (Table S1), could influence the ECM proportions. Our study revealed associations between *Pieris* removal and soil fungal trophic modes and guilds, though the underlying mechanisms remain to be clarified. Although the effects of Ericaceae on soil microbes are being studied (Ward et al. 2022), research on plant species-specific fungal responses is still limited. Therefore, further research is needed to clarify the roles of *Pieris* and other Ericaceae species on soil ecosystems and the effects of their removal.

Dwarf bamboo differences correlated with environmental factors and fungal communities (LMM analyses, Table S2, $p < 0.05$). However, dwarf bamboo leaf litter, EC, NO_3, and Ca did not differ significantly (Tukey's test), except for soil pH. Dwarf bamboo removal influences soil chemistry and increases nutrient availability, particularly nitrogen (Tripathi et al. 2005; 2006). Soil pH differed among treatments, and A3-DBCut had a higher pH than A3-Control (Table S2), contradicting previous studies showing a lower pH (Tripathi et al. 2006). In the fungal community, the phyla of Chytridiomycota and Rozellomycota were affected by dwarf bamboo cutting (Table S6). Additionally, pathotroph proportions were higher in A3-DBCut, whereas symbiotic fungi were unaffected (Table S7). Given the mutualistic AM fungal associations (Fukuchi et al. 2011), removal of dwarf bamboo is expected to alter symbiotic fungal communities. For instance, Kong et al. (2017) reported that the relative abundance of the fungal phylum Ascomycota, specifically the dwarf bamboo symbiotic fungal class of Pezizomycetes was significantly lower in dwarf bamboo removed plots than in intact plots. However, due to differences among dwarf bamboo species (*S. kurilensis*, *S. nipponica* and *P. chino*) and climatic differences, removal effects on fungal taxonomy may vary. In this study, dwarf bamboo manipulation was not significantly associated with soil or symbiotic fungal communities as anticipated by previous studies. Hence, further research on dwarf bamboo removal (including *S. nipponica* and *P. chino*) is needed.

Although our results suggest that *Pieris* and dwarf bamboo cutting was associated with soil environments and fungal communities across proximate plots, inherent tree composition differences may confound these findings. For instance, ECM-AM tree abundances varied among treatments (Table S1), potentially affecting ECM fungal proportions. As this study was not designed to assess the direct effects of cutting, limitations exist in isolating treatment impacts on forest environments and microbiomes. Nonetheless, the observed associations are consistent with previous research, which indicates that understory plant removal is a factor that should be considered as a driver of changes to soil environments and fungal communities. This study thus provides valuable data highlighting the potential importance of understory management in shaping forest ecosystems.

Conclusions

This study demonstrates fungal community variation across forest landscape elements and understory conditions. However, the limited number of plots and treatments in our experimental design resulted in pseudoreplication of one site for each forest type and treatment. Furthermore, due to the lack of pretreatment data, the experimental design could not directly assess the causal effects of understory removal. Additionally, the observed differences between the manipulated plots and the control may reflect the initial variations in tree composition and soil conditions. Further studies are needed to ensure the comprehensive impacts of different tree communities and treatments on soil environments and the fungal communities. Nonetheless, these results provide valuable insights into how understory management can shape belowground soil ecosystems, which are critical for seedling recruitment. Previous studies have shown that removing dwarf bamboo and *Pieris* enhances seedling recruitment (Itô & Hino 2007; Oka & Doma 2016). In line with these findings, our study highlights a potential mechanism through which understory management may promote seedling recruitment, i.e., by altering soil environmental conditions and shaping fungal communities. Therefore, our findings emphasize the importance of diverse forest landscapes and appropriate understory management for both soil ecosystems and, indirectly, seedling recruitment.

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Data availability All raw sequence data of the eukaryotic 18S rRNA genes were submitted in the Sequence Read Archive of DDBJ database under the accession numbers of BioProject PRJDB17624 and Run DRR532674-DRR532701. Environmental data measured in this study was in Appendix1.

Declaration

Competing interest The authors have declared that no competing interests exist.

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