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Research paper

# Long-term P management has limited impacts on soil microbial communities, with unique patterns driven by location, land use, and soil depth

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ABSTRACT

Mineral fertilizers containing phosphorus (P) are widely used in agriculture to enhance soil fertility, yet their impact on soil microbial communities remains unclear. Most studies rely on a single-site approach and observe short-term effects, limiting our ability to extricate long-term P impacts from other drivers of microbial communities. This study aimed to explore the influence of long-term P fertilization on soil microbial communities along the depth gradient across four countries, including grasslands and arable sites. Microbiomes were strongly affected by location, land management, and soil depth. No changes in the composition of prokaryotic communities were detected in response to P fertilization, while fungal communities demonstrated a modest response, but only at 0–10 cm depth in grassland soil. The almost complete absence of P fertilization impacts on communities could be due to a lack of changes in soil properties and nutrient availability after P fertilization. This is likely because of the applied P rate being below the threshold needed to alter soil properties or as a consequence of a legacy from previous P fertilization events. The strongest effect of P fertilization was observed at 0–10 cm depth, where carbon (C) and nitrogen (N) availability was higher. Together, these findings suggest that soil microbial communities are largely resistant to long-term P fertilization, with responses strongly mediated by site-specific conditions. Our study highlights the importance of considering multiple long-term sites, land use types, and soil depths in research focused on P fertilization effects on soil microbial communities.

## 1. Introduction

Soil microbial communities are fundamental to life on Earth through their regulation of global biogeochemical cycles (Aislabie and Deslippe, 2013) and their contributions to soil health and crop production (Wongkiew et al., 2022). Understanding the factors that drive microbiome assembly is therefore essential for elucidating the mechanisms that sustain key ecosystem processes. Advances in next-generation sequencing (NGS) have enabled detailed characterization of soil microbiomes and identification of the abiotic and biotic factors shaping their assembly (DeFord and Yoon, 2024). Previous studies have demonstrated that soil microbiomes respond to changes in soil physicochemical properties (Rousk et al., 2010; Delgado-Baquerizo et al., 2018; Philippot et al., 2024), depth gradients (Eilers et al., 2012), land

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management practices (Richter et al., 2024; Cole et al., 2024), and nutrient inputs, especially P and N (Leff et al., 2015; Francioli et al., 2016). However, because soil is a highly heterogeneous system, the relative importance of these drivers depends on geographic location, environmental conditions, and interactions among factors (Cowan et al., 2022; Knight et al., 2024).

Most studies on soil microbial community dynamics generally obtain data from single sites and focus on surface soil (~ 15 cm depth) without considering changes in physicochemical properties (pH, texture, nutrient availability). Single-site approaches have the advantage of similar initial microbiomes and environmental conditions, with minimal confounding factors. However, it leads to limited biological replication. For example, microbial communities at a single site do not represent the overall microbial diversity and therefore their responses to P fertilization might not either. Moreover, it limits our ability to disentangle nutrient effects from broader drivers such as land management. Effects of nutrient inputs observed at a single site preclude the possibility of determining whether the same trend is consistent among different locations, land use types, and climate conditions.

Microbial diversity typically decreases with increasing soil depth, reflecting changes in physicochemical parameters and nutrient availability along the soil profile (Fierer et al., 2003; Estrada et al., 2024). Concentrations of organic C, N, and P have been shown to consistently decrease with depth (Jobbágy and Jackson, 2000; Morikawa et al., 2022; van der Wal et al., 2007), altering microbiomes. While most microbial ecology studies focus on the topsoil, where plant-microbe interactions and responses to management practices are strongest (Philipp et al., 2025), deeper soil depths remain comparatively understudied, leaving gaps in our understanding of community assembly drivers throughout the soil profile.

Agricultural management strongly influences soil microbiomes: practices such as organic amendments and crop rotations generally enhance microbial diversity and nutrient cycling, improving soil fertility and long-term sustainability (Hartmann et al., 2015; Fernandez et al., 2016). Nutrient inputs, particularly P, play a central role in regulating soil and rhizosphere microbial processes. Phosphorus is an essential element promoting plant growth (Bechtaoui et al., 2021) and microbial activity in soil (Cardinale et al., 2019), yet the observed effects of P fertilization on microbiomes are inconsistent across different ecosystems (Dincă et al., 2022). For instance, long-term P application can increase microbial diversity, biomass, and enzyme activity at low application rates in grasslands (Tan et al., 2013; Shi et al., 2020), but it can also reduce bacterial richness and Shannon diversity (Liu et al., 2020), decrease fungal diversity in arable systems (Lang et al., 2021), suppress arbuscular mycorrhizal fungi (AMF) in grasslands (Gosling et al., 2013; Fornara et al., 2020), and promote pathogenic fungi (Lekberg et al., 2021). Furthermore, it has been shown that P fertilization affects certain prokaryotic and fungal species across multiple sites (Leff et al., 2015; Dincă et al., 2022), with the effect being stronger within fungal communities (Cassman et al., 2016). Mechanisms behind the effect of P fertilization on microorganisms can be attributed to the direct impact of P availability (Oliverio et al., 2020; Ducousso-Détrez et al., 2024) or to changes in C and N availability due to shifted rhizodeposition in topsoil (Margalef et al., 2017; Bicharanloo et al., 2020; Qi et al., 2022). In contrast, some studies report no significant microbial response to long-term P fertilization despite strong effects on plant biomass (Williams et al., 2017; García et al., 2017; Cuhel et al., 2019). These contrasting outcomes highlight the context dependence of P effects, which vary with site conditions and land use types.

Fertilization long-term experiments (LTE) provide an indispensable framework for disentangling the interactions among P, N, and soil C cycling (Bhople et al., 2025). The strength of these LTEs, several decades in duration, lies in the fact that the observed nutrient status reflects the legacy of controlled fertilizer applications, thereby providing a unique basis for assessing nutrient-soil interactions. For example, European LTEs indicate that sustained, moderate P additions (20–30 kg P $ha^{-1}$ $yr^{-1}$) can promote higher plant productivity while, in contrast, consistently high P inputs (>50 kg P $ha^{-1}$ $yr^{-1}$) have been associated with enhanced microbial respiration and accelerated soil organic matter decomposition in temperate grassland systems (Graça et al., 2022).

To date, no study appears to have simultaneously assessed long-term P fertilization effects across multiple sites, land uses, and soil depths. Here, we address this gap by examining microbial responses to long-term P fertilization (up to 89 years) across grasslands and arable sites in four countries within Europe. We sampled soils at three depths (0–10, 10–30, and 30–50 cm) to test three co-occurring hypotheses. We assumed that (i) soil microbial communities would respond to P fertilization and that this effect would be consistent across locations and land use types. We further hypothesized that (ii) microbial response to elevated P would be strongest in topsoil relative to subsoil due to potential shifts in rhizodeposition and that (iii) P fertilization would have a stronger impact on soil fungi than on prokaryotes.

## 2. Methods

### 2.1. Study sites

Soil samples were collected from six LTEs that had been subjected to 29 to 89 years of P fertilization at different rates across four countries in Europe. The LTEs included three grassland experiments, two sites in Ireland and one site in the Netherlands as well as three arable sites, two in Sweden and one in Denmark (Bhople et al., 2025). The grassland LTEs were managed for grazing and silage. Soil texture varied in grasslands from a sandy clay loam in Ireland to a clay soil in the Netherlands. The arable sites were tilled inversely or ploughed annually. The soil texture was a coarse sand in Denmark and a silt clay loam in Sweden.

In Ireland, sites had received P annually as either calcium superphosphate (up to 30 kg P $ha^{-1}$) or as triple superphosphate (up to 45 kg P $ha^{-1}$) in early spring starting from 1968 and 1995, respectively. The Irish grasslands are dominated by perennial ryegrass (*Lolium perenne*) with mean annual precipitation (MAP) of 1000 mm and mean annual temperature (MAT) of 9.6 °C (O'Neill et al., 2021; University of Sheffield, 2021). In the Netherlands, a combination of cattle manure and superphosphate (up to 41 kg P $ha^{-1}$) had been added to soil twice a year, in early spring and after every harvest since 1989. MAP and MAT are 750 mm and 10 °C, respectively, with perennial ryegrass being the dominant plant species (van der Salm et al., 2009). A high dose of superphosphate (105 kg P $ha^{-1}$) had been applied every sixth year at the Swedish sites since 1936 or 1941, respectively (MAP: 584 mm, MAT: 7.3 °C, crops: cereals; Braun, 2022). In Denmark, 15.6 kg P $ha^{-1}$ $yr^{-1}$ had been applied as superphosphate since 1944 (changed to triple superphosphate in 2012) to plots with or without initial addition of 156 kg P $ha^{-1}$ in 1944. Spring barley is the dominant crop in the Danish site, MAP is 890 mm, and MAT is 9 °C (Pedersen et al., 2025). The long-term fertilization history of these LTEs allowed differences in soil P to develop over the years, reflecting the legacy P status at the time of sampling.

Considering absolute P inputs over several years, along with plant available P, and SOC/TP and TN/TP ratios, three P fertilization rates for each site were defined, "Low" (control), "Medium", and "High" (Tables S1-S2), reflecting the legacy P accumulated in the soil rather than immediate responses to fertilization. At the studied sites, the "Low" P fertilization consisted of zero P (0 kg $ha^{-1}$) except in the Netherlands, where the low P application was 23 kg $ha^{-1}$ $yr^{-1}$. The "Medium" and "High" P fertilization rates varied across different LTEs (Table S1) due to the experimental designs, differences in soil types, and the P requirements for plant growth.

### 2.2. Soil sampling and physicochemical analyses

In total, 114 soil samples from three P fertilization treatments (low, medium, high) were collected from the LTEs in September and October 2022. Within each plot, a representative sampling area was selected. A

soil pit (60 × 60 × 60 cm) was excavated at the identified mid-point of the sampling area. The profile face in the pit was cleaned with a sterilized knife, and 500 g of soil was taken from each of three depths, 0–10 cm, 10–30 cm, and 30–50 cm. Subsamples (1–2 g) from each sample were flash-frozen with liquid N or dry ice in the field, followed by storage at −80 °C prior to DNA extraction.

The soil samples were transported to the laboratory facilities in Teagasc Johnstown Castle, Ireland, for physicochemical analysis (Table S2; Bhople et al., 2025). Briefly, roots and stones were removed, the samples were dried at 40 °C and sieved (< 2 mm mesh). Then, soil pH was measured using deionised water (1:5 *w/v*). A TrueSpec C/N analyser (LECO, USA) was used to measure soil total carbon (TC), total nitrogen (TN), and total inorganic carbon (TIC) contents. The SOC contents were calculated based on the difference between TC and TIC. The Mehlich 3 extraction was performed using 20 mL Mehlich 3 reagent consisting of 0.2 M acetic acid ($CH_3COOH$), 0.25 M ammonium nitrate ($NH_4NO_3$), 0.015 M ammonium fluoride ($NH_4F$), 0.013 M nitric acid ($HNO_3$), 0.001 M EDTA (Sigma-Aldrich, USA), and 2 g of dried soil (Mehlich, 1984). The mixture was shaken at 180 rpm for 5 min, and total available soil P was measured using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES).

### 2.3. DNA extraction from soil samples

Extractions of DNA were performed on 0.25 g soil subsamples (avoiding plant material and stones) using a DNeasy PowerSoil Kit (Qiagen, USA) following the manufacturer's instructions. Bead beating was done using the MP FastPrep-24 Tissue and Cell Homogenizer (MP Biomedicals, USA) for 30 s at a speed of 5 m $s^{-1}$. The DNA was eluted in 50 μL of 10 mM Tris-HCl solution (Qiagen, USA). DNA purity and quality were assessed with a spectrophotometer (Thermo Fisher, Ireland), considering both 260/280 and 260/230 absorbance ratios. Yields of DNA ranged from 10.3 to 86.8 ng $\mu L^{-1}$. The DNA extracts were stored at −80 °C until further analysis.

### 2.4. Amplicon sequencing of 16S rRNA and ITS regions

The PCR amplicon libraries targeting 16S rRNA and the ITS encoding regions present in metagenomic DNA were produced using the Earth Microbiome Project barcoded primer set adapted for the Illumina HiSeq2000 and MiSeq (Caporaso et al., 2012; Smith and Peay, 2014). DNA sequence data were generated using Illumina paired-end sequencing at the Environmental Sample Preparation and Sequencing Facility (ESPSF) at Argonne National Laboratory, USA. Each 25 μL PCR reaction contained 9.5 μL of PCR Water (Qiagen, USA; Certified DNA-Free), 12.5 μL of QuantaBio's (USA) AccuStart II PCR ToughMix (2× concentration, 1× final), 1 μL Golay barcode tagged Forward Primer (5 μM concentration, 200 pM final), 1 μL Reverse Primer (5 μM concentration, 200 pM final), and 1 μL of template DNA. The conditions for PCR were as follows: 94 °C for 3 min to denature the DNA, with 35 cycles at 94 °C for 45 s, 50 °C for 60 s, and 72 °C for 90 s; with a final extension of 10 min at 72 °C to ensure complete amplification.

### 2.5. Bioinformatics

Raw sequencing data were processed using the DADA2 package (version 1.26.0, Callahan et al., 2016) in RStudio (R version 4.2.0, R Core Team, 2021). Briefly, forward and reverse reads were demultiplexed, and each sample was split into individual fastq files (one forward and one reverse file per sample). Files were then sorted either by forward or reverse read, filtered and trimmed according to default parameters (maxN = 0, maxEE = c(2, 2), truncQ = 2, rm.phix = TRUE). Paired reads that passed through quality trimming were merged, and an amplicon sequence variant (ASV) table was generated from the merged paired reads. Chimeras were removed from the sequence table, and raw reads were verified by tracking them through the pipeline. After quality trimming and filtering, the 16S amplicons ranged from 175 to 290 bp (median 253 bp), and ITS amplicons ranged from 200 to 338 bp (median 208 bp; Fig. S1-S2). Taxonomy was assigned to ASVs using SILVA (version 138.2) for prokaryotes (Quast et al., 2013) and UNITE (version 10.0) for fungi (Abarenkov et al., 2025). The sequencing data were rarefied to equal read depths of 16S and ITS to 12,000 and 5000 per sample, respectively, using function *rarefy_even_depth* from the "phyloseq" package (McMurdie and Holmes, 2013). Most of the samples collected at 30–50 cm depth in Sweden did not pass the quality trimming and were excluded from the main analysis.

### 2.6. Statistical analyses and data visualization

All statistical analyses of physicochemical data and sequencing data were carried out in RStudio (R version 4.2.0). Principal Component Analysis (PCA) was used to establish the effect of P fertilization rates, site, and depth on soil physicochemical variables. Treatment effects on physicochemical properties were assessed using the non-parametric Kruskal-Wallis test after confirming non-normal distribution with Shapiro-Wilk test and Q-Q-plots.

ASV richness and Shannon diversity were calculated with *estimate_richness* function from the "phyloseq" package. Then, logarithmic response ratio (LRR) analysis was performed using the "SingleCaseES" package (Pustejovsky et al., 2023) to estimate the effect of P fertilization on microbial diversity across sites and depths. Spearman's rank correlation test was used to assess the relationship between microbial diversity and soil physicochemical properties across different depths.

Permutational Multivariate Analysis of Variance (PERMANOVA) and Analysis of Similarity (ANOSIM) were performed using the *adonis2* and *anosim* functions, respectively, of the "vegan" R package (Oksanen et al., 2018) to test variations in soil microbiome structure, associated with P fertilization, land use, site, soil depth, and physicochemical properties. Dissimilarities among microbial communities were assessed with Bray-Curtis distances.

The relative abundances of prokaryotic and fungal taxa across the countries and P fertilization rates were visualized using "microViz" (Barnett et al., 2021), "fantaxtic" (Teunisse, 2022), and "speedyseq" (McLaren, 2020) packages. Kruskal-Wallis test followed by False Discovery Rate (FDR) adjustment to assess the effect of P fertilization on the relative abundance of both prokaryotic and fungal taxa in all countries at all soil depths. Significant differences between P rates ("Low", "Medium", "High") were found using Mann-Whitney *U* test (Wilcoxon sum rank test in R, paired = FALSE). Function *phyloseq_otu_occurrence* from "metagMisc" package (Mikryukov, 2024) was used to calculate Frequency of Occurrence (FOO) of prokaryotic and fungal genera.

All the above tests were performed on a pooled data set, as well as separately for each country and soil depth. Plots were generated using "ggplot2" (Wickham, 2016), "ggrepel" (Slowikowski, 2024), and "ggfortify"(Horikoshi et al., 2024). Preliminary data analysis defined country of origin, but not sampling site, as the strongest grouping factor for soil physicochemical properties and microbiomes. Moreover, no differences in soil or microbial parameters were observed between sites within countries. Considering these preliminary results, our main analysis combined sites within Ireland and Sweden to increase the sample size (Table S1). The amplicon data are available in the NCBI SRA database (PRJNA1337174). Metadata and R scripts are available on GitHub (https://github.com/k-bogdanov/iconica-international-2025).

## 3. Results

### 3.1. Long-term P fertilization does not significantly alter soil physicochemical properties

A principal component analysis of the physicochemical data showed no clustering of samples by P fertilization rate (Fig. 1), with no individual factor strongly correlated with PC1 or PC2 (Table S3). Most soil

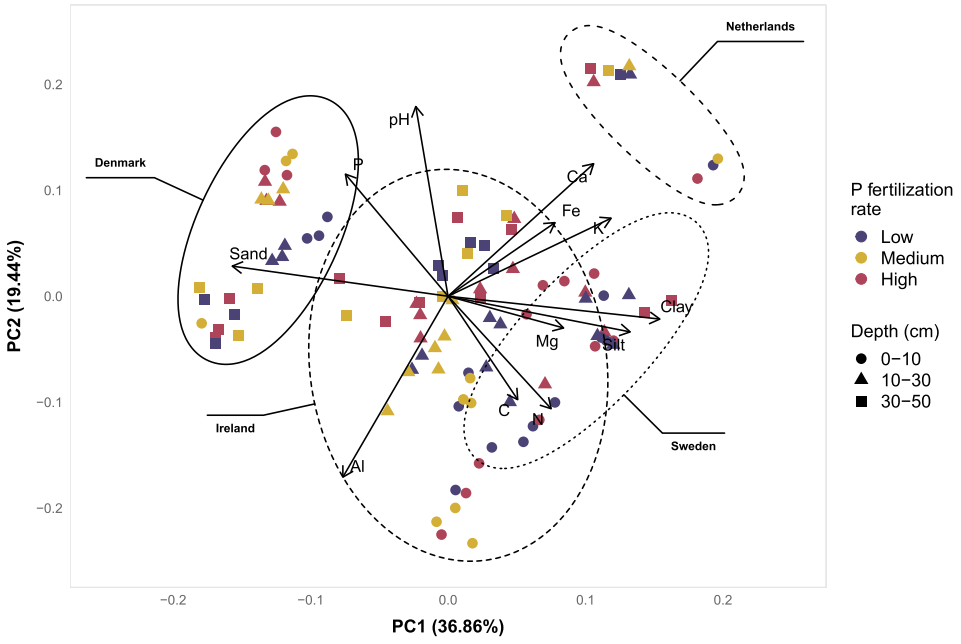


**Fig. 1.** Changes in soil physicochemical properties across the studied countries, soil depths, and P fertilization rates. The plot represents principal component analysis (PCA). Clay, Silt, Sand – content of the fractions (%), C – SOC (%), N – TN (%), P, Al, Ca, Fe, K, Mg – availability of nutrients measured by Mehlich 3 method (mg $kg^{-1}$).

physicochemical parameters varied significantly by country ($p < 0.001$), with the exception of SOC. Median SOC and TN contents declined significantly with depth ($p < 0.001$), decreasing from 2.23% and 0.22% at 0–10 cm to 0.61% and 0.07% at 30–50 cm, respectively. These depth-related differences were more pronounced in grasslands than in arable soils (Fig. S3). No consistent effects of P fertilization on physicochemical properties were detected (Tables S4-S6). When analysed by country and depth, Kruskal-Wallis tests indicated significant positive effects of P application on P availability at 10–30 cm depths in Ireland (median increased from 2.9 to 32 mg $kg^{-1}$, $p = 0.006$) and Denmark (from 68.6 to 166.9 mg $kg^{-1}$, $p = 0.027$) (Tables S1, S7).

### 3.2. *Microbial diversity correlated to land use type rather than P fertilization rate*

Prokaryotic communities exhibited greater ASV richness and Shannon diversity than fungal communities across all countries ($p < 0.05$). In total, 1286 unique prokaryotic ASVs spanning 55 phyla and 992 fungal ASVs spanning 17 phyla were detected across sampled soils (Table 1).

Apart from minor fluctuations, neither prokaryotic nor fungal ASV richness nor Shannon indexes were significantly influenced by P fertilization across countries, land uses, and depths (Fig. 2). In contrast, land use strongly structured microbial diversity. At 0–10 cm depth, median prokaryotic richness was significantly lower in grasslands (701) than in

**Table 1**
The observed abundance of prokaryotic and fungal taxa across land uses, countries, and soil depths.

| Community | Land use | Country | Depth (cm) | Phylum | Class | Order | Family | Genus | Total ASVs |
|---|---|---|---|---|---|---|---|---|---|
| Prokaryotes | Grassland | Ireland | 0–10 | 41 | 111 | 231 | 339 | 557 | 643 |
| | | | 10–30 | 41 | 111 | 237 | 340 | 566 | 656 |
| | | | 30–50 | 44 | 116 | 249 | 354 | 590 | 665 |
| | Grassland | Netherlands | 0–10 | 34 | 91 | 182 | 252 | 400 | 440 |
| | | | 10–30 | 38 | 92 | 191 | 258 | 382 | 412 |
| | | | 30–50 | 43 | 93 | 191 | 259 | 377 | 406 |
| | Arable | Denmark | 0–10 | 44 | 105 | 228 | 334 | 574 | 642 |
| | | | 10–30 | 43 | 107 | 237 | 337 | 553 | 599 |
| | | | 30–50 | 45 | 111 | 236 | 335 | 568 | 638 |
| | Arable | Sweden | 0–10 | 37 | 101 | 200 | 292 | 512 | 559 |
| | | | 10–30 | 36 | 101 | 216 | 320 | 540 | 598 |
| | | | Total unique taxa | 55 | 151 | 362 | 545 | 1039 | 1286 |
| Fungi | Grassland | Ireland | 0–10 | 14 | 41 | 91 | 185 | 309 | 397 |
| | | | 10–30 | 13 | 40 | 93 | 191 | 295 | 373 |
| | | | 30–50 | 12 | 36 | 83 | 167 | 259 | 323 |
| | Grassland | Netherlands | 0–10 | 14 | 30 | 65 | 119 | 178 | 214 |
| | | | 10–30 | 10 | 24 | 44 | 77 | 109 | 128 |
| | | | 30–50 | 10 | 27 | 48 | 89 | 123 | 139 |
| | Arable | Denmark | 0–10 | 12 | 33 | 84 | 177 | 277 | 364 |
| | | | 10–30 | 12 | 36 | 87 | 172 | 273 | 337 |
| | | | 30–50 | 13 | 35 | 88 | 181 | 278 | 349 |
| | Arable | Sweden | 0–10 | 11 | 32 | 76 | 160 | 234 | 294 |
| | | | 10–30 | 11 | 34 | 81 | 162 | 240 | 295 |
| | | | Total unique taxa | 17 | 60 | 151 | 353 | 684 | 992 |

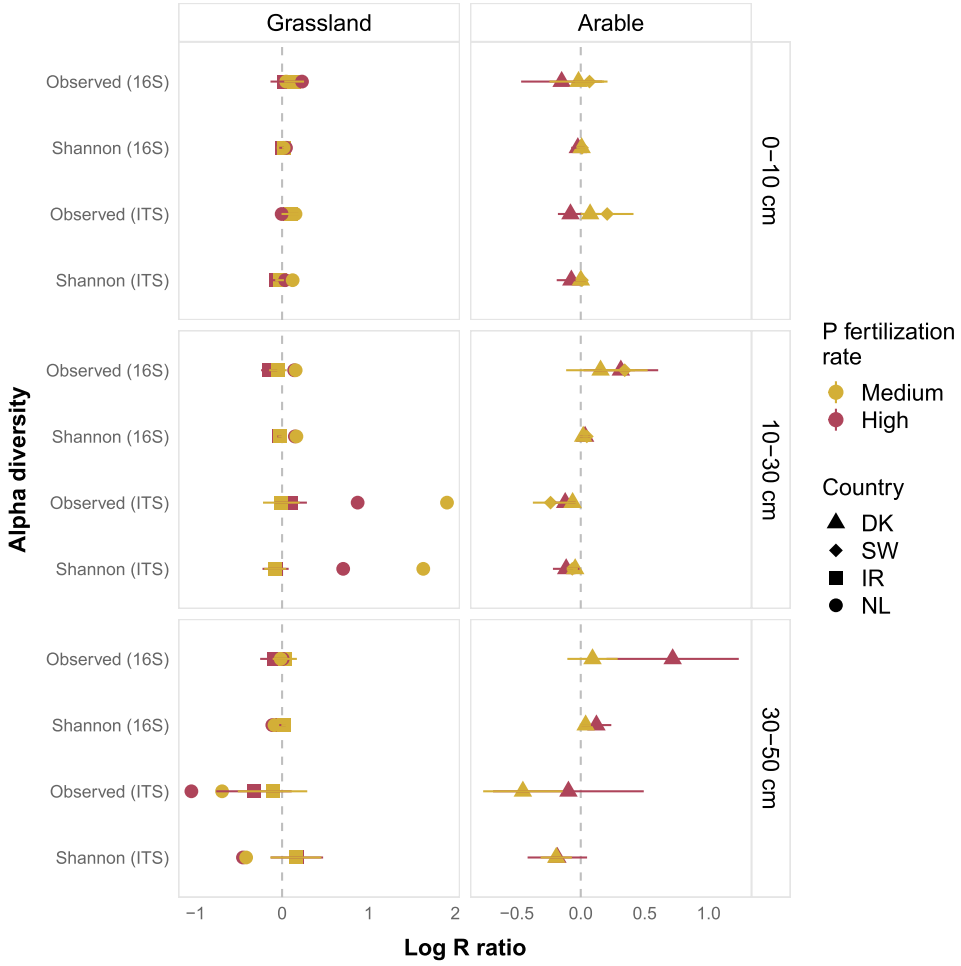


**Fig. 2.** Logarithmic response ratios of alpha diversity (observed ASV richness and Shannon index) under P fertilization, split by depth and land use across four countries, Denmark (DK), Sweden (SW), Ireland (IR), and Netherlands (NL). Error bars represent standard error of mean. Values above 0 show positive response to P fertilization, while values below 0 show a decrease in alpha diversity. "Low" P rate is shown by the dashed line.

arable soils (1001; $p < 0.001$; Fig. S4A). Similarly, the prokaryotic Shannon index was strongly affected by land use across all depths ($p < 0.001$; Fig. S4B). Fungal diversity also varied with land use, being approximately twice as high in arable soils compared to grasslands at 10–30 cm depth ($p < 0.001$; Fig. S4C, D).

### 3.3. *Prokaryotic communities are more resistant to P application than fungi, with effects depending on location and depth*

According to the PERMANOVA results (Fig. 3; Table S8), the community compositions of both prokaryotes and fungi were primarily structured by country of origin (39.1% and 37.2% of variation explained, respectively; $p < 0.001$), followed by land use (17.5%, 19.6%) and soil depth (8.9%, 4.2%). Both prokaryotes and fungi demonstrated strong dependence on SOC and TN contents across countries (Fig. S5-S6). However, given the significant impact of depth on SOC and TN (Tables S4, S6), their effects on microbial communities cannot be decorrelated.

In contrast, long-term P fertilization had a weak but significant effect on fungi (adonis $p = 0.042$, $R^2 = 0.029$), especially in Ireland (adonis $p = 0.011$, $R^2 = 0.068$), with no detectable effect on prokaryotes (Fig. 3). Trends for ANOSIM were consistent with those observed in PERMANOVA (Table S8). When examined by country and depth, PERMANOVA revealed significant ($p < 0.05$) context-specific effects of soil physico-chemical properties on both microbial groups (Table S9).

Prokaryotic communities remained stable under long-term P fertilization across all depths and countries (Fig. S7; Table S9). In Ireland, grassland prokaryotic composition was primarily shaped by soil pH at 0–10 cm (adonis $p < 0.001$, $R^2 = 0.299$) and 10–30 cm (adonis $p < 0.001$, $R^2 = 0.160$), and by Al availability at 30–50 cm (adonis $p = 0.003$, $R^2 = 0.122$). In Sweden, pH in arable topsoil explained 23.7% of variation (adonis $p = 0.014$), while no major drivers were identified in Denmark or the Netherlands.

Fungal communities, in contrast, were slightly more responsive to P inputs. In Ireland, P application significantly influenced fungi at 0–10 cm (adonis $p = 0.002$, $R^2 = 0.220$), though not at other depths (Fig. S8; Table S9). In the same soils, fungi also responded to TP content (adonis $p = 0.002$, $R^2 = 0.183$), TN/TP ratio (adonis $p = 0.009$, $R^2 = 0.144$), and SOC/TP ratio (adonis $p = 0.011$, $R^2 = 0.115$). In deeper soil depths, fungal communities in Ireland were mainly associated with SOC at 10–30 cm (adonis $p = 0.014$, $R^2 = 0.124$) and silt content at 30–50 cm (adonis $p < 0.001$, $R^2 = 0.128$). In Sweden, sand content was the only significant driver of fungi at 0–10 cm (adonis $p = 0.020$, $R^2 = 0.219$). In Denmark, no drivers were identified at 0–10 cm depth. SOC content was the strongest driver at 30–50 cm depth (adonis $p = 0.005$, $R^2 = 0.210$), while SOC/TP ratio was consistently affecting fungi at 10–30 (adonis $p = 0.025$, $R^2 = 0.185$) and 30–50 cm (adonis $p = 0.004$, $R^2 = 0.186$) depths. No major predictors were detected in the Netherlands, likely due to the small sample size.

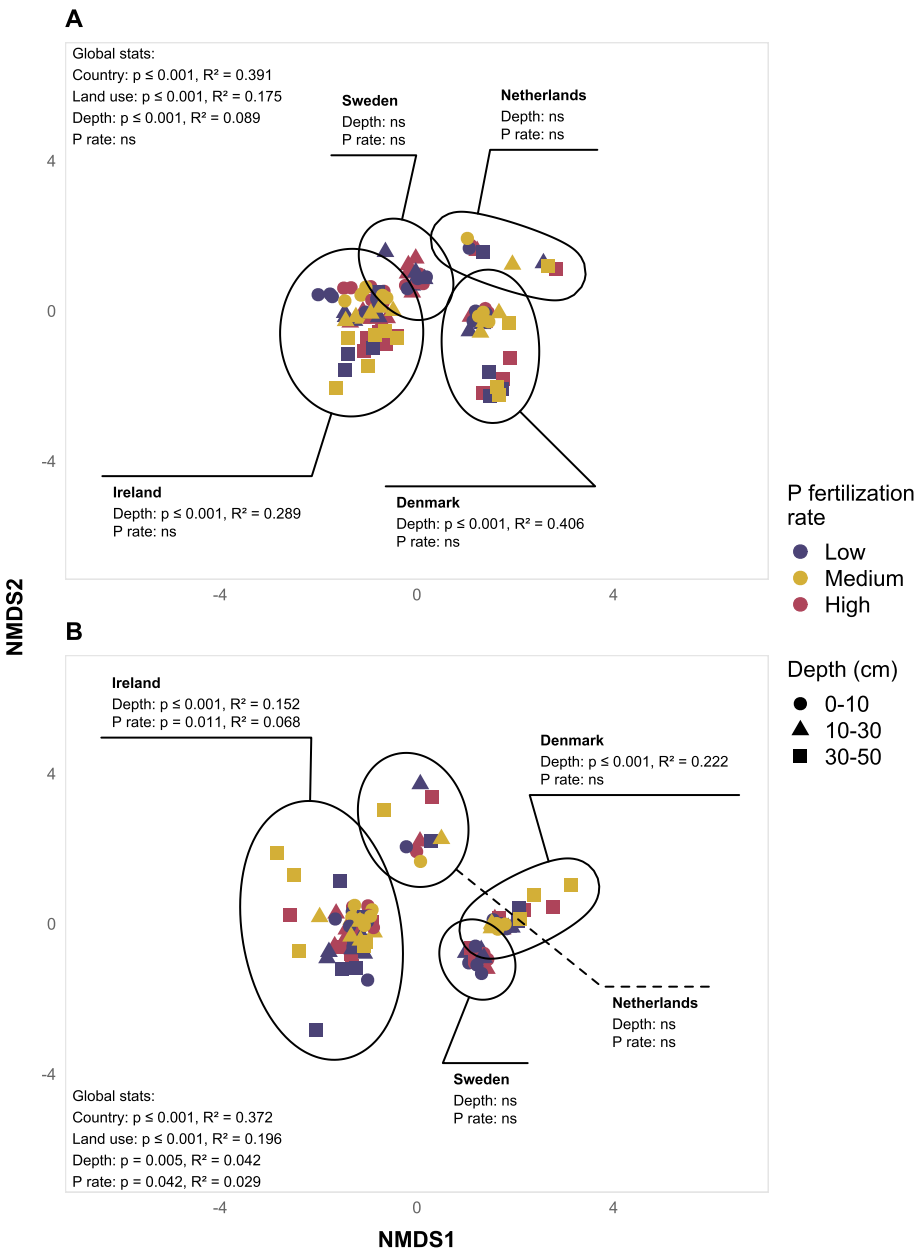


**Fig. 3.** Nonmetric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity showing differences between prokaryotic (A) and fungal (B) communities across the countries (Ireland, Netherlands – grasslands, Denmark, Sweden – arable sites). P and $R^2$ values refer to PERMANOVA test results.

### *3.4. Modest effects of P fertilization on the relative abundance of microbial ASVs*

Despite the observed shifts in community composition, both prokaryotic and fungal communities remained largely consistent across countries, depths, and P treatments at phylum level (Fig. S9). More than 90% of the total prokaryotic abundance was covered by ten dominant phyla: *Pseudomonadota, Acidobacteriota, Actinomycetota, Chloroflexota, Bacillota, Verrucomicrobiota, Methylomirabilota, Planctomycetota*, and *Gemmatimonadota* (Table S10). Although the relative abundance of these phyla was significantly affected by P fertilization across sites and depths ($p < 0.05$), median shifts were small (<1%; Fig. 4).

At the ASV level, Kruskal-Wallis tests identified 32 bacterial ASVs and 670 unidentified bacterial ASVs whose abundance was influenced by P treatment ($p < 0.05$; Table S11). However, changes were generally modest. For example, the abundance of ASVs affiliated with *Arthrobacter alpinus* increased by 1.5% at 30–50 cm in Denmark under a medium P fertilization rate ($p = 0.003$), whereas *Pseudomonas frederiksbergensis* decreased by 2.8% under medium P at the same depth in Ireland ($p = 0.024$). For other bacterial ASVs, the shift did not exceed 1%.

Fungal communities were dominated by *Ascomycota, Mortierellomycota*, and *Basidiomycota*, together representing up to 99% of the total abundance (Table S12). Phosphorus fertilization significantly affected *Ascomycota, Basidiomycota*, and one unidentified phylum across countries ($p < 0.05$), though median shifts remained <1% (Fig. 5). At the ASV level, however, stronger responses emerged. A total of 66 identified fungal ASV and 154 unidentified ASVs were significantly influenced by P fertilization (Table S13). In Ireland, *Trichoderma stromaticum* increased by 4.1% and 3.9% at 0–10 cm under high and medium P fertilization rates, respectively ($p = 0.002$–$0.003$). In Denmark, *Metarhizium robertsii* increased by 2.4–2.8% at 10–30 cm ($p < 0.001$), while *Truncatella angustata* increased by 1.1–2.2% across all depths. Other ASVs showing consistent positive responses (>1% shift, $p < 0.05$) included *Pseudeurotium hygrophilum* (1.7–2.1%), *Keithomyces carneus* (2%), *Exophiala*

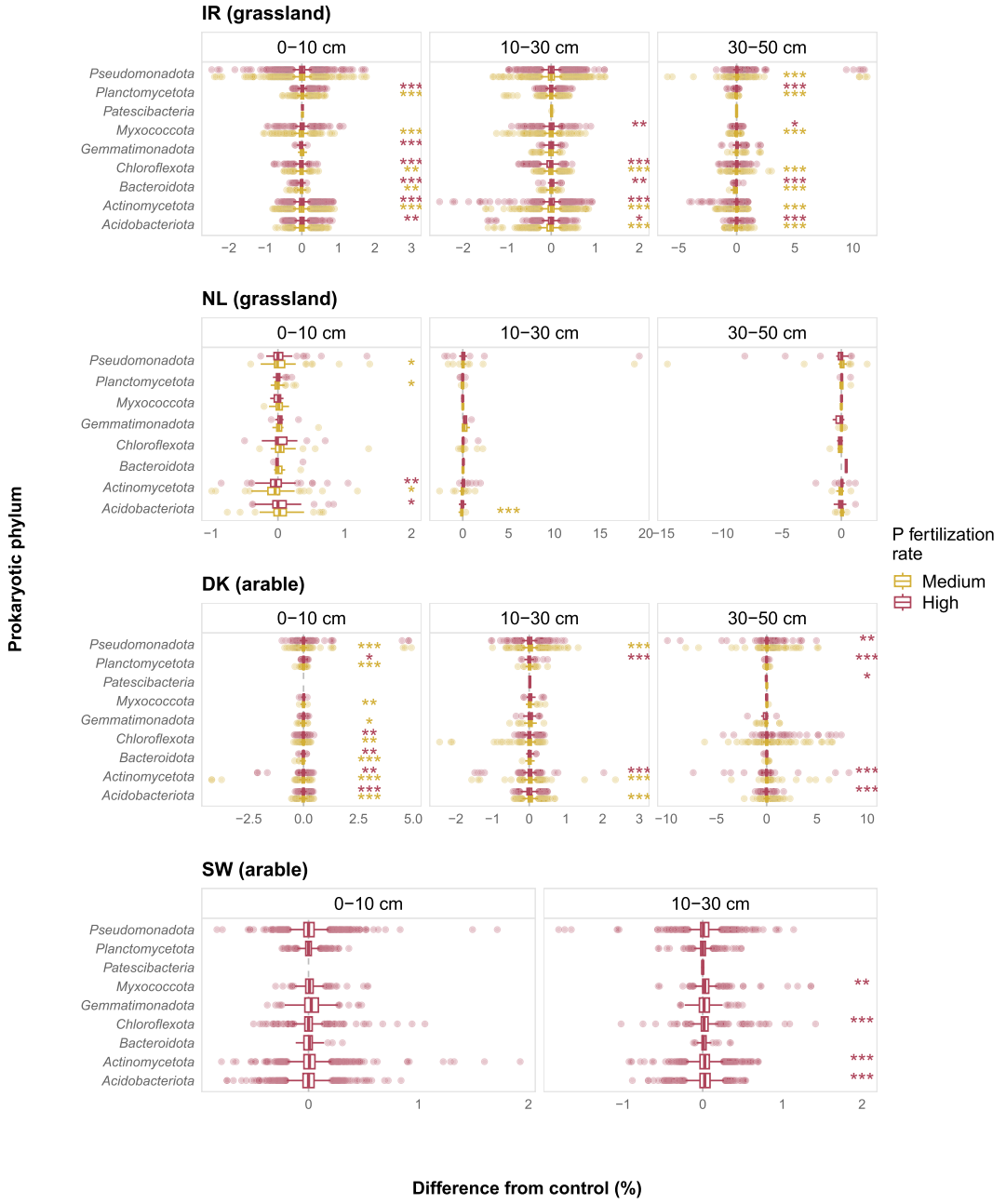


**Fig. 4.** Differences in the relative abundance of detected prokaryotic phyla between "Low" (control), "Medium", and "High" P fertilization rates. The plots are faceted by soil depth and split by country (DK – Denmark, SW – Sweden, IR – Ireland, NL – Netherlands). Boxplots show medians and quartile values for each phylum. Only significantly affected phyla in at least one site are shown. Significance between P rates is marked as follows: $0.05 < p < 0.01$ (*), $0.01 < p < 0.001$ (**), $p < 0.001$ (***).

*salmonis* (1.1–1.8%), *Pyrenochaetopsis decipiens* (1.2–1.3%), and *Fusicolla ossicula* (1.2–1.3%). Conversely, P application reduced *Trichoderma koningiopsis* by 4.2% at 10–30 cm in Sweden ($p = 0.003$) and *Trichoderma multisporum* by 1.5% at 10–30 cm in Denmark under high P input ($p < 0.001$). ASVs assigned to *Exophiala equina* and *Solicoccozyma terricola* exhibited country- and depth-specific responses to fertilization.

Overall, these results indicate that while individual fungal and prokaryotic (bacterial but not archaeal) taxa show measurable shifts in response to P inputs, the magnitude of change remains marginal and does not substantially alter community-level structure.

### 3.5. Frequency of occurrence of fungal genera decreased after P application

No effects of P fertilization were detected on the FOO of prokaryotic taxa. However, two fungal genera, *Clavaria* and *Archaeorhizomyces*, exhibited significant declines in FOO at 0–10 cm depth in Ireland ($p < 0.05$; Fig. S10). In control soils, *Archaeorhizomyces* occurred in 2.5% of samples and comprised 12 unidentified ASVs, but under medium and high P fertilization rates, its FOO declined to 0.3%, and the number of unique ASVs dropped to 2. Similarly, the number of ASVs assigned to *Clavaria* decreased from 13 to 2 under P application, with a corresponding decline in FOO from 3.2% to 0.3% (Table S14).

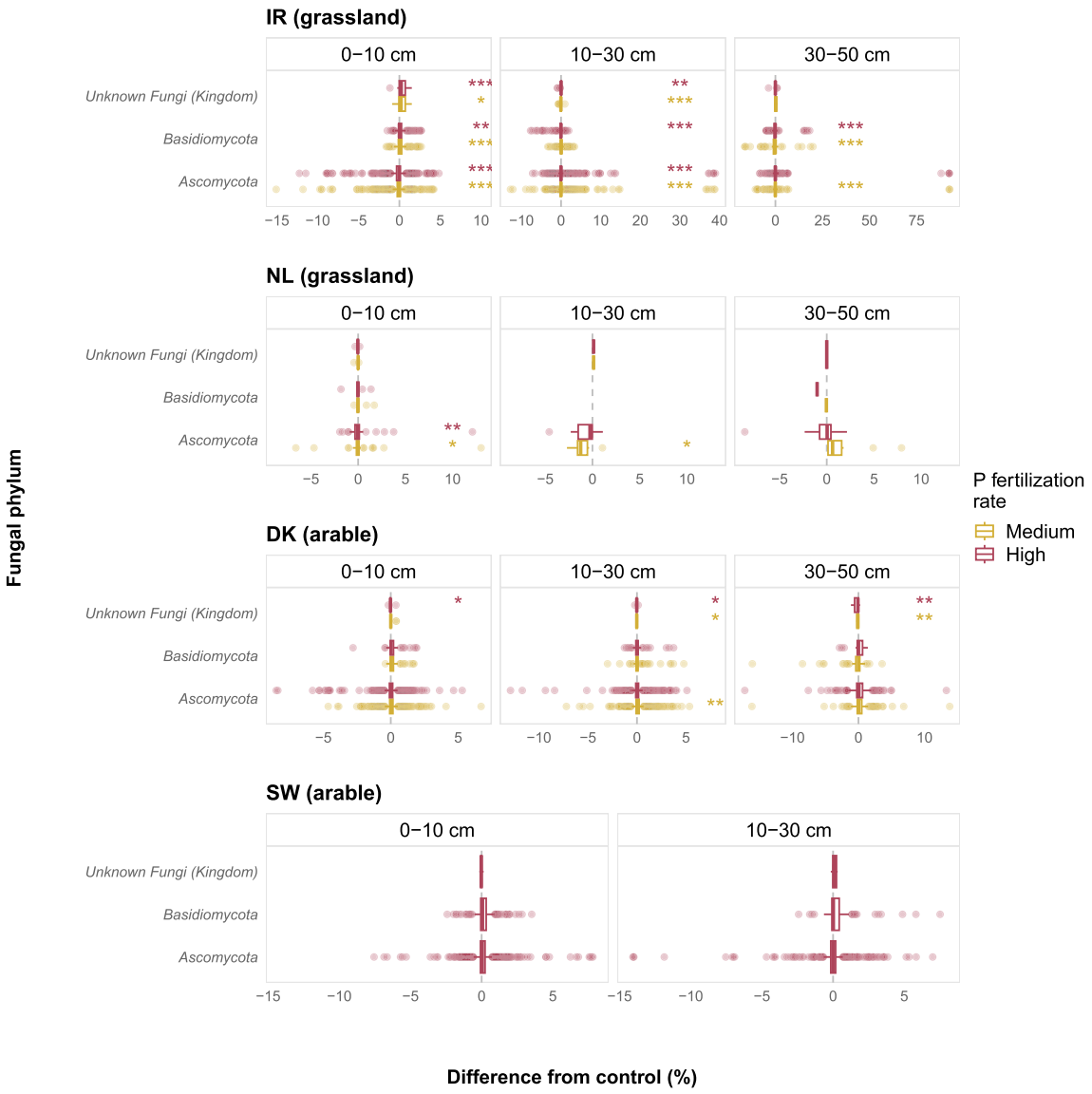


**Fig. 5.** Differences in the relative abundance of detected fungal phyla between "Low" (control), "Medium", and "High" P fertilization rates. The plots are faceted by soil depth and split by country (DK – Denmark, SW – Sweden, IR – Ireland, NL – Netherlands). Boxplots show medians and quartile values for each phylum. Only significantly affected phyla in at least one site are shown. Significance between P rates is marked as follows: $0.05 < p < 0.01$ (*), $0.01 < p < 0.001$ (**), $p < 0.001$ (***).

## 4. Discussion

We evaluated the impact of long-term P fertilization on microbial community composition across multiple countries, land use types, and soil depths. Data from multiple LTEs allowed us to detect a consistent relationship between soil microbial communities and P fertilization among different locations and land uses. We were able to disentangle the effect of P on microorganisms from other strong drivers such as geography and land management. Overall, we found limited and context-specific responses of soil microbial communities to P inputs. Prokaryotic communities were largely unaffected, while fungi showed modest responses at 0–10 cm depth in Irish grassland soils. By combining data from several LTEs sampled at three depths across four European countries, our study highlights that the effects of land use, depth, and country-specific pedoclimatic conditions on microbiomes are far greater than those of long-term P fertilization. This suggests that microbial communities respond primarily to broader edaphic and management drivers, with P inputs playing a minor role.

### *4.1. Long-term P fertilization does not alter microbial communities likely due to lack of changes in soil properties*

Previous research in these LTEs reported no significant changes in C content and plant biomass yields after decades of P fertilization (Bhople et al., 2025). Despite the fact that plant available soil P increased under higher P fertilization rates, we found no major differences in soil properties (pH, nutrient availability, C content), microbial alpha diversity, or community structure (beta diversity) between low, medium, and high P rates. This leads to rejection of our first hypothesis that soil microbial communities change with increasing P rate and that this effect is consistent across countries and land management.

Soil physicochemical properties such as pH, texture, and nutrient availability are known to shape the composition of microbial communities (Labouyrie et al., 2023; Huusko et al., 2024; Panico et al., 2025). In the current study, country of origin and land use, but not P fertilization, explained significant variation in these properties and in microbial communities. For example, pH varied more by country than by P rate, suggesting that fertilization did not alter the chemical environment

in ways that typically influence microbial communities. Furthermore, N and P availability was primarily governed by location but not P fertilization. Considering that N and P are vital for soil microbial communities (Leff et al., 2015; Francioli et al., 2016), this can explain the observed lack of effect of P rate. In addition, apart from N and P, country of origin significantly influenced concentration of other nutrients (Ca, Mg, Fe, Al, K) which also highly impact microbial communities and activity (Jabborova et al., 2021; Zhang et al., 2025). Together, it suggests that the weak microbial response to P fertilization is because of insignificant changes in soil physicochemical properties (Dincă et al., 2022). While P fertilization modestly increased P availability at 10–30 cm in Denmark and Ireland, no associated changes in microbial communities were observed. This suggests that applied P doses may remain below the threshold required to alter soil properties and microbiomes (Moyles et al., 2021). Moreover, legacy P pools sorbed to minerals or bound in organic matter may buffer the impact of new inputs (Wakelin et al., 2012; Doydora et al., 2020; Cerven et al., 2021; Ducousso-Détrez et al., 2024). Microbial stoichiometric homeostasis, whereby microorganisms maintain stable biomass C:N:P ratios under nutrient fluctuations (Allen and Gillooly, 2009; Hall et al., 2011), further explains their resilience. Together, these findings highlight the importance of linking microbial dynamics in LTEs to soil physicochemical properties, particularly nutrient availability.

The studied LTEs differed in their historical P application methods. For example, P was surface-broadcast in grasslands but incorporated by tillage in arable systems. Such differences may have influenced the vertical distribution and local availability of P in the soil profile. Nevertheless, the microbial communities showed only weak and context-specific responses across all countries and depths. This suggests that the initial method of P input becomes less important than the legacy P pool and the influence of soil C, N, and location.

Furthermore, our study integrates data from multiple independently LTEs, each with distinct fertilization rates, durations, and local soil conditions. Although P application levels differed between locations, this heterogeneity allowed us to test whether microbial responses follow a general trend with relative P increases, rather than absolute thresholds. This approach resembles a cross-site meta-analysis and strengthens our conclusions because consistent patterns across contrasting experimental designs indicate robust ecological responses.

### 4.2. The role of land use, depth, and nutrient availability in microbial response to P input

When analysed by depth and country, modest responses to P fertilization were detected for fungi, but not prokaryotes, and this was restricted to the top 0–10 cm in Irish grassland soils. This partly supports our second hypothesis that microbial response to P fertilization would be strongest in surface soils. Tillage is often thought to reduce microbial alpha diversity and homogenize the microbiome, making them less responsive to nutrient inputs (Le Guillou et al., 2019; Romdhane et al., 2022; Khan et al., 2023). However, we observed higher microbial richness and Shannon diversity, arable sites (i.e., Sweden and Denmark) than in grasslands (i.e., Ireland and the Netherlands). Similar findings from other studies have shown that disturbances such as ploughing and crop rotation can create heterogeneous microhabitats and enhance microbial diversity (Kaiser et al., 2016; Szoboszlay et al., 2017; He et al., 2020; Pingel et al., 2023). Arable soil management also promotes plant residue accumulation, which may further support microbial alpha diversity (Degrune et al., 2017). In contrast, microbial activity in grasslands is more frequently limited by P availability (Leff et al., 2015), so P fertilization can indirectly influence microbial composition via plant C allocation (Qi et al., 2022). Legacy P pools in arable soils may buffer microbial responses to fertilization, reducing the relative impact of additional P inputs (Ogilvie et al., 2008; Rowe et al., 2016).

Interestingly, despite lower alpha diversity, the Irish grassland soils showed stronger microbial responses to P inputs than arable LTEs. Higher C and N availability in grassland topsoils likely interacted with P additions to drive these responses. This suggests that C and N availability plays a critical role in mediating microbial responsiveness to P fertilization (Heuck et al., 2015; Fanin et al., 2015). In our study, depth-dependent declines in C and N, but not P, further explained stronger microbial shifts in topsoils relative to subsoils. This is consistent with other studies showing that agricultural practices and nutrient dynamics exert stronger effects on microbial communities in surface horizons than in deeper layers (Eilers et al., 2012; Spohn and Chodak, 2015; Philipp et al., 2025). Moreover, plant species composition, including perennial ryegrass in the grasslands and cereals or spring barley in the arable systems, could have contributed to the distinct microbial communities observed between land uses and countries. Differences in root architecture, exudation patterns, and residue quality likely influenced rhizosphere microbiome assembly and nutrient dynamics (Burrill et al., 2025).

Finally, the climatic context of each site likely influenced P dynamics and microbial activity (MAP ranged from 584 to 1000 mm). Lower precipitation and cooler temperatures, such as in Sweden, can reduce soil moisture and P diffusion rates, potentially constraining microbial access to soluble P compared to warmer, wetter sites in Ireland (Porder and Chadwick, 2009; Gianniny et al., 2024). These climatic differences can also explain why microbial responses to P fertilization were slightly stronger in Ireland, even under long-term management.

### 4.3. The impact of P fertilization on soil fungi and their ecology

Although community-level changes in fungi were limited, ASV-level responses were more pronounced. In line with our third hypothesis, fungi were more sensitive to long-term P fertilization than prokaryotes. This aligns with previous reports attributing fungal sensitivity to their direct role in P acquisition via plant symbioses, enzyme-mediated organic-P cycling, and hyphal foraging (Zeilinger et al., 2015; Cassman et al., 2016). Importantly, ASVs do not precisely correspond to biological species, thus, ASV-level responses observed in our study can be interpreted as shifts in high-resolution sequence-based taxonomic units, rather than definitive species-level dynamics.

We detected P-mediated shifts in 66 identified fungal ASVs and 154 unidentified ASVs, although median shift rarely exceeded 2%. We detected marginal increases (> 2% change) in abundance for ASVs assigned to *Trichoderma stromaticum* (described by Samuels et al., 2000), *Metarhizium robertsii* (Bischoff et al., 2009), *Truncatella angustata* (Arzanlou et al., 2013), *Pseudeurotium hygrophilum* (Minnis and Lindner, 2013), and *Keithomyces carneus* (Mongkolsamrit et al., 2020). In contrast, we observed reductions in the abundance of *Exophiala equina* (Torres-Garcia et al., 2023), *Solicoccozyma terricola* (Yurkov, 2018), and *Trichoderma koningiopsis* (Amerio et al., 2025). The frequency of occurrence of fungal genera *Archaeorhizomyces* (Rosling et al., 2011) and *Clavaria* (Birkebak et al., 2013) also decreased under P fertilization in the Irish topsoils. Furthermore, the observed reduction in the abundance of the mutualistic fungus, *Trichoderma koningiopsis,* and the increasing abundance of the potential pathogenic fungus, *Truncatella angustata,* is consistent with the theory of high P availability favouring competitive or pathogenic fungi over mutualistic partners (Lekberg et al., 2021). Some taxa promoted by increased P, such as *Metarhizium robertsii* and *Keithomyces carneus*, are entomopathogens with potential biocontrol roles. While there was no consistent enrichment of entomopathogens, they have been shown to influence plant P uptake and root development (Oliveira et al., 2025).

Most of the P-responsive fungi were saprotrophs or endophytes, suggesting that observed shifts may reflect plant-mediated changes in C and N allocation under elevated P. High P availability can alter root exudation patterns, indirectly reshaping fungal communities (Margalef et al., 2017; Qi et al., 2022). Declines in the occurrence of certain fungal genera may also reflect competitive exclusion by fast-growing taxa favoured under nutrient-enriched conditions (Egerton-Warburton et al.,

2007).

Finally, the lack of strong microbial responses to increasing P indicates that long-term soil P accumulation, resulting from consistent low fertilizer inputs, provides a sufficient legacy pool to maintain microbial stoichiometric homeostasis and nutrient balance. This suggests that farmers can maintain soil fertility and microbial health without resorting to high P applications. Nevertheless, to support optimal crop growth, it remains important to supply the right amount of plant-available P at the appropriate time during the growing season (Ros et al., 2020). By combining sustained low P fertilization with timely application, farmers not only avoid unnecessary fertilizer costs but also reduce the risk of P runoff, supporting compliance with water quality regulations such as the European Water Framework Directive (Jordan et al., 2012). In this context, additional high P applications are neither required nor harmful, but they offer no clear benefit for microbial stability or nutrient management.

## 5. Conclusion

LTEs, receiving P fertilizer, are a unique resource for examining the effect of fertilization on soil microbiomes. The impact of long-term P fertilization on soil microbiomes was studied across multiple LTEs, with varying land use and depth. We found no significant effects on prokaryotic communities, while fungi exhibited modest but measurable shifts in abundance and frequency of occurrence, particularly in surface soils of Irish grasslands. The absence of strong microbial responses to increasing P indicates that the long-term soil P legacy, built up through consistent low fertilizer inputs, is sufficient to maintain microbial stoichiometric homeostasis. Consequently, additional high P applications are neither detrimental nor required for sustaining microbial equilibrium.

Our findings show that soil depth and C and N availability were consistently stronger determinants of microbial community composition than P fertilization across all studied LTEs. This highlights the importance of applying a multi-site approach in experiments on long-term P fertilization effects on soil microbiomes. The fact that most of the affected fungal taxa were plant-associated saprotrophs, suggests that the observed microbiome changes arise through plant-mediated processes rather than direct microbial responses to P. However, this study relied on 16S rRNA and ITS amplicon sequencing, thus, functional mechanisms remain unresolved. Future work should integrate functional gene and pathway analyses to link long-term P fertilization with microbial metabolism and plant-microbe interactions. Furthermore, the uneven sample distribution across countries, particularly the lower number of replicates from the Netherlands, is a limitation inherent to working with LTEs not originally designed for coordinated microbial sampling. However, by analyzing data both collectively and by country, we ensured that site-specific trends did not bias the overall conclusions. The consistency of the main finding (limited microbial response to long-term P fertilization) strengthens the reliability of our results. Future multi-site studies would benefit from harmonized sampling designs to further balance statistical power across locations.

## CRediT authorship contribution statement

**Kirill Bogdanov:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Parag Bhople:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Giulia Bondi:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Naoise Nunan:** Writing – review & editing, Project administration, Conceptualization. **Lars Elsgaard:** Writing – review & editing, Project administration, Conceptualization. **Anke M. Herrmann:** Writing – review & editing. **Karl G. Richards:** Writing – review & editing, Conceptualization. **Mart Ros:** Writing – review & editing. **David Wall:** Writing – review & editing. **Fiona Brennan:** Project administration, Conceptualization. **Sergio E. Morales:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Timothy J. Clough:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2026.106877.

## Data availability

R scripts and input files are provided on GitHub: https://github.com/k-bogdanov/iconica-international-2025. The 16S and ITS amplicon sequencing data are available in the NCBI SRA database (accession No PRJNA1337174).

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