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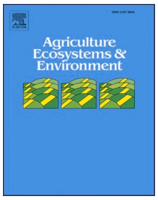

Arable soil microbial communities are affected by plant community and agricultural management

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ABSTRACT

Plants shape soil microbiomes, yet this interaction is underexplored in the cultivated farmlands of the boreal region. We assessed the soil microbiome of seven differently managed major crop types in the region (pasture, ley, oat, rye, faba bean, oilseed, and cabbage), alongside a long-term environmental fallow, in 73 fields in Southern Finland. Microbial data were cross-analyzed with plant community data, which combined the cultivated and other vascular plants observed in the fields. Amplicon sequence analysis indicated that crop type, plant richness, plant coverage, and agricultural management affect the soil microbiome's taxonomic and predicted functional composition. The most dissimilar microbial communities were under fallow and cabbage, which represented the management and plant diversity extremes. Plant richness influenced the community composition and predicted functional potential of bacteria and fungi. Microbial diversity was a poor indicator of the putative beneficial fungal functional group, arbuscular mycorrhizal fungi (AMF), and of bacterial predicted genes related to soil ecosystem functions, inorganic-phosphorus (Pi) solubilizing and nitrogen-fixing genes. Fallow with lowered microbial diversity had the highest proportions of nitrogen-fixing and Pi solubilizing genes, and AMF. Similarly, organic production method with lowered fungal richness in perennial crop types (pasture and ley) had high proportion of AMF and nitrogen-fixing genes across crop types. Tillage intensity was positively associated with the proportion of bacterial beta-glucosidase genes involved in carbon cycling. We show that in the boreal region, crop type and plant community (especially richness), and agricultural management all affect soil microbial communities, with potential implications for microbial-mediated soil functions.

1. Introduction

Soil microbiome is a major component of the overall biodiversity in agroecosystems and contributes to important ecosystem functions, such as nutrient and carbon cycling, with implications for food production (Bardgett and van der Putten, 2014; Dainese et al., 2019; de Graaff et al., 2019). As plant community closely interacts with the soil microbiome (Lange et al., 2015; Leff et al., 2018; Muhammad et al., 2025; Schmid et al., 2021a) combining soil microbial analysis with the study of plant communities enhances our understanding of overall agroecosystem biodiversity. Addressing this requires consideration of both the crop species and the other plant species found in the field, along with their management. Such plant-soil microbiome interactions in boreal agroecosystems, however, remain poorly characterized.

Plants shape the soil microbiome by altering the soil environment with their root structure, by producing root exudates, other rhizodeposits, and litter, and by plant-mediated nutrient cycling and forming intimate associations with the soil microbiome (Cappelli et al., 2022; Hu et al., 2018; Ke et al., 2015). Different aspects of plant community, such as diversity, density, and taxonomic and functional groups, mediate these impacts (Lepinay et al., 2024; Schmid et al., 2021a). For instance, crop species richness correlated positively with fungal diversity

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(Shrestha et al., 2025) and enhanced positive associations within the bacterial community, with cascading effects that increase soil organic carbon (SOC) in the rhizosphere (Domeignoz-Horta et al., 2024). These findings highlight the critical role of plant-soil microbial interactions in shaping carbon dynamics within agroecosystems (Cappelli et al., 2022). In cropping systems, crop species play a key role in determining soil microbiome (Azeem et al., 2020; Wagg et al., 2021; Wen et al., 2016) but, we lack the knowledge of many of the important boreal crop species such as, rye, oat, faba bean, and oilseed (*Natural Resources Institute Finland, 2021*). The key factors affecting differences among crop species are rooting depth (Pietola and Alakukku, 2005), crop life cycles (perennial vs annual; Roumet et al., 2006), the crop rotations they are involved in (Palojärvi et al., 2020), and other functions like nitrogen fixation (Roumet et al., 2008). For instance, perennial crop types were shown to increase the ratio of fungi and bacteria as well as the abundance of arbuscular mycorrhizal fungi (AMF) in relation to annual wheat, and leguminous crops to increase the abundance of N-fixing genes as well as different C decomposing microbes in relation to gramineous plants due to differences in plant residue C/N ratios (Li et al., 2025; Rousk and Bååth, 2007; Tao et al., 2024; Taylor et al., 2023; Thapa et al., 2018). In addition to crop species, arable weed community may comprise a substantial share of the total plant biomass of a cropping system (e.g. up to 20% in organic cropping) as well as species diversity (Hyvönen et al., 2003; Salonen et al., 2023). Moreover, weed species diversity and identity influence the transmission of root microbiota between weeds and crop plants (Hu et al., 2023). Although several studies of natural or seminatural plant communities have highlighted the importance of including the whole plant community in soil microbial analysis (Leff et al., 2018; Lepinay et al., 2024; Porazinska et al., 2018), this is rarely done in the microbial analysis of agricultural soils. Notable exceptions include Cassman et al. (2016), who included whole plant community composition and diversity in their analysis of agricultural grasslands, and Hu et al. (2023), who studied the impact of weed species identity and diversity on the wheat root mycobiome. However, both studies were conducted in temperate regions, leaving the boreal region, and the impact of its whole plant community under major crop species on the soil microbiome largely unexplored. Results from a study conducted in the boreal region across cultivated crop richness levels (Shrestha et al., 2025) align, however, with those from temperate region study covering the whole plant community analysis (Cassman et al., 2016) both showing that plant community affects fungal communities more than bacterial communities.

Whereas the boreal region harbors distinct microbial communities shaped by biogeographic factors such as moderate precipitation and low soil pH (Tedersoo et al., 2014), agricultural management creates a distinct habitat within this biome that requires specific attention (Vahter et al., 2022). Identification of the exact drivers of crop management is challenging, as multiple management factors—including tillage, crop rotation, fertilization, and pesticide use—may collectively influence the outcome (Martínez-García et al., 2018; Peltoniemi et al., 2021). Yet, evidence of specific management practices, such as pesticide usage, contributing to microbial community differences does exist (Walder et al., 2022). Soil disturbance related to tillage can negatively impact some microbial groups, especially the hyphal symbiotrophic and saprotrophic fungi (Hydbom et al., 2017). The effect of fertilization can vary greatly. However, a meta-study without other management practice differences indicated that, compared to non-fertilized controls, organic fertilization with manure had a positive effect on microbial diversity, whereas mineral fertilization had no effect (Bebber and Richards, 2022). Similarly, microbial functions are impacted by agricultural management practices. The AMF are shown to respond positively to manure and negatively to pesticides (Riedo et al., 2021; J. Wang et al., 2018), bacterial nitrogen fixation (N_2 fixation) negatively to nitrogen (N) fertilization and pesticides (L. Liao et al., 2021; Walder et al., 2022), and bacterial solubilization of inorganic phosphorus (Pi) negatively to N fertilization (Dai et al., 2020). Together, these findings indicate that some beneficial soil microbial functions may be induced by organic farming compared with conventional farming. Furthermore, the substantial differences in weed species richness and biomass between organic and conventional cropping systems (Hyvönen et al., 2003; Hyvönen and Salonen, 2005; Salonen et al., 2023) suggest that shifts in the plants community may indirectly drive some management effects on the soil microbiome.

Bacterial and fungal functional potential can be estimated from amplicon sequencing based on annotation databases such as PICRUSt2 and FUNGuild, respectively (Douglas et al., 2020; Nguyen et al., 2016). FUNGuild fungal functional guilds are curator-reviewed and commonly applied in agricultural soil microbiome analysis (Peltoniemi et al., 2024). Although predictive gene annotation based on 16S rRNA data is limited by incomplete phylogenetic information and does not match the accuracy of shotgun metagenomics for characterizing gene content (Toole et al., 2021a), it offers a valuable exploratory tool. For instance, PICRUSt2 predictions have been shown to correlate significantly with qPCR-derived gene abundances in soil (Manter et al., 2023) and often outperform other predictive methods (Toole et al., 2021b). Consequently, this approach is now widely applied in agricultural soil research (e.g., Guo et al., 2025; Lee et al., 2025; C. Wang et al., 2021). Nevertheless, care should be taken when interpreting these predictions.

In this study, we assessed plant-soil microbiome interactions in differently managed agricultural fields of the boreal region by combining soil microbial analyses with previously published data on plant species richness and coverage of cultivated and non-cultivated species (i.e., plant community; Toivonen et al., 2022). We used amplicon sequencing to assess microbial community composition and diversity, as well as the proportions of predicted bacterial genes related to SOC decomposition, N and P cycling, and the proportions of fungal saprotrophs, potential plant pathogens, and AMF. The objective was to determine how crop type and overall plant richness shape soil bacterial and fungal communities in arable land, and how production method (organic vs. conventional) and other management practices influence these relationships. The studied crop types represent distinct plant functional groups: legumes (faba bean), cereals (oat, rye), Brassicaceae (oilseed, cabbage), perennial grasses (pasture, ley), and a long-term environmental fallow as a reference. Across most crop types, there was variation in production methods and other management practices, including tillage, N fertilization rate, fertilization type, pesticide use, and crop rotation diversity. Our hypotheses were:

H1. Crop type, as the dominant component of the plant community, shapes microbial community composition, diversity, and potential functions, regardless of management.

H2. Plant richness impacts microbial communities, and that the effect is more prominent on fungi, which are known to be more responsive to plant effects.

H3. Organic production increases microbial diversity and the microbial potential for beneficial soil functions, particularly those related to AMF, N_2 fixation, and P availability.

H4. Tillage negatively impacts hyphal fungi, especially AMF.

2. Methods

2.1. Study design and sampling

The study was conducted in field parcels of farms in southern Finland (60.09936–61.01251°N, 23.40421–25.14284°E) (see Toivonen et al., 2022). The study fields included seven actual crop types and long-term environmental fallow, which are collectively referred to as ‘crop types’ in this paper from here on. The crop types were: spring cereal (oat; *Avena sativa* L.), winter cereal (rye; *Secale cereale* L.), legume (faba bean; *Vicia faba* L.), spring oilseed crops (oilseed; oilseed rape *Brassica napus* L. subsp. *oleifera*, turnip rape *Brassica rapa* L. subsp. *oleifera*, and camelina

Camelina sativa (L.) Crantz), field vegetable (cabbage; *Brassica oleracea* L. var. *capitata*), grass ley (ley), arable pasture (pasture), and long-term environmental fallow (fallow) (Toivonen et al., 2013). The fallows had perennial vegetation and were unmanaged except for mowing (see 2.3. for details on management).

For each crop type, we aimed to sample five fields from conventional farms and five from organic farms. This goal was achieved for other crop types than oilseeds and cabbage, which are unusual crops in organic farms in the region. For oilseeds, soil samples were taken in five conventionally managed fields and three organically managed fields. For cabbage, five conventional and no organic fields were sampled. Thus, the total number of study fields was 73. The fields were located across 33 farms, with a maximum of five study fields per farm. The study fields of the same crop type were separated by at least 1 km. For the fields that represented different crop types, the minimum distance was 500 m.

In each field, a 50 m × 50 m plot was established, which was placed parallel to, and at 5 m distance from, the field edge farthest from the forest. All vascular plant species were recorded and their coverage by species as a percentage of the area of the entire plot was determined visually by using a nine-step scale: $1 = x < 0.125\%$, $2 = 0.125\% < x < 0.5\%$, $3 = 0.5\% < x < 2\%$, $4 = 2\% < x < 4\%$, $5 = 4\% < x < 8\%$, $6 = 8\% < x < 16\%$, $7 = 16\% < x < 32\%$, $8 = 32\% < x < 64\%$ and $9 = x > 64\%$. Soil sampling was conducted by collecting three replicate samples from each plot (one from the middle and two from the corners). Each replicate sample was formed by pooling ten soil samples taken from the topmost 0–15 cm soil layer using a 2 cm soil corer. Replicate samples were stored in cooler bags in the field and finally in the freezer (-20C) for further analysis. Vegetation and soil sampling were conducted between 29th June and 7th July 2020.

2.2. DNA extraction and processing of sequence data

For DNA analysis, a representative composite sample was mixed from the replicate samples prior to the DNA isolation, resulting in one soil sample for each field. Composite soil samples for DNA isolation were free of debris such as rocks and plant material, and DNA was isolated with DNeasy PowerSoil Pro kit (Qiagen, Germany) as described by the manufacturer with the following modification. Cell lysis was performed with FastPrep-24 (MP Biomedicals, USA) homogenizer by mixing PowerBead Pro tubes twice at 5.5 m/s for 30 s, and DNA was removed from the spin column with two consecutive 50 μl solution C6 elution. The DNA concentration and quality were measured with NanoDrop One (ThermoFisher Scientific, USA), diluted to a 7.5 ng/μl concentration and shipped for sequencing. Paired-end sequencing was performed as a service at DNA Sequencing and Genomics Laboratory (BIDGEN) at the Institute of Biotechnology with AVITI (Element Biosciences, USA) device. Bacterial and fungal diversity were targeted with primers f341 & r785 (Klindworth et al., 2013) and gITS7 & ITS4 (Ihrmark et al., 2012), respectively. Sequences were demultiplexed based on sample, and the raw sequences were submitted to GenBank SRA (BioProject ID: PRJNA1345405).

Primer sequences were trimmed from the raw reads using Cutadapt 4.9 (Martin, 2011). ASVs were then obtained in a denoised, chimera-free, non-singleton form with the DADA2 1.28 pipeline (Callahan et al., 2016). The ASVs were classified using the Silva SSU 138.1 reference database (McLaren and Callahan, 2021) for bacterial taxonomy, and UNITE 10.0 dataset (Abarenkov et al., 2023) for fungal taxonomy. After removal of singletons and non-target domain ASVs, 77, 366 bacterial ASVs and 85 million reads, and 7891 fungal ASVs and 80 million reads remained in the dataset. Bacterial and fungal ASV counts were normalized by library size (proportions) for all other analyses except for the alpha-diversity calculations. Fungal ASVs were assigned to fungal functional groups with FUNGuild database (Nguyen et al., 2016; downloaded November 12th, 2024). FUNGuild categorizes fungal taxa into trophic modes which can be unimodal (saprotroph, pathotroph, symbiotroph) or their multimodal combinations (e.g. pathotroph-saprotroph). Trophic modes are further classified into unimodal and multimodal functional guilds, such as plant pathogen within the pathotroph trophic mode (unimodal) or soil saprotroph-plant pathogen within pathotroph-saprotroph trophic mode (multimodal). Only annotations with confidence ranking level ‘highly probable’ or ‘probable’ were included, amounting to 51% of the ASVs and 61% of the reads being assigned. In addition to saprotroph trophic mode, AMF, defined as the unimodal and multimodal arbuscular mycorrhizal guilds, and potential plant pathogens, defined as the unimodal and multimodal plant pathogen guilds, were specified and used in statistical analyses. Predicted bacterial functional gene proportions were retrieved based on 16S reads with PICRUSt2 v 2.6.1 (Douglas et al., 2020) following the default pipeline with the command picrust2_pipeline.py, which uses EPA-NG (Barbera et al., 2019), gappa (Czech et al., 2020), and HMMER (Eddy, 2011) for phylogenetic placement of reads, castor (Louca and Doebeli, 2018) for hidden-state prediction (hsp) to predict gene family abundances, and MinPath (Ye and Doak, 2009) for pathway inference. Abundances of the retrieved KEGG Orthologues (KOs) were normalized sample wise by KO library size (proportion of all genes). Six categories of KOs were selected for further analysis due to their important roles in nutrient and C cycling, with implications for agricultural soil health and crop performance (Bakhshandeh et al., 2017; Ladha et al., 2016; T. Ma et al., 2024; H. Wang et al., 2024). Categories included 1) C cycling genes defined as beta-glucosidases (*bglX* and *bglB*), which work at the last rate-limiting step of cellulose degradation (Zang et al., 2018) and their activity has been shown to positively correlate with SOC in agricultural soil (Zhu et al., 2024); 2) inorganic P (Pi) solubilizing gene defined as pyrroloquiniline-quinone synthase (*pqqC*), a marker for the biosynthesis of the PQQ cofactor required for the Pi solubilizing enzyme PQQGDH, which is associated with bioavailable phosphorus in soil (Liang et al., 2020; Rawat et al., 2021; Wu et al., 2022); 3) organic P solubilizing genes, defined as acid phosphatase (*appA*), alkaline phosphatases (*phoA*, *phoD*), and class A acid phosphatase (*phoN*) any of which can mediate P decomposition and whose activity positively correlates with agroecosystem available P (Fan et al., 2025); 4) N_2 fixing genes defined as nitrogenase Fe protein (*nifH*), nitrogenase Mo-Fe protein (*nifD*), and nitrogenase Mo-Fe protein (*nifK*); 5) nitrifying genes defined as methane/ammonia monooxygenases (*pmoA-amoA*) or hydroxylamine dehydrogenase (*hao*); and 6) denitrifying genes defined as nitrate reductases (narG and *narH*), nitrite reductases (*nirK* and *nirS*), nitric oxide reductases (*norB* and *norC*) and nitrous-oxide reductase (*nosZ*). The N_2 fixing, nitrifying, and denitrifying genes are based on the KEGG database (Kanehisa et al., 2025) following a previous study on agricultural soil nutrient cycles (Dixon et al., 2025).

2.3. Plant community, management, and soil variables

Plant community variables used in this study were plant community composition, plant Shannon diversity, and plant total coverage, all based on coverage values of individual plant species, and plant species richness in the 50 m × 50 m area in each field (see Toivonen et al., 2022). For the plant community composition, Bray-Curtis dissimilarity matrix with Vegan’s (v2.6-2) vegdist function was formed (Oksanen et al., 2012). Agricultural management variables were compiled from the information obtained from farmers. Among the crop types, cabbage and oilseeds were cultivated most intensively in terms of fertilization and pesticide use, whereas fallows were managed most extensively (Table S1). The studied fallows had grassland swards of eight years old or older (mean 18.2 years), and their only management was mowing, which is usually performed once a year or every two years. Pastures were grazed by cattle, sheep, or horses with various intensities. They were, on average, older (mean 7.5 years) than leys (mean 3.5 years). The leys were cut two or three times per year. Variables on agricultural management practices recorded and used in the statistical models were: 1) production method: organic or conventional; 2) tillage: till, reduced till, perennial (no-till), and no-till, which was excluded from statistical analysis due to lack of replicates (n = 1); 3) N fertilization rate (range 0–430 kg/ha); 4) fertilization type: no fertilization, organic fertilization, and mineral fertilization; 5) pesticide usage times per year within herbicide, fungicide, and insecticide spraying, and all pesticides combined (range 0–8) and seed dressing (yes/no); and 6) the number of crop species and crop types in the crop rotation. Fields in organic production were either not fertilized (23) or received a manure fertilization (10) in the sampling year, whereas fields in conventional production mostly received mineral fertilizer (31) or received combined (2), manure (1), or no fertilizer (6). Tillage practices varied similarly between the production methods.

Soil analyses were conducted on three replicate samples, and the average value was calculated for each field. Soil variables included pH_{H2O} (pH), soil total carbon (C), and total nitrogen (N) content, as well as Particulate Organic Matter Carbon (POMC) (Table S1). C and N were determined from air dried, ground samples sieved through a 2 mm sieve and analyzed using the Leco CN-2000 analyzer (LECO, St. Joseph, MI, United States). The ratio of C and N (C/N) was calculated and used in the analysis. The POMC was analyzed based on wet sieving (Cambardella and Elliott, 1992).

2.4. Statistical analysis

Statistical analyses were conducted for two overlapping sample sets. To compare crop types, all samples from the eight crop types (fallow, pasture, ley, oat, rye, faba bean, oilseed, and cabbage) were used. To compare organic and conventional cropping and other management practices, a subset of five crop types (pasture, ley, oat, rye, and faba bean) were used. Despite our efforts, organically farmed cabbage fields could not be included in the study, as this production practice is rare in the region. Likewise, a comparison of production methods was not feasible for oilseed crops, due to the small number of organic fields (n = 3) and, more critically, a confounding species difference: the organic oilseed was camelina, while the conventional was either oilseed rape or turnip rape. The full set of eight crop types facilitated the comparison of all crop types, including the soil management intensity extremes of fallow (least intensive), oilseed, and cabbage (most intensive). The subset of five crop types included agriculturally relevant crop types (excluding fallow), which had a balanced representation of both organic and conventional management (excluding oilseed and cabbage) enabling a focused analysis of farming practices.

2.4.1. Bacterial and fungal community composition

All analyses were done in RStudio with R version 4.2.2 (R Core Team, 2022). To analyze the dissimilarities in bacterial and fungal communities among samples, Bray-Curtis distance was calculated with the vegdist-function (Oksanen et al., 2012). To see if the overall plant community composition (beta diversity) influences microbial community composition, a Mantel correlation test was conducted against the plant species dissimilarity matrix separately for bacterial and fungal ASV dissimilarity matrix with Vegan’s mantel function with 9999 permutations (Oksanen et al., 2012). The microbial distance matrices were used in Principal Coordinates Analysis (PCoA) with base R function cmdscale, which was visualized with Vegan’s ordiplot-function (Oksanen et al., 2012). To investigate the effect of crop type, soil variables, and plant community variables on bacterial and fungal communities, a permutational multivariate analysis of variance (PERMANOVA) was carried out with Vegan’s adonis2-function (Oksanen et al., 2012) with 9999 permutations. First, the significance of the variables was determined with partial PERMANOVA models. Next, a full model was constructed with all significant variables. Finally, the final model only with significant ($p \leq 0.05$) terms was obtained with backward selection method for the marginal PERMANOVA model (option by = “margin”), where the variation explained by each term is assessed considering the other terms in the model. Vectors of soil variables and plant community variables in the final PERMANOVA model were fitted to the PCoA figure with Vegan's envfit-function with 9999 permutations (Oksanen et al., 2012). To investigate pairwise differences between crop types, pairwise PERAMANOVA was performed with pairwise.adonis (Martinez Arbizu, 2020) with Bonferroni p-value adjustment.

To assess how agricultural management practices (production method, tillage, fertilization, and pesticide use) affected bacterial and fungal communities, a marginal PERMANOVA was conducted with the subset of five crop types (see above). Only the significant variables among production method and crop type or crop life cycle (perennial/annual) and their interaction, and soil and plant community were included in the final PERMANOVA model.

Prior to all PERMANOVA, the homogeneity of variance was tested for the crop type with the full set of data and for production method, fertilizer type, and tillage type with the subset data by utilizing the betadisper-function, followed by ANOVA and Tukey tests. For bacteria, variances were similar between crop types (ANOVA; $p = 0.617$), production methods (ANOVA; $p = 0.690$), fertilizer types (ANOVA; $p = 0.716$), and tillage types (Tukey; $p = 0.309$). For fungi, variances were similar between crop types (Tukey; $p > 0.1$), except for cabbage, which had a significantly different variance compared to all other crop types (Tukey; $p < 0.05$), production methods (ANOVA; $p = 0.642$), fertilizer types (ANOVA; $p = 0.900$), and tillage types (Tukey; $p = 0.271$).

2.4.2. Microbial diversity, predicted bacterial functional genes, and fungal functional groups

Bacterial and fungal diversity was calculated as richness (number of ASVs) with the microbiome package v1.18.0 (Lahti et al., 2017). To examine the effects of crop type, soil variables and plant community variables on microbial diversity and the proportion of predicted bacterial genes and fungal functional groups, mixed models were fitted using the function glmmTMB of the R package glmmTMB (Brooks et al., 2017) using data from the full set of eight crop types. Generalized linear mixed models (GLMMs) were fitted separately for the bacterial and fungal richness with Poisson distribution or with negative binomial distribution (nbinom2) in case the data were overdispersed. For the proportion data (predicted bacterial genes and fungal functional groups), a suitable model was chosen based on the dependent variable distribution and model fit. Either a gamma-distribution with log-link function for right-skewed data, a Beta-family distribution for left-skewed data or a Gaussian distribution for normally distributed data was used. Farm was included as a random effect with random intercept structure. First, the significance of the soil and plant community parameters with and without the crop type in the model were assessed in individual (G)LMMs with a type II Wald $\chi2$ test by function Anova() of the R package car (J. Fox and Weisberg, 2019), and a full model was constructed with all significant variables. The final model was obtained by removing non-significant parameters in the full model context sequentially and estimating the model fit. To detect overdispersion and singularity (i.e., overfitting), and to obtain conditional and marginal R-squared values (R^2), functions check_overdispersion, check_singularity, and performance of the performance package (Lüdecke et al., 2019) were used, respectively. In addition, the functions simulateResiduals together with testResiduals of the Dharma package were used for residual diagnostics (Hartig et al., 2024). In case overfitting was detected with low random effect variation ($< 1 \times 10^{-6}$), the random effect of farm was removed and a linear model (LM) or generalized linear model (GLM) was used instead. Post hoc pairwise comparison was conducted with Tukey’s p-value adjustment for multiple comparisons using the emmeans function (Lenth, 2017) to determine significant differences between crop types. The emmeans function was also used to obtain estimated marginal means (EMMs) of each continuous predictor in the model so that results were averaged over the levels of crop type.

In order to assess how plant parameters, community (beta diversity), species richness, Shannon index, and coverage, correlated with the microbial parameters, bacterial and fungal richness and Shannon index, and the proportions of the fungal functional groups and bacterial predicted genes, a Mantel test (Oksanen et al., 2012) with 9999 permutations and Pearsons pairwise correlations were conducted using Benjamini-Hochberg (BH) p-value adjustment. The results were visualized together with Pearson's correlation matrix, which included the soil property variables.

To examine how agricultural management practices, together with soil and plant community variables, were associated with microbial diversity and the proportions of predicted bacterial genes and fungal functional groups, another set of (G)LMMs was fitted using the subset data. First, the significance of the interaction with production method and crop type was tested in (G)LMM with a type II Wald $\chi 2$ test. Then, the remaining management practice, soil variables, and plant community variables associated with the dependent variable were selected with individual (G)LMMs and the final model was constructed and tested for model diagnostics as before.

The difference in the proportion of bacterial and fungal phyla between crop types were examined with one-way analysis of variance (ANOVA) followed by a Tukey Honest Significant Difference test (Tukey) for multiple pairwise comparison between the means of groups in case of homoscedasticity (Levene’s test $p > 0.05$), and with Kruskal-Wallis one-way analysis of variance (Kruskal-Wallis) followed by a pairwise Wilcoxon test (Wilcoxon) in case of heteroscedasticity (Levene’s test $p < 0.05$). The BH method was used for p-value adjustment in the Wilcoxon test. The statistical significance level was set to $p \leq 0.05$.

3. Results

3.1. *Effects of crop type on soil bacterial and fungal community composition, phyla, diversity, and potential functions*

Crop type impacted both bacterial (PERMANOVA; R^2=0.12) and fungal (R^2=0.14) community composition, with the most dissimilar communities being in fallow and cabbage (Fig. 1**;** Table S2). Bacterial communities in fallow were significantly or marginally different from all other crop types (p.adjusted = 0.028–0.056) except for pasture (p.adjusted = 0.168), and in cabbage significantly or marginally different from all other crop types (p.adjusted = 0.028 – 0.084) except for rye (p.adjusted = 0.252) (Table S3). Fungal communities in fallow and cabbage crop types differed significantly or marginally from all other crop types (p.adjusted $\leq$ 0.056) (Table S4).

The most common bacterial phylum in all crop types was Actinobacteriota followed by Proteobacteria and Acidobacteriota (Fig. 3**A**). The proportions of bacterial phyla differed mostly between fallow and other crop types (Table S7). Fallow had a higher proportion of Acidobacteriota compared to pasture, rye, and cabbage, and a higher proportion of Verrucomicrobiota compared to all other crop types except for oilseed. The proportion of Firmicutes was lowest in fallow and highest in pasture, which also had a higher proportion than in oat, faba bean, and oilseed. Ascomycota was the most common fungal phylum in all crop types, followed by Basidiomycota and Mortierellomycota (Fig. 3**B**). The greatest differences in the proportions of fungal phyla were found between fallow and cabbage crop types (details in Table S8).

Both bacterial and fungal richness in soil were significantly associated with crop type (Fig. 2; Table S5). The crop types with the highest mean bacterial richness were cabbage, oilseed, faba bean, and oat, whereas the lowest were fallow and rye (Fig. 2**A**; Table S6). In post hoc analysis, however, significant pairwise differences were only found between fallow and oilseed after considering the positive and significant effect of C/N on bacterial richness. The highest mean fungal richness was found in pasture, ley and oilseed, and the lowest in fallow and rye (Fig. 2**B**; Table S6). However, no significant pairwise differences between crop types ($p > 0.05$) were found when the negative and significant effect of pH on fungal richness was considered.

The proportions of predicted bacterial genes related to P and N cycling in the soil were significantly impacted by crop type (Fig. 4; Table S9A), while the impact on C cycling genes, represented by beta-glucosidases, was marginal. In addition to crop type, soil variables significantly impacted the proportions of the C, P, and N cycling genes. Specifically, the C cycling genes were negatively impacted by soil pH, with no differences found between crop types in the post hoc analysis. The N_2 fixing genes were negatively impacted by soil N, and higher proportions were found in fallow compared to rye, faba bean, and cabbage. Although the mean proportion of nitrifying genes was highest in fallow and lowest in rye (Fig. 4; Table S10), most of the differences between crop types could be explained by their negative association with soil pH. Thus, the model indicated cabbage with high soil pH (pH = 7.2; Table S1) to increase the proportion of nitrifying genes over pasture, ley, and oilseed with lower pH ($pH < 6.3$) and over rye with moderately low pH (pH = 6.5). The proportion of denitrifying genes was significantly higher in oat, rye, and cabbage compared to fallow, with no further soil variable impact. Soil pH affected the two P cycling gene groups in opposite ways. The proportion of Po mineralizing genes was positively correlated with pH and was significantly higher in pasture, ley, and faba bean soil compared to the fallow. The Pi solubilizing genes,

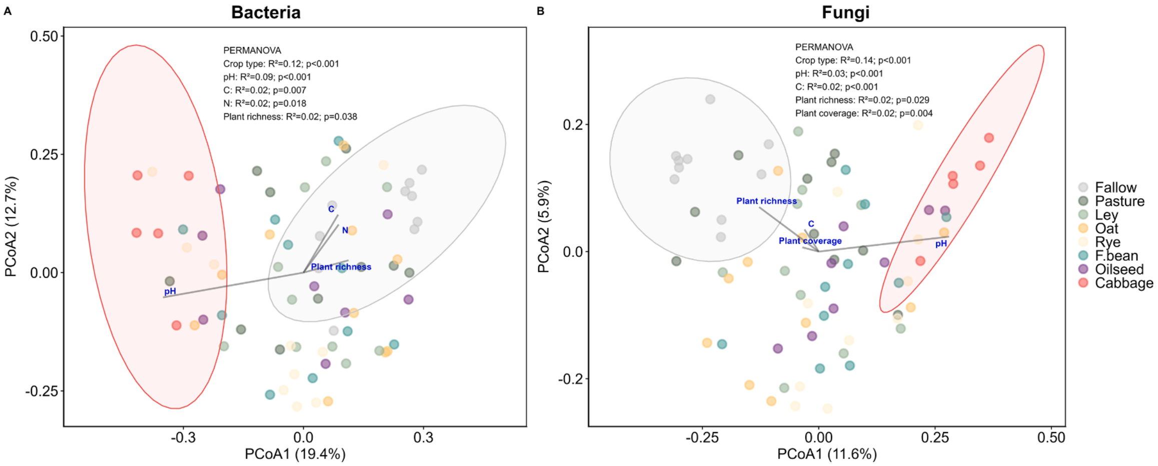

Fig. 1. Soil bacterial and fungal community (dis)similarities. Ordinations show principal coordinates analysis (PcoA) with the Bray–Curtis distance for bacteria (A) and fungi (B). The PERMANOVA results are shown on top of the PcoAs and vectors of the PERMANOVA model variables apart from crop type are fitted to the PcoA with Vegan’s envfit-function. Pairwise PERMANOVA analysis indicated distinct bacterial and fungal communities in fallow and cabbage (Table S3**;** Table S4) and the 95% confidence ellipses based on multivariate t-distribution are shown only for them.

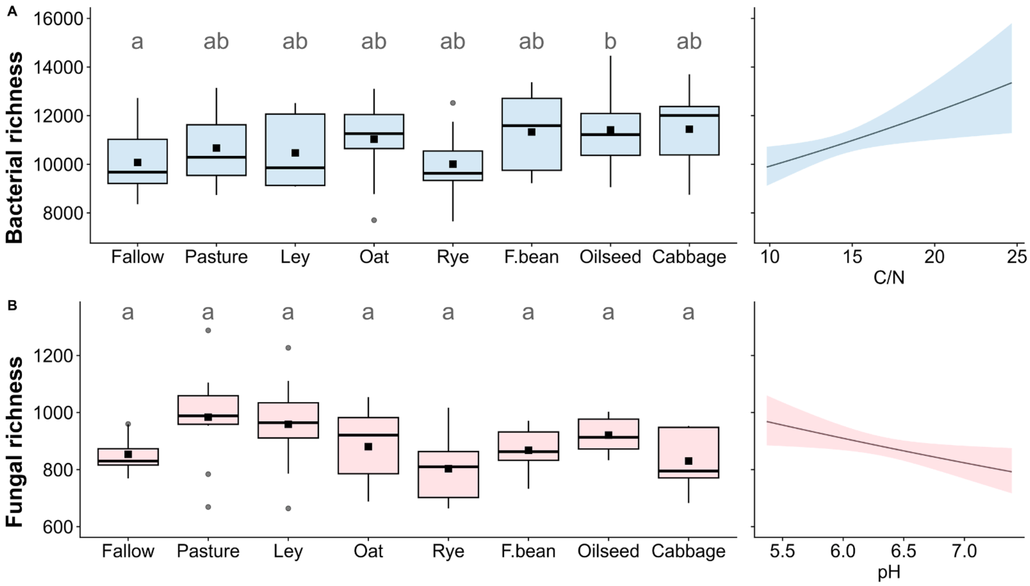

Fig. 2. Soil bacterial and fungal richness in crop types and the significant soil property associations. Different letters indicate statistically significant differences in the whole model context between crop types in post hoc test of the generalized linear mixed model (GLMM) ($p < 0.05$). Black square indicates the mean value. The Estimated Marginal Means of the significant soil property associations are shown in separate graphs. In addition to crop type, bacterial diversity and fungal richness were linked to C/N and pH, respectively. The mean and standard error of mean values for bacterial and fungal richness, and the post-hoc test results for the crop types outside model context are given in Table S6.

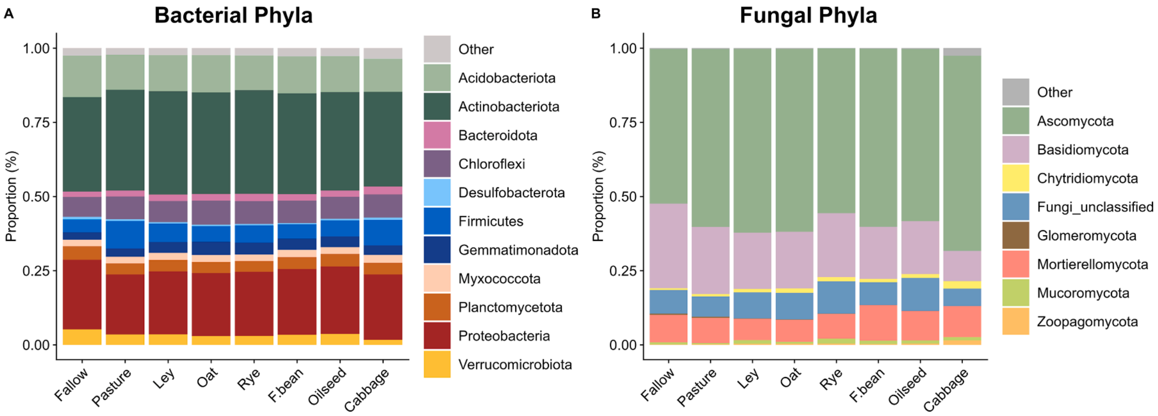

Fig. 3. Soil bacterial and fungal phyla in crop types. Phyla with relative abundance below 1% are grouped in "Other.".

conversely, were negatively correlated with soil pH but positively linked to soil N. Furthermore, the proportion of these genes was significantly higher in fallow compared to all other crop types. A strong negative correlation was found between the Pi and Po mobilizing genes (Spearman $\rho = -0.635$; $p < 0.001$) (Fig. S2).

Among soil fungal trophic modes, saprotroph fungi were the most common in all crop types, followed either by saprotroph-symbiotroph or pathotroph-saprotroph fungi (Fig. S3; Table S11). The proportions of all three fungal functional groups of interest—saprotrophs, AMF and potential plant pathogens—varied with crop type. However, only AMF showed significant differences between crop types in the post hoc analysis (Fig. 5). Saprotrophs were negatively impacted, and potential plant pathogens were positively impacted by soil C/N. AMF proportion decreased across the crop sequence: fallow > pasture > ley/oat > rye/faba bean/oilseed > cabbage, with crops grouped by statistically similar abundances.

3.2. *Impact of other plant community parameters on microbial communities*

In addition to the crop type, bacterial community composition was influenced by plant richness ($R^2 = 0.02$) as well as pH ($R^2 = 0.09$), C ($R^2 = 0.02$), and N ($R^2 = 0.02$), and fungal community composition by plant richness ($R^2 = 0.02$) and plant coverage ($R^2 = 0.02$), as well as pH ($R^2 = 0.03$), and C ($R^2 = 0.02$) (Fig. 1; Table S2). The overall plant community composition did not significantly affect bacterial community composition (Mantel test; $r = -0.009$; $p = 0.599$) but did impact fungal community composition marginally with a weak correlation ($r = 0.055$; $p = 0.060$) (Fig. S1). Out of the plant community parameters, plant richness, Shannon diversity, and coverage, only plant richness significantly correlated with the other microbial parameters studied (Fig. 6). Particularly, plant richness was positively associated with the proportions of AMF ($r = 0.29$; $p = 0.009$) and predicted N_2 fixation ($r = 0.26$; $p = 0.009$) and Pi solubilization ($r = 0.17$; $p = 0.029$) genes. Microbial diversity measures (richness and Shannon diversity) showed no significant associations with plant community parameters. Instead, bacterial diversity measures were significantly correlated with some of

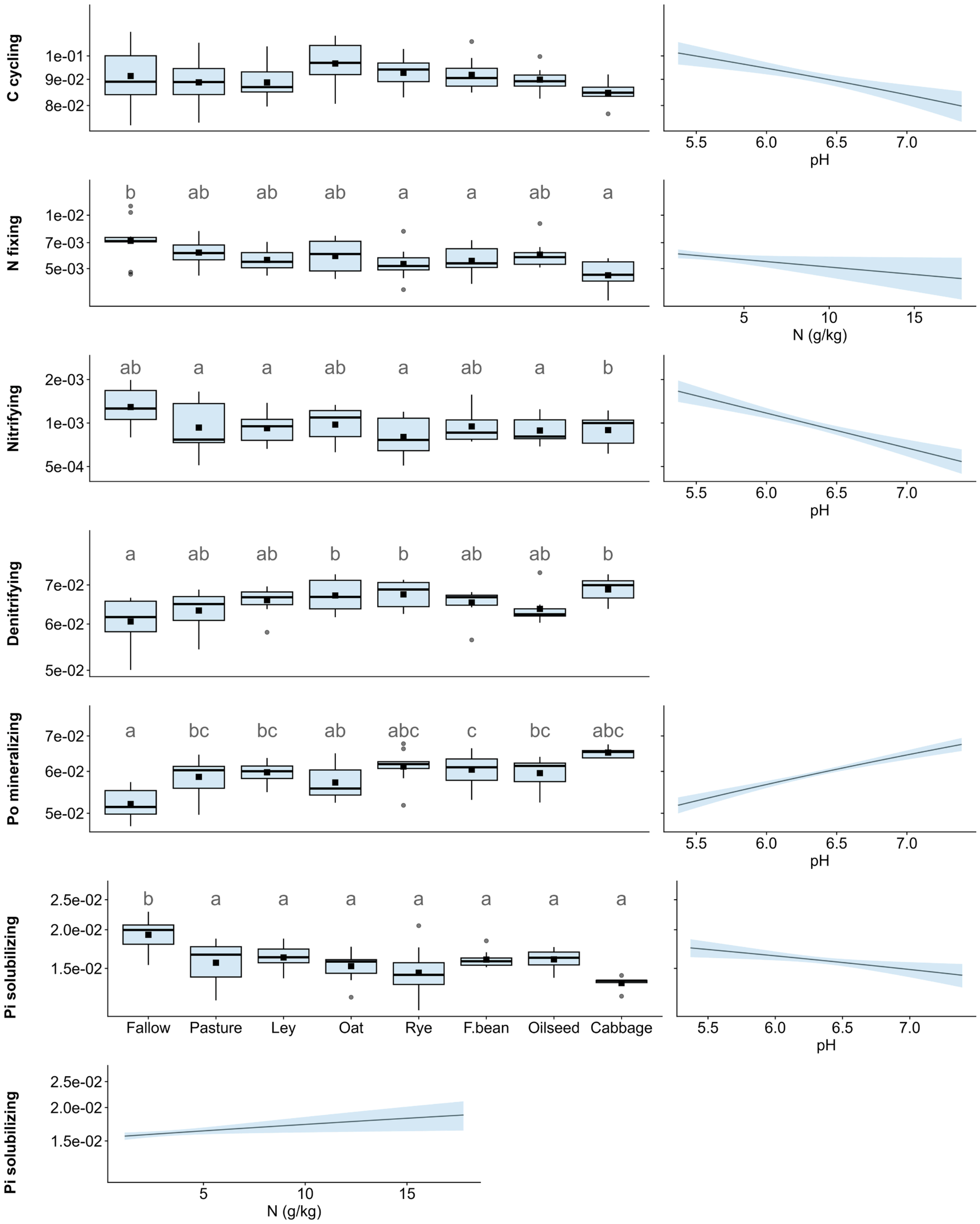

Fig. 4. Selected predicted bacterial functional genes in soil related to carbon (C), nitrogen (N) and phosphorus (P) cycling in the crop types. The boxplots show the proportions of the C cycling (represented by beta-glucosidases), N_2 fixing, nitrifying, denitrifying, organic P (Po) mineralizing, and inorganic P (Pi) solubilizing genes out of all predicted KEGG orthologs. The C cycling genes include *bglX* and *bglB*, nitrogen fixing genes *nifH*, *nifD*, and *nifK*, nitrifying genes the *pmoA-amoA* and *hao*, denitrifying genes the narG , *narH*, *nirK*, *nirS*, *norB*, *norC* and *nosZ*, Pi solubilizing genes the *pqqC*, and Po solubilizing genes the *appA*, *phoA*, *phoD*, and *phoN*. Different lower-case letters indicate statistically significant differences between the crop types in the whole model context in post hoc test ($p \geq 0.05$). The Estimated Marginal Means of the significant soil property associations are shown in separate graphs. Details of the statistical models are given in Table S9A. The mean and standard error of mean values for the proportions of the selected genes, and the post-hoc test results for crop types outside model context are given in Table S10.

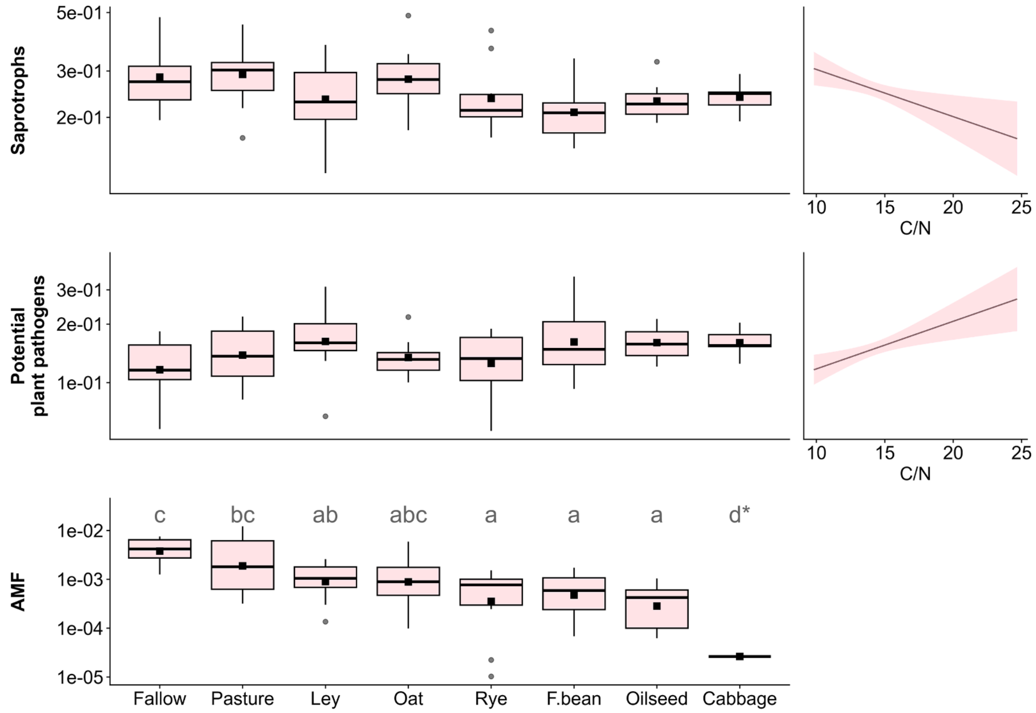

Fig. 5. Selected soil fungal functional groups in crop types. Proportions of the saprotrophic, potential plant pathogenic and arbuscular mycorrhizal fungi (AMF) are shown. Different lower-case letters indicate statistically significant differences between the crop types in the whole model context in post-hoc test ($p \leq 0.05$). (*) For the AMF model, cabbage was excluded due to incidences of zero proportion which are not accepted with Gamma log-link distribution and the difference of AMF proportion between cabbage and the other crop types was determined with Wilcoxon test (Table S11). The significant soil property associations (Estimated Marginal Means) included in the models are shown in separate graphs. Details of the statistical models are given in Table S9B. The mean and standard error of mean values for the proportions of the selected fungal functional groups, and the post-hoc test results for crop types outside model context are given in Table S11.

the soil parameters. Specifically, bacterial richness was positively linked to C:N ratio ($r = 0.33$; $p = 0.005$) and bacterial Shannon to C:N ratio ($r = 0.25$; $p = 0.033$) and pH ($r = 0.37$; $p = 0.001$). Soil pH also showed a significant correlation with the proportions of predicted bacterial genes. The denitrification ($r = 0.39$; $p < 0.001$) and Po mineralization ($r = 0.79$; $p < 0.001$) genes were positively associated with pH, whereas C cycling ($r = -0.40$; $p < 0.001$), nitrification ($r = -0.60$; $p < 0.001$), and Pi solubilization ($r = -0.60$; $p < 0.001$) showed negative associations. Fungal diversity measures were not significantly correlated with soil properties, however, the proportion of AMF was negatively correlated with pH ($r = -0.37$; $p = 0.001$), potential plant pathogens positively correlated with C:N ratio ($r = 0.33$; $p = 0.005$), POMC ($r = 0.28$; $p = 0.015$), and C ($r = 0.25$; $p = 0.032$), and saprotrophs negatively correlated with C:N ratio ($r = -0.27$; $p < 0.021$).

3.3. *Effects of agricultural management on the soil microbial community composition, richness, and potential functions in the subset analysis of pasture, ley, oat, rye, and faba bean*

In the subset analysis of pasture, ley, oat, rye, and faba bean, soil fungal community composition was significantly affected by production method (PERMANOVA; $R^2 = 0.026$, $p = 0.036$). Furthermore, crop type, soil pH, C, and plant coverage influenced fungal community composition (Fig. S4B; Table S12). Soil bacterial community composition was not significantly affected by the agricultural management practices studied, but by soil C, C/N, pH, and plant richness (Fig. S4A; Table S12). In addition, crop life cycle (annual or perennial) was found to have a more significant influence on bacterial communities than crop type. Whereas fungal richness was influenced by an interaction between crop type and production method, with the highest levels observed in conventionally farmed pasture and ley soils, bacterial richness was solely driven by a positive relationship with the C/N ratio (Fig. 7; Table S13).

Out of the selected soil fungal functional groups and bacterial predicted genes, agricultural management impacted AMF, and bacterial C cycling (represented by beta-glucosidases) and N_2 fixing genes (Fig. 8; Table S14). Organic farming increased the proportion of AMF and N_2 fixing genes over conventional farming, whereas the proportion of C cycling genes responded positively to tillage intensity, with these being higher in tilled soils compared to perennial (no-till) soils. Under reduced tillage, the proportion of C cycling genes was intermediate between that of till and perennial (no-till) systems and was not significantly different from either. The annual no-till system also had a low proportion, but its data could not be statistically tested due to low replicate number ($n = 1$). Furthermore, the proportions of predicted bacterial functional genes and fungal functional groups of interest were not associated with agricultural management practices (Table S14).

4. Discussion

4.1. *Crop type had a stronger impact on microbial community composition and on potential functions predicted by PICRUSt2 and FUNGuild than on microbial diversity*

The above ground plant community is known to interplay with the below ground microbial community (Cappelli et al., 2022). However, the influence of crop plants on the soil microbiome is typically more pronounced in rhizosphere than in bulk soil, which can be more prone to soil property effects (Domeignoz-Horta et al., 2024; Tkacz et al., 2020). Here, we show that across farms, soil properties, and agricultural management, crop type influences microbial communities in the bulk soil. We found crop type to have a greater influence on bacterial and fungal community composition than any studied soil property (pH, POMC, C, N, C/N). We found fallow and cabbage to contribute most to the microbial community differences between crop types (Fig. 1; pairwise PERMANOVA; Table S3; Table S4), which was reflected in

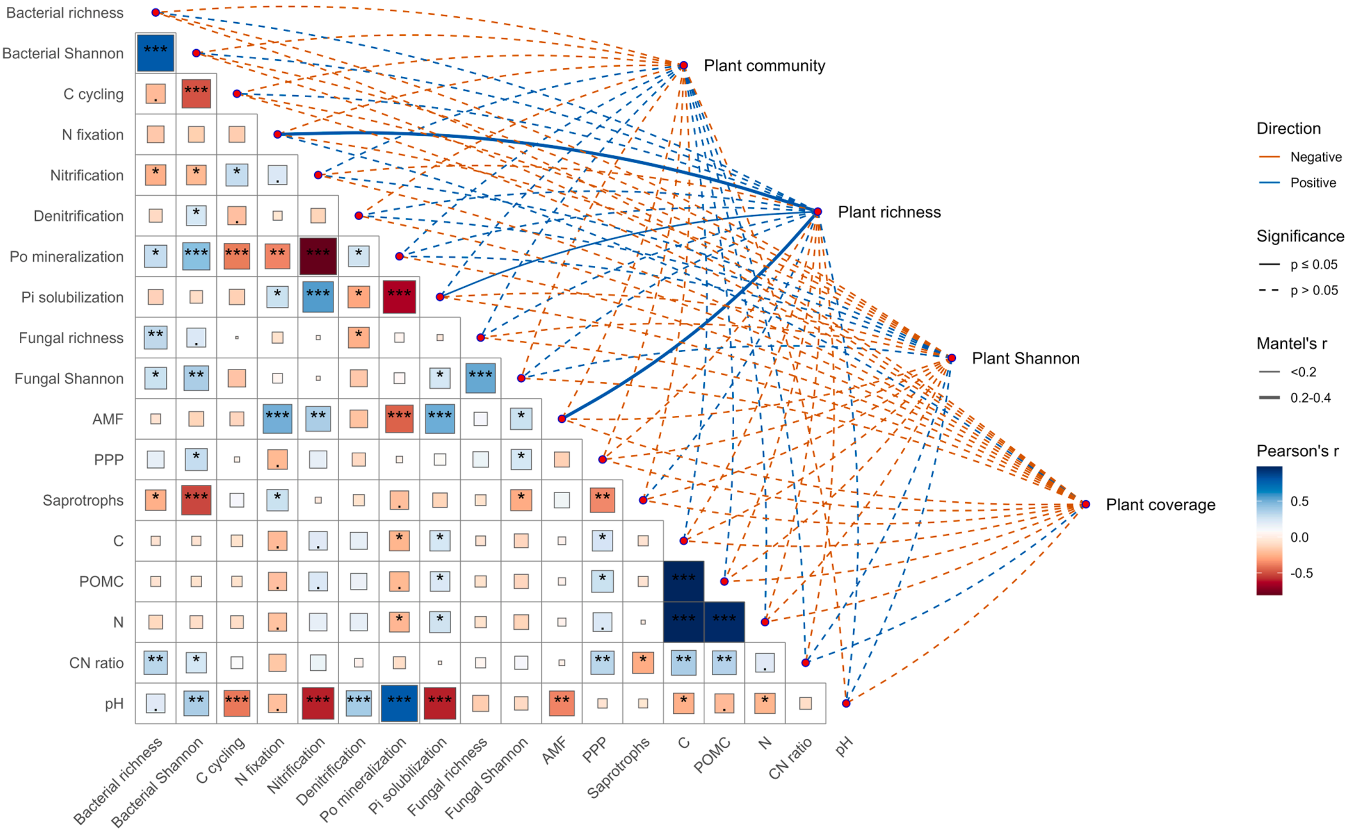

Fig. 6. Mantel tests and Pearson's correlation matrix illustrating the relationships between plant community parameters and microbial diversity, functional groups and soil properties. Plant community parameters include plant community (plant species beta Bray-Curtis dissimilarity), plant richness (plant species richness), plant Shannon (Shannon index based on plant species coverage values), and plant coverage (total plant coverage). The line type corresponds to the Mantel’s Benjamini-Hochberg adjusted p values solid line indicating significance level ≤ 0.05. Line width indicates Mantel's r statistic and line color the direction of the association (positive or negative). The Pearson's correlation coefficient matrix shows the associations between microbial diversity and fungal functional group and predicted bacterial gene proportions, as well as soil properties. The C cycling, N fixation, nitrification, denitrification, Po mineralization, and Pi solubilization represent the proportions of the PICRUSt2 predicted genes involved in these bacterial functions, whereas AMF, PPP, and saprotophs represent the represent the proportions of arbuscular mycorrhizal fungi, potential plant pathogens and saprotrophic fungi, respectively, according to the FUNGuild database. Red color represents negative and blue positive correlation, and the significance level is indicated with asterisks: *** < 0.001, ** < 0.01, * < 0.05,. < 0.1. The Mantel correlation between plant community and microbial communities (beta diversities) is provided in Supplementary data (Fig. S1).

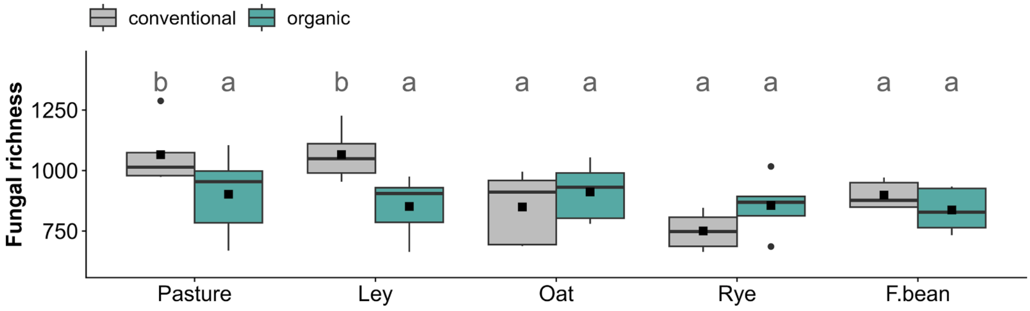

Fig. 7. The significant agricultural management impact on soil fungal richness. Fungal but not bacterial richness was impacted by crop type, production method and their interaction. Different letters indicate statistically significant differences in the whole model context in post hoc test of the generalized linear mixed model (GLMM) ($p < 0.05$). Black squares indicate mean values. Details of the statistical models are given in Table S13.

differential proportions of soil bacterial and fungal phyla (Fig. 3; Table S7; Table S8; Supplementary discussion), fungal functional groups (FUNGuild) and predicted bacterial functional genes (PICRUSt2). The impacts of cabbage may be attributed to glucosinolates produced in the Brassicaceae family, which inhibit microbial growth and shape bacterial and fungal communities (Bressan et al., 2009; Tagele et al., 2021). However, as we did not find oilseed to have divergent microbial communities, our results indicate either plant species specific influence within Brassicaceae or other factors specific to the cabbage crop type. When the crop types representing the management extremes (cabbage and fallow) were excluded (subset analysis), bacterial community composition was impacted by crop life cycle (annual vs perennial) rather than by crop type (Fig. S4). The effect of crop life cycle may indicate root trait effect on soil microbiome (Nunez-Mir and McCary, 2024) as annual plants typically have more acquisitive (high specific root length and root nitrogen concentration) root traits and perennials more conservative

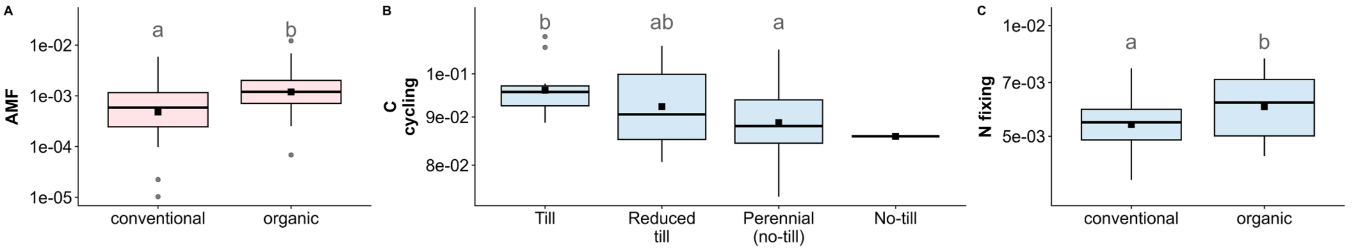

Fig. 8. Agricultural management impact on selected predicted bacterial functional gene and fungal functional group proportions. Only significant management effects are shown. Details of the whole models are given in Table S12. Different lower-case letters indicate statistically significant differences between production methods or tillage systems in the whole model context in post-hoc test ($p < 0.05$).

(high root tissue density) root traits (Roumet et al., 2006; Wicaksono et al., 2024) and a long period of root exudate production (Li et al., 2025; Ma et al., 2022). Fungi, however, were impacted by crop type after the exclusion of management extremes. Our results support H1, confirming that crop type shapes microbial community composition, with fungal communities exhibiting heightened sensitivity. Given the well-established link between microbial communities and soil functionality, this finding emphasizes that crop type, independent of rotation, should be considered a factor shaping the soil microbiome in boreal regions.

Opposite to community composition, the crop type influence on microbial diversity was overshadowed by the strong effects of C/N on bacterial diversity and pH on fungal diversity, a pattern consistent with previous findings (Delgado-Baquerizo et al., 2016; Rousk et al., 2009). The lowered fungal diversity in fallow agrees with previous findings where unmanaged meadow had lower fungal richness compared to conventional and organic crop rotations in topsoil (Häkkinen et al., 2025). The reason behind the low microbial diversity in fallow remains to be verified, but it is possible that disturbances caused by management (e.g. fertilization, harvest, tillage) create more niches for microbes than natural, relatively steady-state conditions. Our results are consistent with a meta-analysis showing reduced bacterial and fungal diversity in less-disturbed environments (Labouyrie et al., 2023b). As only fallow differed from the other crop types in bacterial diversity, and fungal diversity showed no differences among any crop types, our results do not support the component of H1 predicting that crop type impacts microbial diversity but rather suggest that soil properties are the primary driver.

Although a positive association with soil biodiversity and ecosystem functions has been found (Delgado-Baquerizo et al., 2020), it has been proposed that rather than the overall microbial diversity, certain microbial functional groups or traits better describe soil ecosystem functioning in agricultural soils (Bardgett and van der Putten, 2014; K. Fan et al., 2021; Peng et al., 2024). Bacterial functions, such as P solubilization and N_2 fixing, and the fungal symbiosis by AMF may enhance plant nutrition and resilience against drought and pathogens (Elhaissoufi et al., 2022; Pandey et al., 2017; Weng et al., 2022). Consistent with a previous meta-analysis (Zhou et al., 2020), we found high microbial taxonomic diversity to be a poor indicator of predicted functions with putative beneficial roles. Specifically, high bacterial diversity in cabbage fields coincided with the lowest proportions of predicted Pi solubilizing and N_2 fixing genes, whereas low bacterial diversity under fallow coincided with the highest proportions of these genes. Similarly, in fungi, fallow had among the lowest fungal diversity but the highest proportion of AMF. Predicted bacterial gene or fungal functional group proportions, however, do not indicate their absolute abundances nor activities. Rather, the proportionality of sequencing data can show how large a proportion a given functional potential represents within a community. Thus, the proportional increase in the Pi solubilization and N_2 fixing genes and AMF in fallow soil suggests that this low-input management is enriched in the soil's inherent functional potential for nutrient cycling relative to other functions. However, similar to our findings, extensively managed grassland was previously shown to increase N_2 fixing bacteria compared to croplands (Labouyrie et al., 2023b) which may be driven by the absence of fertilization and higher plant richness (Fig. 6; L. Liao et al., 2021; Smercina et al., 2019). The leguminous faba bean did not show increase in predicted N_2 fixing gene proportion indicating our sampling approach may have excluded these important N_2 fixers and mainly included N_2 fixing by free-living bacteria. However, it has been estimated on a global scale that free-living N_2 fixing bacteria contribute to 24% of maize, rice and wheat total N (Ladha et al., 2016).

Based on the proportions of predicted bacterial genes, fallow and the other crop types appeared to employ partially differential strategies for soil P mobilization: fallow inducing Pi solubilizing and agricultural crops the Po mineralizing predicted functions. Differences in fertilization may partially explain this—fallow being non-fertilized and agricultural crops generally fertilized—and is supported by the finding that fertilization increases the abundance of the *phoA* gene related to Po mineralization (Liao et al., 2023). One possible explanation is the greater input of plant residue Po in fertilized systems (Nuruzzaman et al., 2005), which may in turn stimulate Po mineralization (Randhawa et al., 2005) and reduce the need for Pi solubilization from mineral soil. Consistent with this, faba bean, which has an enhanced capacity to take up soil P and therefore produces P-rich residues (Liao et al., 2022; Nuruzzaman et al., 2005), increased predicted potential for Po mineralization compared to oat. In addition to crop type, pH impacted the two predicted P mobilization strategies. In comparison to a study where Pi solubilization gene (*gcd*) was found to decrease together with N fertilization associated decreases in pH (Dai et al., 2020), our results indicate a negative association between pH and the predicted Pi solubilization marker gene (*pqqC*) and a positive association with pH and predicted Po mineralizing genes. In fact, predicted Pi solubilizing and Po mineralizing genes were strongly negatively correlated indicating that soil functions related to P availability may shift in relation to environmental conditions. In boreal agroecosystems, agricultural practices such as liming are used to increase soil pH, which in turn enhances P availability through the chemical desorption of P from mineral surfaces (Hingston et al., 1967). Our results indicate that, beyond this direct chemical effect, pH may also play a role in shaping the microbial pathways that control P cycling. The Pi solubilizing, Po mineralizing and N_2 fixing bacteria form close interactions with roots and rhizosphere and are impacted by root exudates, which can explain the influence of crop type on the proportions of these predicted functions (Pantigoso et al., 2023).

Although the end product of nitrification, nitrate, is readily available N source for plants, both nitrifying and denitrifying functions are related to N losses in agricultural soils and are positively linked to N fertilization (Pan et al., 2022). We found the non-fertilized fallow to have the highest proportion of predicted nitrification genes, however, the low pH explained the differences compared to other crop types. Although, pH optimum for nitrification is quite high (7.9–8.2) (Park et al., 2007) and nitrification is typically decreased in acidic soils (Pan et al., 2022), nitrification by chemolithoautotrophic and possibly by heterotrophic bacteria occur in lower pH soils (De Boer and Kowalchuk, 2001). Our results from the predicted genes indicate considerable bacterial nitrification potential in more acidic fallow soil conditions. After considering the differences in soil pH (Table S9), predicted nitrifying genes were increased under cabbage compared to pasture, ley, rye, and oilseed and denitrifying predicted functions were increased under the cereal crops (oat and rye) and cabbage compared to fallow. These suggest that the perennial pasture and ley may have decreased risk for microbial-induced N losses in the boreal agroecosystems similarly as shown in temperate regions (Iqbal et al., 2015; Smith et al., 2013). Overall, our results indicate that among the studied predicted microbial functions, Po mineralization and nitrification potential were influenced by cultivated crop types (excluding fallow). This supports the component of H1 predicting that crop type impacts potential bacterial soil functions.

It is important to note that although PICRUSt2 based bacterial functional prediction used here has been shown to work better (i.e. more similarly with shotgun metagenomics) than some other annotation methods, it still relies on incomplete phylogenetic information from 16S marker gene sequences and genomic content and underestimates the metabolic diversity of bacterial function in complex environments such as soils (Douglas et al., 2020; Toole et al., 2021b), and thus results should be interpreted with caution. Further studies, such as metagenomic analyses, are needed to confirm these results.

Fungal functional groups—specifically putative pathogens, mycorrhizal fungi, and saprotrophs—have been identified as primary regulators of plant-soil feedback (Semchenko et al., 2018), highlighting their relevance for crop performance. We found fungal saprotroph and potential plant pathogen proportions to be influenced only by C/N, the former with a negative and the latter with a positive association. Similarly, strong impact of C/N on saprotrophic fungi in general and the negative association of C/N with some specific saprotrophic taxa in agroecosystems have been previously shown (Ning et al., 2021). Soil-borne fungal plant pathogens have been shown to positively associate with SOC and straw amendments, which have a high C/N ratio (Du et al., 2022). However, a high C/N may not directly indicate increased disease occurrence; rather, disease incidence may be more closely linked to soil N levels (Bi et al., 2022), which highlights the difference between microbial presence and activity. Consistent with studies comparing extensive grasslands and croplands (Häkkinen et al., 2025; Labouyrie et al., 2023b), we found that fallow induced the proportion of AMF. The differences in AMF proportion between fallow and other crop types may be partially driven by plant richness (Toivonen et al., 2022; Fig. 6; Table S9), a known driver of AMF communities (Lepinay et al., 2024). As AMF is shown to be connected to enhanced soil aggregation (Lehmann et al., 2017; Leifheit et al., 2014), the results suggest a possible positive interaction between plant diversity and soil structure. Among agricultural crop types, we found a decreasing trend from perennial through non-Brassicaceae-annual to Brassicaceae-annual crop types in the proportion of AMF. However, oat was partially an exception as the AMF proportion could not be differentiated from ley and pasture. This oat-specific promotion of AMF community was also found in a previous study, where oat cover crops had the highest AMF abundance out of eight planted monocultures and similar or higher compared to the planted four or eight plant species mixtures (Finney et al., 2017). Our results indicate that oat as a main crop marginally induces soil AMF over other annual crops but not over perennial multispecies crops (ley and pasture). The non-AMF host status of Brassicaceae plants (Sharma et al., 2023) is the probable reason for the proportionally less abundant AMF community in oilseed and especially in cabbage, where in some fields no AMF were detected. The cultivation of Brassicaceae plants has been shown to negatively impact AMF colonization of the succeeding crops (García-González et al., 2023). Our results indicate that the negative AMF legacy effect in Brassicaceae may be partially weakened with a more diverse crop rotation as the oilseed with relatively diverse crop rotations (mean number of crops in rotation: 4) showed less drastic differences in soil AMF proportion compared to the non-Brassicaceae crop types than cabbage grown in simple rotations or monocultures (mean number of crops in rotation: 2) (Table S1). Our results support the component of H1 predicting that crop type impacts potential fungal soil functions, although this was true only for AMF among the studied fungal functional groups. However, the fold differences in AMF proportions between crop types were large, indicating that AMF could be strongly affected by crop type.

Based on the results, our H1 was largely supported. Crop type, as the dominant component of the plant community, influenced microbial community composition and predicted potential functions, and these effects persisted despite variation in management practices. However, for microbial diversity, crop type effects were overshadowed by soil properties. Additionally, only a subset of the predicted potential microbial functions studied were impacted by crop type, and pairwise differences between agricultural crop types (excluding fallow) were few, namely the nitrifying and Po mineralization functions. This may be attributed to the legacy effect of previous crops in the rotation. Plants in general (Schmid et al., 2021b) and crop plants specifically (García-González et al., 2023) can shape microbial communities in the following year. In the crop rotations studied here, the influence of the current crop type on the soil microbiome was significant but limited.

4.2. Whole plant community attributes shape microbial diversity and predicted functional potential

Although the role of the whole plant community in shaping soil microbiome is well established for natural and semi-natural soil ecosystems (Leff et al., 2018; Lepinay et al., 2024; Porazinska et al., 2018), it is rarely included in studies of agricultural soil (but see Cassman et al., 2016; J. Hu et al., 2023) and, to our knowledge, has never been investigated in the boreal region. We found that both bacterial and fungal community composition were influenced by plant species richness in addition to the crop type and soil property impacts (Fig. 1). Total plant diversity has previously been shown to impact root fungal community composition in agricultural soils (Hu et al., 2023), but here we show that these effects also cover the bacteria and reach the bulk soil. Our study suggests that the aboveground and belowground alpha diversities are not tightly linked in the studied boreal agroecosystems, as no correlation between plant and microbial diversity was found. Overall, this link is ambiguous: both negative (Schlatter et al., 2015), positive (Lange et al., 2015) and neutral (Prober et al., 2015) relationships have been observed, and these may be ecosystem- and microbial domain-specific (Lepinay et al., 2024; Porazinska et al., 2018). For example, Lepinay et al. (2024) found a positive association between plant and fungal diversity but not between plant and bacterial diversity in a semi-natural grassland ecosystem. However, in Lepinay et al. (2024), the bacterial biomass was positively associated with plant diversity, indicating a decoupling between microbial diversity and biomass, which can occur at moderately low-C soils (Bastida et al., 2021), such as the soils in this study. The low bacterial and fungal diversity in fallow thus may not indicate low microbial biomass. This has implications for soil C accrual, which is believed to increase together with microbial biomass (Kallenbach et al., 2016). Previous research has shown that soil perturbation strongly influences microbial diversity (Labouyrie et al., 2023a) and that the link between plant and soil microbial diversity strengthens over time in the absence of disturbance (Schmid et al., 2021b). Consequently, this link may be weakened in agricultural soils due to continuous perturbation.

We found a positive correlation between plant species richness and the proportions of AMF, as well as the predicted bacterial N_2 fixation and Pi solubilization genes, suggesting that plant diversity in boreal agricultural soils may enhance beneficial microbial-mediated functions. The positive link between plant richness and AMF is supported by studies in grassland soils (C. Wang et al., 2022) and, for crop species richness, in agricultural soils (Guzman et al., 2021; Shrestha et al., 2025). However, to our knowledge, this relationship has not been demonstrated for the full plant community in agricultural settings. The positive plant diversity-AMF relationship found in this study suggests a potential mechanism for enhancing soil organic carbon (SOC) stabilization, a pathway supported by previous research on plant diversification (E. Zhang et al., 2025). The found association between predicted bacterial N_2 fixation potential and plant diversity may be driven by changes in rhizosphere metabolite profiles that enhance nitrogen fixation by free-living bacteria, thereby increasing nitrogen availability, as demonstrated in a crop diversification study (Qiao et al., 2024). Moreover, N_2 fixation is an energy-intensive process, which may be favoured by the increased availability of easily accessible energy sources derived from more diverse root exudates (Schmid et al., 2021b). Direct evidence for plant diversity effects on bacterial inorganic phosphorus (Pi) solubilization remains limited. However, our findings point to two potential indirect pathways: (1) mediation through arbuscular mycorrhizal fungi (AMF), given their positive correlation with predicted Pi-solubilizing genes here and their known interactions (Zhang et al., 2019), and (2) the general induction of Pi solubilization by diverse root exudates (Pantigoso et al., 2023).

Overall, our results largely support the component of H2 stating that plant richness impacts microbial communities. This was evident for microbial community composition (beta-diversity) and predicted potential functions, but not for alpha-diversity. The other component of H2, stating that the effect of plant richness is more prominent on fungi, was not supported. However we did find that plant community parameters in general had a stronger effect on fungi than on bacteria, which is consistent with previous research (Hannula et al., 2020; Lepinay et al., 2024). This was reflected in the marginal correlation between overall plant community composition and fungal community composition (Fig. S1), and a significant influence of plant coverage on fungal community composition (Fig. 1**B**). These plant community parameters likely impact root biomass and composition of root traits and exudates (Lin et al., 2014; Roumet et al., 2008), whose influence on fungal communities has been previously documented (Broeckling et al., 2008; Hou et al., 2023; Newberger et al., 2023). Thus, the plant community composition and coverage, in addition to the plant species richness, appear to modulate the impacts on soil fungal communities.

4.3. Agricultural management practices influenced fungal community composition and richness, as well as microbial predicted functions

Agricultural management practices affected bacteria and fungi differently. Bacterial diversity and community composition were unaffected by the studied agricultural management practices—production method, tillage, fertilizer type, N fertilization rate, pesticide usage, and crop sequence diversity—whereas fungal diversity and community composition were influenced by the production method. We found that under perennial crops (pasture and ley), soil fungal richness was higher in conventional than organic farming, whereas no such difference was observed for annual crops (oat, rye and faba bean). In contrast to our results, organic farming has been shown to increase microbial richness, but similarly to here in a crop life cycle dependent manner (Peltoniemi et al., 2021). The increased fungal richness in conventional over organic pasture and ley soil support the previously found neutral to positive land-use intensity effects on fungal diversity specifically in grasslands (Gossner et al., 2016). The stronger effect of production method on fungi relative to bacteria supports previous findings by Hartman et al. (2018), who reported that farming practices altered fungal communities in bulk soil but affected bacteria only in the root-associated compartment. Yet, we found organic farming to increase the proportion of predicted bacterial N_2 fixing genes as well as AMF. Whereas AMF have been shown to respond negatively to mineral fertilization compared to manure (Wang et al., 2018), to higher soil management intensity in general (Banerjee et al., 2019; Thiele-Bruhn et al., 2012), and positively to the higher plant diversity associated with organically managed fields (Fig. 6; Shrestha et al., 2025), the effects of management on N_2 fixing remain less understood apart from the known negative impact of N fertilization and positive influence of organic manure (Liao et al., 2021; Shi et al., 2021). Our results suggest that the predicted N_2 fixing potential in boreal agricultural soil is enhanced under organic production as a whole, not just due to the lack of mineral fertilization, further supporting the potential negative impact of pesticide use (Walder et al., 2022). These findings support the component of H3 predicting that organic production enhances the predicted potential for beneficial soil functions, but they do not support the component predicting an increase in overall microbial diversity. Instead, these results further illustrate the ambiguous link between microbial diversity and ecosystem functioning. Whereas a positive association may exist at low diversity levels, this relationship becomes less clear at high diversity, where greater microbial richness may no longer indicate improved ecosystem functions (summarized in Bardgett and van der Putten, 2014). Our results with predicted functions are consistent with this nonlinear relationship between microbial diversity and putative beneficial functions (described in 4.1.).

The predicted bacterial C cycling gene proportions were elevated in more intensively tilled soils. This aligns with some earlier genomic studies (Tyler, 2021) but contrasts with research on enzyme activities (Zhu et al., 2024). Lower tillage intensity may impact the soil physical properties and promote increased retention of plant residue C in macroaggregates and thus lower the available C for decomposition (White and Rice, 2009). However, as the C cycling potential was estimated based on beta-glucosidase gene abundance, which is the rate-limiting enzyme of degradation of cellulose (Zang et al., 2018), it does not cover the full C cycling genomic machinery. Moreover, bacterial processes represent just one component of microbial organic matter turnover, as fungi often play a dominant role, particularly in less disturbed soils where their biomass is associated with higher SOC (Yang et al., 2022). Thus, the increased bacterial genomic potential for degrading labile cellulose in tilled systems may not reflect a higher potential for overall microbial turnover of soil organic matter. We hypothesized that tillage intensity would negatively impact hyphal fungi, particularly AMF (H4). No such effect was detected. The absence of a detectable tillage effect on AMF may be due to the need to exclude no-till annual crops with low replication number ($n = 1$), and further research is needed to confirm these findings. Nevertheless, our results provide tentative support for a shift towards more bacterial-dominated carbon cycling under higher tillage intensity. This has implications for sustainable soil management in the boreal region, suggesting that organic production, through its positive effect on plant diversity and AMF, may help maintain fungal-based carbon pathways even under tillage, supporting long-term soil health.

We recognize limitations of this study. First, not all crop types were represented under both organic and conventional management, which limits the generalizability of our findings across the full range of boreal cropping systems. Specifically, the management impacts on cabbage and oilseed could not be assessed due to the lack of organically farmed cabbage fields and a confounding plant species effect for oilseed (different oilseed species under organic compared to conventional farming). Nevertheless, the setup is consistent with the common crop types and their management in the region. Second, our measurements represent a single time point, providing only a snapshot of microbial communities and limiting the ability to assess temporal variability or seasonal fluctuations. However, previous work showed that agricultural system (including crop type and management) was a stronger driver of soil microbial communities than sampling time, with many system-related microbial markers persisting throughout the year (Fox et al., 2022). Third, bacterial gene prediction, despite expanding genomic databases, does not indicate microbial functional potential as robustly as metagenomic studies. Even so, this study offers a useful reference point for understanding how crop type, plant community and agricultural management shape soil microbial communities, and identifies patterns for further exploration in long-term studies.

5. Conclusions

In this study, we investigated how crop type, overall plant richness, as well as agricultural management influence plant-soil microbial interactions in boreal systems. We found that microbial community composition was shaped by crop identity. In addition to the fallow and cabbage, which had the most distinct microbial communities, the other cultivated crop types also shaped fungal community composition, and the crop life cycle (perennial vs annual) influenced the bacterial community composition. Crop type also influenced potential microbial functions, as predicted by PICRUSt2 (bacteria) and FUNGuild (fungi). For instance, faba bean increased the proportion of genes associated with organic phosphorus mineralization, cabbage the nitrification-related genes, and pasture, ley, and oat promoted arbuscular mycorrhizal fungi (AMF). Whereas aboveground and belowground diversity were not tightly coupled, plant diversity did impact the microbial community composition, and enhanced the proportion of AMF and predicted bacterial genes involved in nitrogen fixation and inorganic phosphorus solubilization. Management practices further shaped microbial communities. Organic farming, likely partially through its positive effect on plant diversity, promoted AMF and predicted nitrogen-fixing genes. In contrast, tillage appeared to shift carbon cycling toward a more bacterial-dominated pathway. These functional predictions provide valuable insights. However, metagenomic or activity-based measurements are needed to confirm them. Despite this limitation, our findings have several implications for boreal agriculture. First, they highlight the importance of crop identity as a driver of microbial community structure and function. Second, the observed decoupling between overall microbial diversity and beneficial functions suggests that specific functional groups, such as AMF and nutrient-cycling bacteria, may be more relevant targets for management. In particular, organic farming and crop diversification could support key soil processes. Third, our results provide a foundation for future studies using metagenomic or activity-based approaches to further explore plant-soil microbiome dynamics in boreal cropping systems.

CRediT authorship contribution statement

Terho Hyvönen: Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization. **Tero Tuomivirta:** Writing – review & editing, Validation, Conceptualization. **Marjaana Toivonen:** Writing – review & editing, Validation, Data curation, Conceptualization. **Juha-Matti Pitkänen:** Resources, Investigation, Formal analysis, Data curation. **Ansa Palojärvi:** Writing – review & editing, Conceptualization. **Jussi Heinonsalo:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Laura Häkkinen:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110440.

Data availability

Data will be made available on request.

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