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Pedological classification as a key determinant of arable soil microbial communities and effects of cash-crop management

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Abstract. Climate and soil-related variables, along with soil management practices, have been identified as key determinants of soil microbial composition and, consequently, soil ecosystem functioning. While numerous biogeographic studies at local to continental scales have identified several variables such as pH, soil carbon quality and quantity and total precipitation as important predictors of microbial composition and diversity, these observations have not been validated by similar biogeographic research within agricultural systems, limiting our ability to compare microbiomes from cultivated sites. This observational study of topsoil microbial composition in Quebec's cash crop fields is one of the rare biogeographical studies conducted in arable land that investigates a wide range of soil, climate, and farming-related variables. In this study, the taxonomic and predictive carbon-related functional composition of microbial communities was investigated in 80 cultivated mineral topsoils across 38,000 km^2 in Quebec, Canada. Using multivariate statistics, we examined how two climatic variables (precipitation and growing degree-days), 9 soil-related variables (pedological classification, soil texture and structure, pH, carbon and nutrient concentrations), and 6 agricultural management practices (crop diversity indexes, tillage intensities, organic fertilization type and compaction risk) influenced community variation (represented by the robust Aitchison beta diversity). Pedological classification, based on the Canadian System of Soil Classification, emerged as one of the strongest and most consistent predictors of prokaryotic and fungal community structure and of the structure of inferred prokaryotic carbon-cycling functional potential, whereas farming practices showed little relative influence. All six climate- and soil-related variables that significantly explained microbial variance in the biogeographic analyses were also significantly different between pedological soil classifications. We also hypothesized that the strong predictive power of soil classification indicates that it serves as a proxy for additional key variables. Further taxonomic analyses revealed that stratifying samples by pedological groups provided a more nuanced understanding of the specific effects of organic fertilizer type and soil tillage intensity, with distinct taxonomic families responding within each soil classification and some soils showing distinct sensitivities to specific farming practices. This evidence supports integrating soil classification as a foundational framework for assessing microbial responses to farming practices across soil types and for monitoring the soil microbiome at large geographic scales.

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1 Introduction

Interpreting variation in soil microbial community composition across soil environments and agricultural perturbation gradients remains a significant challenge because these patterns emerge from the interplay of numerous pedoclimatic and biological factors, coupled with complex responses and feedback loops (Jansson & Hofmockel, 2020; Philippot et al., 2023). Developing a better understanding of the drivers of soil microbial community composition in such complex systems is crucial because microbial community structure underpins key soil functions and informs ecosystem-based strategies for restoring and conserving ecosystem services (Crowther et al., 2019; Fierer and Walsh, 2023; Fierer, 2017).

Tremendous progress in the study of microbial biogeography has led to identifying the main drivers of soil microbial composition, such as pH (Tedersoo et al., 2020; Griffiths et al., 2011; Lauber et al., 2009; Bahram et al., 2018), carbon–nitrogen ratio (C:N) (Labouyrie et al., 2023; Fierer et al., 2009; Kuramae et al., 2012) and redox status (Husson, 2012; Lipson et al., 2015; Pett-Ridge and Firestone, 2005). Organic carbon content (Griffiths et al., 2011; Waldrop et al., 2017), moisture availability (Griffiths et al., 2011; Frindte et al., 2019), nitrogen and phosphorus availability (Leff et al., 2015; Lang et al., 2020; Cederlund et al., 2014), soil texture and structure (Xia et al., 2020; Hartmann and Six, 2023), and temperature (Frindte et al., 2019) have also been identified as relevant drivers of prokaryotic community structure across natural landscapes (Fierer, 2017). In contrast, fungi have been recognized as more sensitive to land use, plant populations (Tedersoo et al., 2020; Labouyrie et al., 2023) and climate (Labouyrie et al., 2023; Tedersoo et al., 2020; Tedersoo et al., 2014; Vetrovsky et al., 2019; Bahram et al., 2018; Banerjee et al., 2024). Despite these advances, these studies often rely on a limited set of environmental descriptors and rarely consider soil classification systems that integrate long-term pedogenetic processes and the resulting edaphic characteristics (Food and Agriculture Organization of the United Nations et al., 2020).

Comparatively to natural landscapes, little research has been conducted on the biogeography of soil microorganisms in cultivated soils, where crop rotation and farming practices, such as tillage intensity and organic and mineral fertilization, further interact with these factors to shape soil microbial communities. Soil tillage has been hypothesized to alter fungal community composition by breaking hyphal networks, thereby negatively affecting filamentous fungi (Hartmann and Six, 2023). Additionally, tillage alters edaphic properties, further shaping soil microbial composition (Degrune et al., 2017; Young and Ritz, 2000). However, the specific effects of tillage on microbial taxa vary across studies and appear context-dependent (Degrune et al., 2019). Organic fertilization has also been reported to shape a part of microbial communities in the short term by providing nutrient-rich organic substrates to soil microbiota (Semenov et al., 2021) and, in the long term, by modifying soil properties, such as carbon content and C:N. On the other hand, mineral fertilizers supply inorganic nutrients to soil, reducing the dependence of nutrient cyclin on microbial decomposition of organic matter. As a result, they generally induce smaller changes in soil carbon and nitrogen content than organic fertilizers and, thus, exert weaker effects on soil microbial community composition, similar to unfertilized soils (Li et al., 2017).

Growing scientific interest in soil microbiomes mainly rests on the fact that soil microorganisms play central roles in a myriad of soil processes, ensuring many different soil ecosystem services such as crop health and protection, pollutant

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degradation, nutrient cycling and climate regulation (Hartmann and Six, 2023; Iqbal et al., 2025). Because soil microorganisms mediate most soil biogeochemical processes (Falkowski et al., 2008), changes in soil microbial communities can often also indicate functional changes. To this end, an increasing body of research has aimed, beyond describing microbial amplicon sequence variants (ASVs) or taxonomic composition, to link microbial communities to soil ecosystem functioning, particularly functions related to soil carbon and nitrogen cycling (Azevedo et al., 2024; Geisseler et al., 2010; Schuur et al., 2015; Dang et al., 2024). Inferring soil functions from microbial community composition is inherently complex, as multiple biological and methodological caveats weaken the link between microbial taxonomic composition and realized ecosystem processes. Thus, functional inferences based on rRNA amplicon sequencing reflect the potential functional capacity of microbial communities rather than the functions measured under field conditions at the time of sampling (Prosser, 2015). Still, it can be useful as an exploratory approach to generate hypotheses about broad functional shifts in omnipresent functions (Toole et al., 2021), such as broad biogeochemical cycles. Nonetheless, in agricultural soils, it has been demonstrated that while inferring functions from 16S rRNA gene amplicon sequencing systematically underestimates soil functional abundance, it is sensitive to omnipresent functions, with a case study reporting correlations of 0.76 to 0.86 with functional profiles obtained via shotgun sequencing (Toole et al., 2021).

In North America, intensive agriculture, associated with the production of cash crops, mainly corn, wheat, canola and soybean, has been linked to declining soil health (Smith et al., 2024; Bedolla-Rivera et al., 2023; Gasser et al., 2023b). Agricultural intensification has also been linked to significant changes in soil microbial communities, such as a decrease in fungal diversity and the decrease or disappearance of rare fungal groups (Banerjee et al., 2024; Hartmann et al., 2015), and soil biotic health indicators, such as a decrease in a health-microbial index (Xu et al., 2024). Because of the soil microbiome's predominant role in biogeochemical cycles and the production of soil ecosystem services, these changes in soil microbiome under intensive agricultural management have definite repercussions for microbiome functions and soil ecosystem functions (Hartmann and Six, 2023). The most promising practices for restoring and maintaining organic matter in arable soils have been proposed to be soil tillage reduction, the use of organic fertilizers (OFs), residue retention and the use of cover crops and perennials (Liptzin et al., 2022; King and Blesh, 2018). Research shows conflicting evidence on the effects of implementing beneficial management practices on soil health indicators and ecosystem services, depending on specific pedoclimatic contexts (Samson et al., 2019; Sun et al., 2020). As a result, developing agronomic recommendations tailored to specific field conditions that maintain or improve soil health remains a challenge. Only limited research has examined how management practices influence soil health indicators in cold, humid climates (e.g.Lavergne et al., 2025; Mann et al., 2019). Developing broadly applicable recommendations is particularly challenging in regions characterized by high pedoclimatic heterogeneity, such as Quebec (Eastern Canada), where substantial variation in soils and climate can influence agricultural system responses. Moreover, even fewer resources have been allocated to studying microbial responses to these practices, limiting our understanding of the mechanisms underlying changes in soil health and ecosystem services driven by agricultural management across Quebec's varied pedoclimatic environments.

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This study investigated the overall and specific effects of multiple climatic, farming, and pedological variables on the composition of soil microorganisms spanning 38,000 km^2 in the province of Quebec (Canada), a warm-summer humid continental climate region characterized by diverse pedogenetic conditions. While many studies focus either on agricultural practices in small-scale controlled plots or on pedoclimatic conditions at large scales, few have investigated both together. Furthermore, few studies have simultaneously examined how agricultural practices and pedoclimatic conditions interact, and almost none have considered pedological classification in studies of the soil microbiome. This study had two main objectives. First, it sought to determine the relative importance of climatic, farming, and soil-related variables in shaping prokaryotic and fungal ASV composition, as well as the inferred carbon cycling functional potential of prokaryotes in cash crop soils of Quebec. Second, it aimed to investigate the specific effects of soil tillage intensity and OF type on microbial taxonomic families and groups involved in carbon cycling in these soils, while accounting for the confounding influences of the key variables identified in the initial phase of the research.

2 Materials and Methods

2.1 Study area

Data collection was conducted as part of the Quebec 2020 Soil Health Inventory (*Étude sur l'état de santé des sols agricoles du Québec*; QSHI), which is documented in Gasser et al. (2023b). The QSHI surveyed Quebec's agricultural landscape, a temperate, cold, and humid province in eastern Canada. These soils are relatively young, having formed over the last 8,500 to 10,800 years since the last glaciation (Richard and Occhietti, 2005) and cover a wide range of textures and pedological classifications, due in part to the varied topography and deposition modes. Many of these soils have been converted to agriculture within the past 100 to 300 years, mainly from mixed or deciduous forests.

For this inventory, 71 soil series as defined by the Canadian Soil Classification System (CSSC) (Soil Classification Working Group, 1998) were selected, allowing a comprehensive representation of Quebec's diverse pedogeographic farming regions in terms of agricultural land coverage and parent material characteristics. The CSSC is a hierarchical framework for categorizing soils based on their physicochemical properties, reflecting the environmental conditions in which they formed and the pedogenetic processes that have and continue to occur. The order is the highest categorical level, containing 10 different categories, followed by the great group, subgroup, family and, ultimately, the soil series. Soils within a series all have similar colour, texture, structure, consistence, thickness, reaction and composition for each of their horizons (Soil Classification Working Group, 1998).

For each selected soil series, 12 agricultural fields deemed pedologically homogeneous and representative of their respective series, which had not undergone recent levelling and were cultivated with cash crops, pasture, prairie, vegetable crops, or potatoes, were identified as potential study sites. Four of these 12 sites were randomly selected to conduct the QSHI. For each soil series, two non-forested, pedologically intact and ideally uncultivated control sites were also sampled. The QSHI resulted in the sampling of 431 sites, distributed within a 250,000 km² polygon spanning over a 700 km east-west axis and a

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550 km north-south axis. Amongst these sites, 231 were cultivated. Those sites covered Quebec's three geological provinces: the Saint-Laurent platform, a calcareous sedimentary area; the Appalachians, with metamorphic bedrock; and the Canadian Shield, an igneous and metamorphic region dating to the Precambrian era. Across these provinces, soils developed predominantly on marine and fluvial sediments in the Saint-Laurent Platform, glacial and post-glacial lacustrine deposits in the Appalachians' lowlands, and glacial till and morainal materials overlying crystalline bedrock in the Canadian Shield, resulting in a wide range of soil textures from heavy clay to skeletal soils.

Eighty sites out of the original 231 cultivated sites surveyed in the QSHI were selected for the present study, specifically those that had been cultivated with soybean or corn crops at least once during the sampling year or in the preceding four years. Sites without data regarding fertilization and tillage practices were excluded. Sites with potato production in their five-year history were also excluded due to considerable differences in management practices, resulting in disproportionately different microbial compositions, as revealed by preliminary analyses.

Most of the 80 selected sites spanned the Montreal Plain (n = 53), the St. Lawrence Upper Terraces (n = 14) and the St. Lawrence Coastal Plain and Islands (n = 4), all within the St. Lawrence Lowlands. Additional sites encompassed the Appalachians (n = 10), resulting in a total of 32 distinct soil series surveyed (Fig. 1). This spatial distribution reflects agricultural crop patterns observed in Quebec, with more than 60% of soybean and corn surfaces being cultivated in the Montreal Plain in 2021 (Statistics Canada, 2022a, b; Lamontagne and Nolin, 1997). This site selection does exclude the Laurentian pedological province, which hosted around 2% of the soybean production area and 4% of the corn production area in 2021 (Statistics Canada, 2022b, a; Lamontagne and Nolin, 1997).

2.2 Soil sampling and analysis

2.2.1 Soil sampling

Sites were sampled between May and September 2017 and 2018. Ap and B horizons, as defined by the Canadian System of Soil Classification (Soil Classification Working Group, 1998), were characterized through a soil profile (60 to 100 cm width; 40 to 60 cm depth), with the Ap horizon being subdivided into Ap1 and Ap2 when deeper than 17 cm. Ap1 was sampled at a depth of 1 to 10 cm, and Ap2 at 15 to 25 cm when present (see Gasser et al. (2023b) for more details).

Each site was sampled at four sampling points, located at least 80 m apart. First, a visual assessment was performed on the soil profiles dug at each sampling point to evaluate the structural quality of each horizon using the Visual examination of soil structure (VESS) method (Guimarães et al., 2011; Ball et al., 2007). Second, six to eight soil samples were collected within a 5 m radius around every soil profile using a 4 cm-diameter Edelman auger. These samples were combined to create composite bulk soil samples of every horizon. The first centimetre of soil and a few centimetres around the horizon interface were removed and discarded from these bulk samples to exclude the surface litter and contamination from other horizons. All samples were kept cool in the field by storing them in coolers with ice packs and brought back to the laboratory, where they were kept at 4 °C. Bulk soil samples were weighed, air-dried, and sieved to 2 mm within 14 days. The bulk soil was

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subsampled, ground to 100 mesh, and stored at -20 °C pending DNA extraction. In the same year as sampling, crop dry yields were estimated by manual harvests using a 1 m^2 quadrat near each of the four sampling points at crop maturity.

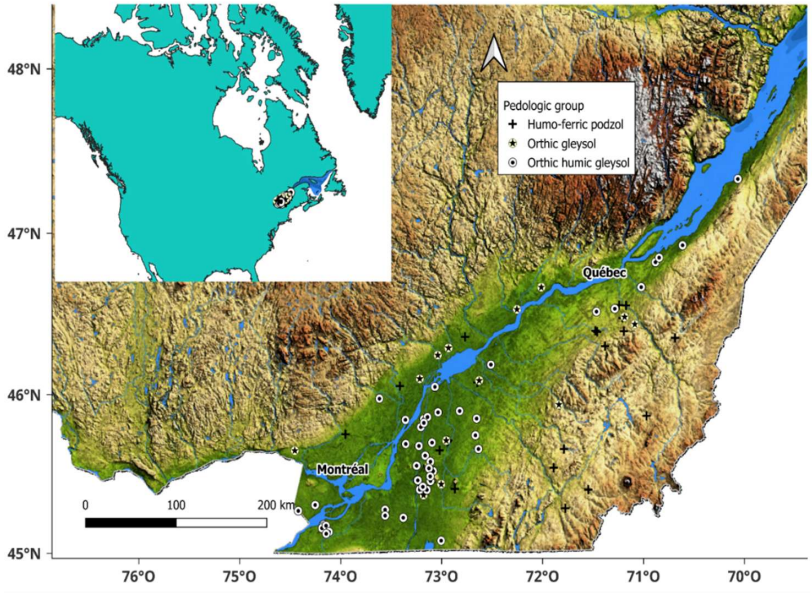


Figure 1: Physiographic context and pedological categorization of the sites included in this study across the Saint-Lawrence lowlands (green area) and the Appalachians (South-East brown area) of southern Quebec. Major cities are indicated for geographic reference. The base map was designed and developed by Quebec's Ministère des Ressources naturelles et des Forêts. For more information on this map, visit https://www.donneesquebec.ca/recherche/dataset/carte-du-relief-a-l-echelle-de-1-2-000-000 (last access: April 1st, 2026).

2.2.2 Pedological and climatic classification

The pedological classification of each site, as defined by the Canadian Soil Classification System (CSSC) (Soil Classification Working Group, 1998), was confirmed during sampling. Soils selected from the QSHI were classified into three categories: the humo-ferric podzol (HF.P) great group (21 sites), the orthic humic gleysol (O.HG) subgroup (46 sites), and the orthic gleysol (O.G) subgroup (13 sites). The great group level was initially chosen for the present study because it was the most detailed classification, yielding groups with at least five sites, ensuring a reasonable balance between taxonomic resolution and the grouping of similar sites. It should however be noted that all sites corresponding to the humic gleysols great group and the gleysols great group also belonged to the same subgroups (O.HG and O.G).

HF.Ps, O.HGs and O.Gs are respectively associated with the podzol group, mollic or humic gleysols, and haplic gleysols in the World Reference Base for Soil Resources (Bedard-Haughn, 2011; Sanborn et al., 2011; Iuss Working Group, 2022). HF.Ps form on sandy, acidic parental material, most commonly under coniferous forest vegetation. Their surface horizon is

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eluviated, while their B horizon is enriched in surface organic matter and in iron and aluminum oxides (Sanborn et al., 2011). They are known for their low fertility and water retention potential, although their fertility can be improved through liming and fertilization (Laverdière et al., 1977). O.HGs and O.Gs, primarily characterized by the visible presence of oxidation-reduction reactions, are often tile-drained in agricultural contexts, making them highly productive for agriculture (Bedard-Haughn, 2011). In contrast to O.Gs, O.HGs have organic matter accumulation as a secondary pedogenetic process, leading to the presence of a surface horizon enriched in organic matter (Ah).

The average annual precipitation (PPT) and average annual growing-degree days (GDD) were determined for each site using Daymet satellite data collected over the past five years (Thornton et al., 2021; Thornton et al., 2022; Thornton et al., 1997). GGDs ranged from 1640°C-days to 2270°C-days, and PPTs ranged from 598 mm to 872 mm at the sites surveyed as part of this research.

2.2.3 Management practices history

Agricultural management data were collected through a written survey completed by each producer, encompassing the sampling year and the four preceding years. The survey captured the use of radial tires and real-time kinematic positioning technologies, the types and models of machinery employed, the dates of mechanical operations, and the use of cover crops (if used) and crop rotation. Data was compiled on the provenance and type of OF and the machinery used for tillage and seeding operations. Survey data were used to calculate annual values for various indicators, which were then averaged over the five-year period. Among these indicators were the soil tillage intensity rating (STIR) and a compaction risk index, as fully described by Gasser et al. (2023a), and a crop diversity index (CDI).

The STIR index was derived from the Revised universal soil loss equation, version 2 (RUSLE2) (Dabney et al., 2012), and field data collected by Wall et al. (2002) to characterize the extent of disturbance caused by machinery, as described in Appendix A. The compaction risk index quantified the intensity of factors such as the weight of the largest tractor used, the use of radial tires across all machinery, the implementation of reserved circulation roads, the use of real-time kinematic positioning GPS, and the total number of machinery passes. It is further described in Appendix A. CDI was calculated using the total number of different crop and cover crop types over the five years. Silage corn, sweet corn, and grain corn were all considered as corn crops. Prairies were considered to consist of four to six different crops. Dominant grass or legume prairies were considered to have four grass or legume species, respectively, and mixed prairies had four grass species and two legume species.

The total number of years with perennials was calculated. The organic fertilizer (OF) type used was divided into the following classes: liquid dairy manure, liquid hog manure, solid poultry manure, other or multiple OF sources, and no use of OF over the five-year survey period.

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2.2.4 Physicochemical analyses

Laboratory analyses were performed on air-dried and sieved bulk soil samples unless otherwise specified. Phosphorus (P_{M3}) and iron (Fe_{M3}) concentrations were quantified using the Mehlich-3 method (Carter and Gregorich, 2007; Greenberg et al., 1992; Eaton and Franson, 2005). The pH was measured using a 1:1 soil–water ratio. Total carbon and nitrogen content were assessed on a 0.2 g crushed and sieved (100 mesh) sub-sample using dry combustion on a LECO CN828 analyzer set at 950° C.

For granulometry analysis, 40 g of soil was mixed with 100 mL of sodium hexametaphosphate, diluted to 1 L with distilled water, following the modified Bouyoucos hydrometer method (CPVQ, 1997; Gee and Bauder, 1986; Kroetsch and Wang, 2007). This procedure included adding H_2O_2 solution to samples containing more than 5% SOM and acetic acid to carbonate-rich soils before analysis.

2.2.5 Soil DNA extraction, amplicon sequencing and bioinformatics

Soil DNA extraction and sequencing were conducted on bulk samples from the Ap horizon(s) as detailed by Jeanne et al. (2022). DNA was extracted from subsamples using a FastDNA SPIN Kit for Soil (MP Biomedicals, Solon, OH, USA) according to the manufacturer's instructions. The extracted DNA quality and quantity were assessed via absorbance spectrometry at 230, 260, 280 and 360 nm (Biophotometer, Eppendorf, Mississauga, ON, Canada) using a G1.0 microcuvette (mCuvette, Eppendorf). For prokaryotic 16S rRNA gene amplification, primers 515FB and 806RB were employed (Apprill et al., 2015; Parada et al., 2016), while the fungal ITS1 rRNA region was amplified using primers BITS and B58S3 (Bokulich and Mills, 2013). Sequencing processing adhered to the methodology outlined by Jeanne et al. (2022). In brief, sequencing employed a dual-indexed PCR approach and a paired-end approach with 300-base reads on the Illumina MiSeq at Laval University *Institut de biologie intégrative et des systèmes* (IBIS) genomic analysis platform.

Bioinformatics are also detailed in Jeanne et al. (2022). Briefly, the determination of ASVs was performed using the QIIME 2 platform (Bolyen et al., 2019) and its DADA2 plugin (Callahan et al., 2016). For prokaryotes, primers were removed with DADA2 by length. ITS primers were removed from each sequence using the Cutadapt tool (Martin, 2011). Taxonomic assignments were based on SILVA version 138 (Quast et al., 2013) for prokaryotes and UNITE version 8 (Kõljalg et al., 2013) for fungi. Functional inferences for prokaryotes were performed using PiCRUST2 (Douglas et al., 2020). Only functions related to carbon cycling were investigated. 183 orthologs and modules were selected and grouped into eight carbon cycling functional groups, following the approach used by Wang et al. (2022) in a study of carbon cycling in soil biocrusts, and supplemented with the Kyoto Encyclopedia of Genes and Genomes (Kanehisa et al., 2024; Kanehisa and Goto, 2000). For prokaryotes, orthologs related to labile carbon degradation (54 orthologs), recalcitrant carbon degradation (58 orthologs), fermentation (26 orthologs), anaerobic respiration (2 orthologs) and aerobic respiration (22 orthologs), as well as modules representing methanotrophy (3 modules), methanogenesis (7 modules) and carbon fixation (9 modules)

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processes were selected and grouped under these categories as detailed in Table S1. The sequence data for the sites in this study are part of a larger dataset deposited in the NCBI Sequence Read Archive (BioProject PRJNA1210483).

2.3 Statistical analyses

Specific climate, farming, and pedological variables were preselected for statistical analyses based on their biological relevance and low collinearity. The selected variables showed an absolute Pearson's correlation of less than 0.9, a variance inflation factor of less than 10, and a condition index of no more than 30. All continuous environmental variables were centred and scaled. Data aggregation was performed at the site level to derive average values. It was performed after the bioinformatic process, but prior to any data transformation or analysis. All statistical analyses were conducted in RStudio version 2026.08.1+195 (Posit Team, 2026) using R version 4.4.1 (R Core Team, 2024). Analyses used the vegan R package version 2.7-5 (Oksanen et al., 2026) unless otherwise specified.

2.3.1 Overall microbiota response to environmental factors

Variables identified for analysis were categorized into three distinct groups: climatic variables (PPT and GDD), farming variables (CDI, number of years with perennials, crop at sampling, STIR, compaction risk index and OF type), and soil-related characteristics (pH, clay and silt proportions, carbon concentration, C:N, P_{M3}, Fe_{M3} and VESS and pedological group). This last group will be referred to as the "soil variables".

To ascertain the significance of each preselected variable, distance-based redundancy analyses (dbRDAs) (Legendre and Anderson, 1999) were performed using the *capscale* function with the robust Aitchison dissimilarity measure (Martino et al., 2019) separately on ASVs for both prokaryotes and fungi and with the Aitchison dissimilarity measure (Aitchison et al., 2000) for carbon cycling functional inferences. The overall significance was tested using ANOVA-like permutation tests with the *anova.cca* function (Oksanen et al., 2026; Legendre et al., 2010) with 9,999 permutations. Individual variable significance was assessed by testing the marginal effects for each variable using the same function. Adjusted R-squared values were derived from partial dbRDAs for each variable to provide estimates of the total effect size attributable to each variable.

Following the dbRDA, variance partitioning analyses were used to elucidate the independent and shared variances attributable to climatic, soil, and farming variables (Borcard et al., 1992), using the *varpart* function on robust-centred log-ratio-transformed abundance tables for 16S ASVs, ITS ASVs, and the carbon cycling functions. The marginal significance of individual variable groups was again assessed using ANOVA-like permutation tests with 9,999 permutations on partial dbRDAs for each variable group, with the effects of other variable groups removed.

2.3.2 Pedological classification potential to summarise other variables

Results from the analyses detailed in 0 indicated that pedological classification plays a significant role, alongside other soil-related and climatic variables. This raised questions about how much of the R^2 of these variables is directly associated with

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the pedological classification itself. To further explore this issue and better select covariates for downstream analyses of farming variables, a permutational multivariate analysis of variance (PERMANOVA) using Euclidean distances was conducted. In this analysis, all climatic and soil-related variables identified as significant in prior dbRDAs were treated as response variables, with pedological classification serving as a predictor variable through the *adonis2* function. The multivariate homogeneity of group dispersions was verified using a permutational version of the PERMDISP2 procedure (Anderson, 2006) via the *permutest.betadisper* function. Given that the model was significant, permutational analyses of variance (permutational ANOVAs) were performed on the individual response variables using the *perm.anova* function from the MVAideMemoire R package (Herve, 2025). Permutational ANOVAs p-values were corrected for multiple comparisons using the Holm method. When significant differences were detected, they were further examined using pairwise permutation t-tests with the *pairwise.perm.t.test* function from the MVAideMemoire R package, again using the Holm method for p-value correction. All permutational tests used 9,999 permutations.

2.3.3 Exploration of the effects of agricultural practices

To explore the specific effects of STIR in conjunction with the OF type as they pertain to pedological influences, encapsulated as pedological groups, Analyses of composition of microbiomes with bias correction, version 2 (ANCOM-BC2) were conducted using the ANCOMBC R package version 2.8.1 (Lin et al., 2022; Lin and Peddada, 2024) for prokaryotic and fungal taxonomic families. Individual analyses were conducted on subdatasets of each pedological group on taxonomic families present in at least 5 samples within each subdataset. Taxa were deemed significantly different among groups when they met the sensitivity analysis criteria stipulated by ANCOM-BC2 and had an adjusted p-value fixed at 0.017 (0.05 divided by 3) to correct for multiple testing across the datasets by conducting stratified analyses. ANCOM-BC2 results are expressed in log fold change (base *e*). These results were converted into fold changes to facilitate interpretation. Since these analyses were performed on relatively small data subsets (n = 21, 46 and 13), these analyses should be considered as exploratory despite the applied p-value correction.

To investigate the specific effects of STIR and OF type on functional inference groups for prokaryotes, and their interaction with the pedological group, a PERMANOVA was conducted as described previously (Sect. 0), but using a robust Aitchison distance (Martino et al., 2019) and marginal effects to determine significance. In case of significant effects, pairwise PERMANOVAs were executed on the significant categorical terms using the *pairwise.adonis2* function from the pairwiseAdonis R package version 0.4.1 to evaluate which values differed from the others. The OF type value "Other-OF" was not evaluated in downstream analyses because significant effects could not lead to biological interpretations. Permutational ANOVAs and t-tests were also conducted as described in Sect. 0 to further investigate the specific effects of significant PERMANOVA terms.

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3. Results

3.1 Overview of study sites

The physicochemical properties of soil exhibited significant variation among the 80 sites studied, particularly in terms of clay (mean = 30%, range: 6.5–75%), silt (mean = 31%, range: 2.6–68%), and carbon content (mean = 1.9%, range: 0.6–4.3%). There were also notable differences in the Mehlich-3 extractable elements P_{M3} (mean = 76 kg/ha, range: 9.2–419 kg/ha) and Fe_{M3} (mean = 249 kg/ha, range: 117–473 kg/ha). Soil pH showed relative homogeneity across sites and horizons, with a mean of 6.6 (SD = 0.5) and a maximum deviation of 1.2 units (range: 5.5–7.8). O.HG soils were characterized by higher levels of clay, pH, and GDD, while O.Gs exhibited notably higher Fe_{M3} and silt than other pedological groups (Table S2). In contrast, HF.Ps showed significantly lower values for clay, Fe_{M3}, GDD, silt, and pH, but had much higher P_{M3} contents than both gleysolic groups. Both HF.Ps and O.Gs had similar carbon concentrations, which were slightly higher than those in O.HGs.

STIR varied significantly across sites, ranging from 0.15 to 274, with a mean of 74 and a standard deviation of 48. Over the five-year survey period, a minority of sites were cropped with perennials (20 %) or cover crops (25 %) at least once. The distribution of OF types was as follows: no OFs (27 %), liquid dairy manure (21 %), liquid hog manure (15 %), solid poultry manure (9 %), and other OFs (27%). Notably, sites without OFs were overrepresented in the O.HG sites (Table 1). Among the sites that received OFs, 47% had been last fertilized with organic materials in the same year as the sampling, while 31% had received their last dose of organic fertilizer in the previous year. Additionally, 19% and 3% had received OFs two and three years prior, respectively. All sites, except for two, had received mineral fertilizers at least once within the past five years.

Table 1: Number of sites per type and source of organic fertilizer across the pedological groups encountered in this study

Pedological group	No organic fertilizers	Liquid dairy manure	Liquid hog manure	Solid poultry manure	Other organic fertilizers
Ortic humic gleysols	16	6	6	5	14
Ortic gleysols	3	4	2	3	1
Humo-ferric podzols	3	7	4	0	7

The six most abundant prokaryotic phyla included Actinobacteriota (30.7%), Proteobacteria (24.2%), Chloroflexi (11.4%), Acidobacteriota (8.5%), Firmicutes (4.9%), and Crenarchaeota (4.4%). In contrast, the remaining 45 phyla accounted for < 16% of the total abundance. Amongst fungi, 12.1% of ASVs were unidentified, while 65.8% belonged to the Ascomycota phylum and 14.5% to Basidiomycota, with the remaining 7.6% distributed across 15 other phyla.

The most prevalent prokaryotic families were Xanthobacteraceae (5.6%; phylum Proteobacteria), KD4-96 (5.5%; phylum Chloroflexi), Nitrososphaeraceae (4.3%; phylum Crenarchaeota), and Gemmatimonadaceae (3.3%; phylum Gemmatimonadota). In the fungal domain, the prevalent families were Lasiosphaeriaceae (8.2%; phylum Ascomycota),

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Piskurozymaceae (6.9%; phylum Basidiomycota), Mortierellaceae (4.7%; phylum Mortierellomycota), and Chaetomiaceae (4.5%; phylum Ascomycota). 11.6% of prokaryotic and 32.5% of fungal ASVs remained unidentified at the family level (see Table S3 and Table S4).

For the prokaryotic carbon cycling functional groups, 119 of the 181 selected prokaryotic modules and orthologs were identified in the dataset. All eight carbon cycling functional groups were detected in all samples.

3.2 Microbiota responses to environmental characteristics

3.2.1 Biogeographical importance of individual variables

The dbRDA conducted on prokaryotic ASVs, fungal ASVs, and inferred prokaryotic carbon-related functional profiles showed overall p-values of 0.0001 for the ANOVA-like permutation tests, with an adjusted R^2 of 78%, 82%, and 63%, respectively.

From the 17 preselected environmental variables used in the dbRDAs, the same four variables were found to be significant for both prokaryotic ASVs and prokaryotic carbon cycling functional potential, while eight variables were significant for fungal ASVs (Fig. 2; Table S5). Only fungal ASVs showed a significant response to climatic or farming practice variables. Among the eight variables related to climate and agricultural practice intensity, the OF type (partial $R^2 = 0.23$; $p = 0.005$), CDI (partial $R^2 = 0.14$; $p = 0.02$) and GDD (partial $R^2 = 0.36$; $p = 0.0001$) were the sole variables influencing ASV composition, only for fungal ASVs.

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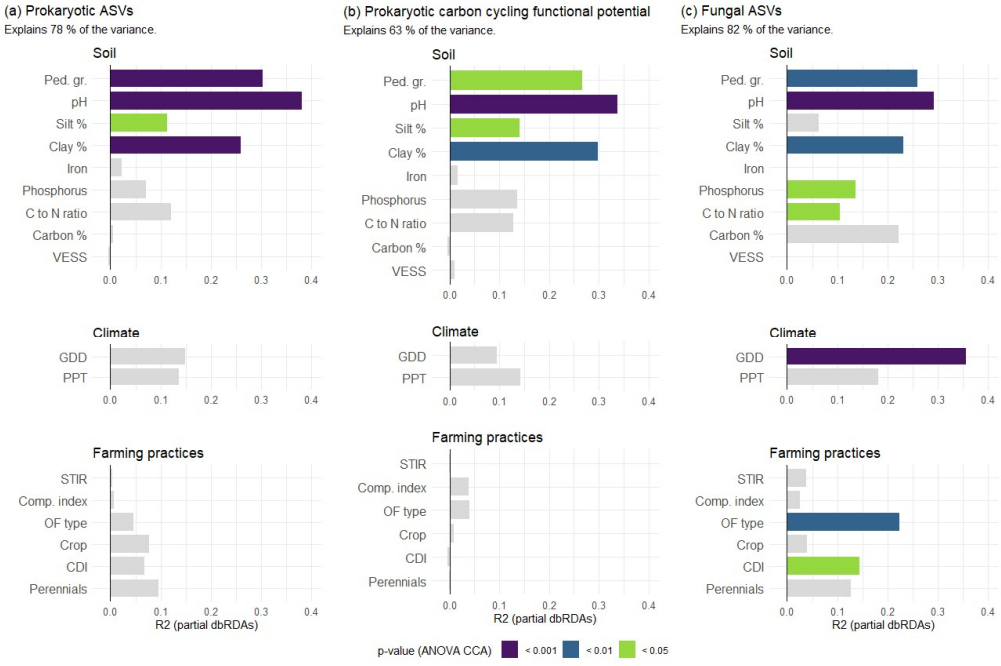


Figure 2: Results of analyses based on the dbRDAs to determine the relative importance of 17 climatic, soil and farming factors on the (a) prokaryotic (16S) ASV structure, (b) selected potential prokaryotic carbon cycling functions and (c) fungal (ITS) ASV structure across Quebec. The total variance explained corresponds to the R2 of the dbRDAs using all variables. Significance of individual variables corresponds to the adjusted p-values from permutation ANOVA-like tests (ANOVA CCAs) run on the dbRDAs using all 17 variables. The effect size of an individual variable corresponds to the R2 from a partial dbRDA (a dbRDA run with that variable as the only explanatory variable). Analyses were conducted individually for prokaryotic ASVs, fungal ASVs, and potential carbon cycling functions.

The prokaryotes ASV and carbon cycling potential were highly influenced by soil pH (ASV partial $R^2 = 0.38$; $p = 0.0001$; functions partial $R^2 = 0.34$; $p = 0.0001$), pedological group (ASV partial $R^2 = 0.30$; $p = 0.0001$; functions partial $R^2 = 0.27$; $p = 0.015$) and clay concentration (ASV partial $R^2 = 0.26$; $p = 0.0001$; functions partial $R^2 = 0.30$; $p = 0.008$). Furthermore, silt concentration moderately influenced these two groups (ASV partial $R^2 = 0.11$; $p = 0.01$; functions partial $R^2 = 0.14$; $p = 0.02$). As observed with prokaryotic ASVs, the fungal ASVs were highly influenced by soil pH (partial $R^2 = 0.29$; $p = 0.0001$), pedological group (partial $R^2 = 0.26$; $p = 0.006$) and clay content (partial $R^2 = 0.23$; $p = 0.006$). However, three other variables significantly influenced the variance of fungal ASVs; GDD explained the highest effect with a partial R^2 of 0.36 ($p = 0.001$), followed by the OF type (partial $R^2 = 0.23$; $p = 0.005$) and then CDI, which showed the lowest (partial $R^2 = 0.14$; $p = 0.02$). Additionally, P_{M3} (partial $R^2 = 0.14$; $p = 0.03$) and C:N (partial $R^2 = 0.11$; $p = 0.03$) were both moderate contributors to fungal ASV structure, while carbon concentrations (partial $R^2 = 0.22$), PPT (partial $R^2 = 0.18$) and the number

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of years with perennials (partial R^2 = 0.13) had respectively high to moderate effect sizes on ITS ASVs but were not significant.

3.2.2 Relative importance of soil, climate and farming management practices

Permutation ANOVA-like tests on the partial dbRDA, which tested the marginal significance of each variable group (soil, climate, and farming management), showed that the soil variable group was significant across prokaryotic ASVs, carbon cycling functions, and fungal ASVs (p_{adj} = 0.0004). Soil individual variance, represented by its adjusted R^2, accounted for more than 2/3 of the explained variance for prokaryotic ASVs and functions, and 52% of the fungal ASV explained variance (Fig. 3, Table S6). For both prokaryotic groups, climate was not significant. In contrast, the farming practices variable group was only weakly significant (p_{adj} = 0.04) for carbon cycling functional potential, and the two variable groups' unshared variance explained only a marginal portion of the total explained variance, consistent with the previous dbRDA analysis. For fungal ASVs, a moderate and statistically significant portion of the variance was explained by climatic (adj. R^2 = 0.08, p_{adj} = 0.0004) and farming practices (adj. R^2 = 0.04, p_{adj} = 0.002) variable groups (Fig. 3c). Thus, fungal ASVs differed from prokaryotic results by having a greater individual variance of climate and farming practices, and greater shared variance of these two groups with soil variables.

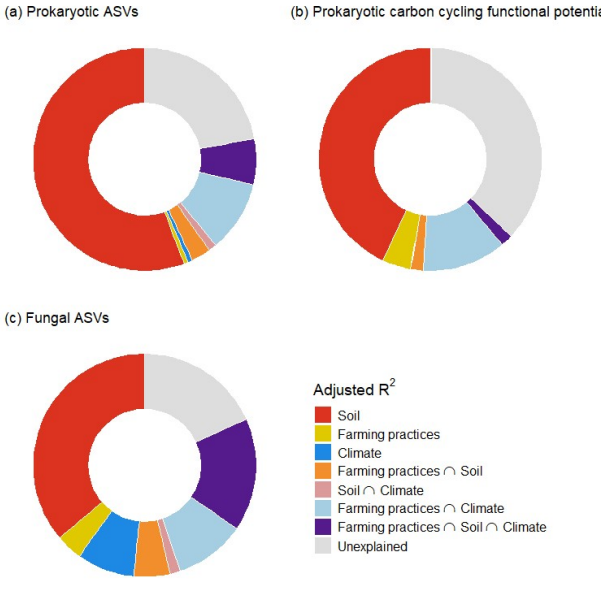


Figure 3: Microbial structure variance portions explained independently and conjointly by the three groups of variables for (a) Prokaryotic (16S) ASVs, (b) potential carbon cycling functions and (c) fungal (ITS) ASVs.

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3.3 Effect of pedological grouping on the significance of soil and climatic variables

The PERMANOVA was performed using the six significant climatic and soil-related variables previously identified in the dbRDAs' ANOVA CCA. It revealed a significant relation between the pedological groups and at least one of the climatic and soil-related variables (R^2 = 0.20; p = 0.0001). Follow-up permutational ANOVAs with adjusted p-values indicated that all variables differed significantly among pedological groups (Fig. 4; Table S7). Permutational pairwise t-tests indicated that O.Gs often had values falling between HF.Ps and O.HGs, but were often more similar to O.HGs (Fig. 4). The multivariate homogeneity of group dispersions was respected, with a p-value of 0.81 for the permutational version of the PERMDISP2 procedure.

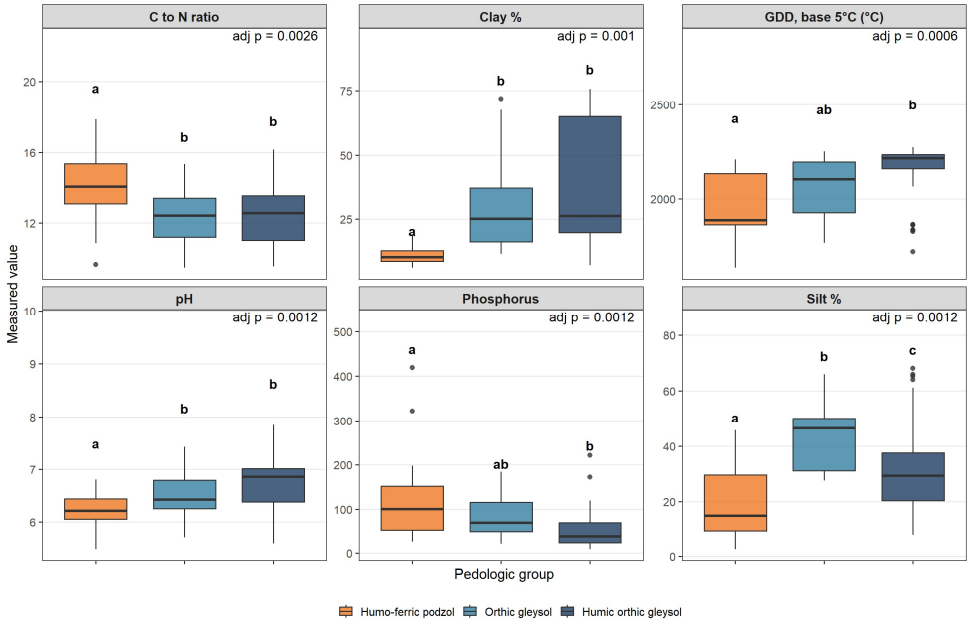


Figure 4: Distribution of the measured values and significant differences in selected physicochemical and climatic characteristics among pedological subgroups. Only significant (adj. p < 0.05) variables for prokaryotic ASV, fungal ASV or prokaryotic carbon cycling potential composition identified in the dbRDAs are shown. Indicated p-values correspond to the adjusted p-value of the permutational ANOVAs run on individual variables. Letters indicate which pedologic groups differed across variables in permutational post hoc multiple comparisons, and boxplots display the observed distribution of values across the dataset.

3.4 Microbial responses to farming management

In separate analyses of prokaryotic and fungal taxonomic families and pedological groups aimed at identifying microbial families with differential abundances in response to OF type and STIR, no family demonstrated a significant effect across

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multiple pedological groups (Fig. 5; Table S8). Specifically, 19 prokaryotic and nine fungal families were identified, yielding 31 separate treatment effects for prokaryotic families and 11 for fungal families.

In the prokaryotic analysis, no significant effects were observed in HF.Ps. Conversely, the O.G group exhibited twice as many significant taxa compared to the O.HG group, even though its sample size was 3.6 times smaller. Several prokaryotic taxa exhibited a similar response to both liquid manure treatments (hog and dairy) when compared to solid poultry manure or no OFs in O.Gs. This pattern was observed for A0839 (phylum Proteobacteria; more abundant with liquid OFs), WD2101 soil group (phylum Planctomycota; less abundant with liquid OFs) and Micromonosporaceae (phylum Actinobacteriota; less abundant with liquid OFs). A similar pattern was observed for Paenibacillaceae (phylum Firmicutes), which was favoured by both liquid OFs compared to no OFs and for Azospirillaceae (phylum Proteobacteria) as well as Roseiflexaceae (Chloroflexi), which were both favoured by no OFs and solid poultry manure respectively compared to liquid dairy manure and liquid dairy manure in O.Gs. Indeed, 29 of the 31 significant differences between OF types for procaryotic communities were between liquid OFs and solid poultry manure, or between liquid OFs and no OFs. The ANCOM-BC2s of fungal taxa produced only a few results, and no such patterns were identified.

Amongst all prokaryotic and fungal taxa aggregated to the taxonomic family level that exhibited significant responses, three had an overall relative abundance exceeding 1%: Roseiflexaceae (from the Chloroflexi phylum, with an overall relative abundance of 1.14%) and Xanthomonadaceae (from the Proteobacteria phylum, with an overall relative abundance of 1.48%) and Sporormiaceae (from the Ascomycota phylum, with an overall relative abundance of 1.09%). Roseiflexaceae declined with liquid hog manure compared to no OFs (-8.7-fold change, adj. $p = 0.001$) and solid poultry manure (-11.8-fold change, adj. $p = 0.001$) in O.Gs. Xanthomonadaceae increased with liquid hog manure when compared with no OFs (2.9-fold change, adj. $p = 0.01$) in O.Gs. Sporormiaceae increased with liquid dairy manure when compared with no solid poultry manure (12.7-fold change, adj. $p = 0.01$) in HO.Gs. Several taxa exhibited extreme sensitivity to specific treatments. Notably, the prokaryotic family A00839 (Proteobacteria phylum), along with fungi from the families Sanchytriaceae (phylum Monoblepharomycota), Strophariaceae (Basidiomycota phylum), Leotiaceae (phylum Ascomycota) and Onygenaceae (Ascomycota), and the order Cantharellales (Basidiomycota phylum), displayed absolute fold change values ranging from 40 to 157 (see Table S8).

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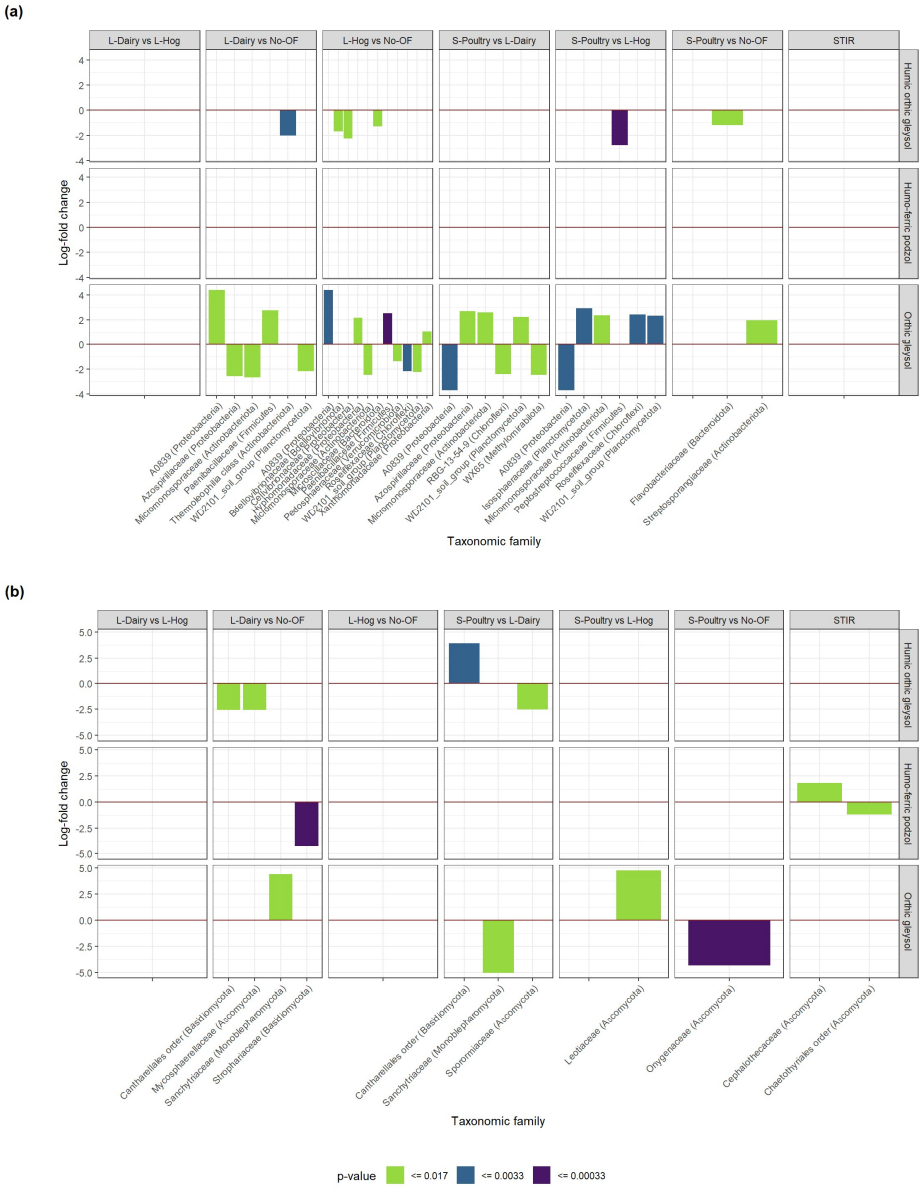


Figure 5: (a) Prokaryotic and (b) fungal taxonomic families with a significant and robust effect for each ANCOM-BC2, expressed as log fold change (base e). Each row represents an individual analysis, as ANCOM-BC2 were run separately on each pedological group. There are 21 observations for humo-ferric podzolsites, 13 observations for orthic gleysols and 46 observations for orthic humic gleysols. L-Dairy: liquid dairy manure, L-Hog: liquid hog manure, S-Poultry: solid poultry manure, other-OF: other or multiple organic fertilizer sources, no-OF: no use of organic fertilizer over the five-year survey.

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The PERMANOVA performed on the eight prokaryotic carbon cycling functional groups was significant (R^2 = 0.44, p = 0.0001). Further analysis revealed that STIR and OF type interactions with the pedological group were not significant (p = 0.91 and 0.62, respectively), but that the pedological group (R^2 = 0.27, p = 0.0001) and, less importantly, OF type (R^2 = 0.08, p = 0.03) had significant effects once taken individually, while the individual effect of STIR was not significant (R^2 = 0.01, p = 0.55). Pairwise PERMANOVAs revealed that all pedological groups differed, with both gleysols having adjusted p-values = 0.0003 when compared to the H.FP, and an adjusted p-value of 0.042 when compared together. The pairwise PERMANOVA on OF type indicated that only liquid hog manure weakly differed from no OF application (R^2 = 0.17, adj. p = 0.046). Subsequent permutational ANOVAs with the pedological group as the only explanatory variable revealed significant effects across all functional groups, whereas no significant effect was detected for the OF type. Pairwise comparisons indicated that HO.Gs tended to be similar to HF.Ps rather than to O.Gs in terms of functional abundances, and that O.Gs were more similar to HF.Ps than to HO.Gs (Fig. 6).

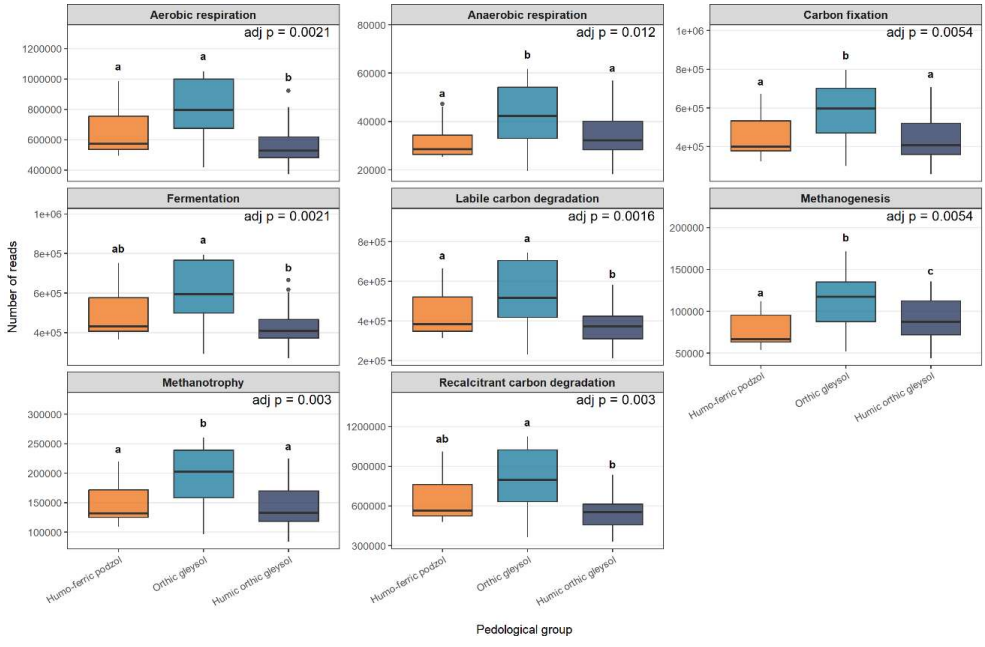


Figure 6: Differential abundances of the eight carbon-related prokaryotic functional groups. Adjusted p-values are reported from permutational ANOVAs conducted on significant terms and interactions found in previous PEMANOVAs. Letters indicate which pedological groups differed across variables in permutational post-hoc multiple comparisons, while the boxplots represent the observed abundance of the inferred functions across the data set.

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4 Discussion

4.1 Soil is the microbiome's main biogeographic regulator, with additional secondary drivers for fungal structure

The first objective was to identify the main biogeographic drivers of Quebec's cash crop soil microbiome composition, first by using dbRDA models. These models performed remarkably well, given that this study relied on observational data, encompassing a large geographic range and multiple pedoclimatic contexts, compared with other studies, where similar or substantially lower R2 values are reported (Constancias et al., 2015; Degrune et al., 2019; Li et al., 2024). By relying on real cash crop fields and leveraging information directly reported by farmers, this study captures the heterogeneity and complexity inherent to real-world cash-crop agricultural systems, thereby strengthening the practical relevance of the observed patterns for farmers and practitioners despite the limited number of independent observations (n = 80). As is inherent to large-scale observational studies, some sources of variability could not be resolved. Obtaining more detailed information on farming practices using an unsupervised survey proved to be challenging. It would probably have helped resolve some of the unexplained variance in the dbRDA models. Model performance may also have been improved by accounting for sampling depth, which varied with A horizon depth. Additionally, because this study primarily relied on deterministic environmental drivers, a portion of the unexplained variance could reflect stochastic processes that contribute to microbial community assembly in agricultural soils (Zhang et al., 2016) and are not explicitly accounted for in the modelling framework that we used. However, we expect to have largely reduced the influence of such stochastic processes, which are associated with field-scale heterogeneity, by aggregating samples at the site level (Averill et al., 2021).

Soil properties emerged as the dominant source of drivers of microbial ASVs and inferred carbon cycling functional composition, explaining substantially more variance than climatic or farming-related variables in the variance partitioning analysis (Fig. 3). This was true across all groups but was especially pronounced for prokaryotic ASVs and carbon-cycling functional structure. It is consistent with other observations from Europe and Great Britain (Labouyrie et al., 2023; Griffiths et al., 2011; Kuramae et al., 2012). We found that most of the explained variation in soil prokaryotes, fungi, and prokaryotic carbon cycling potential functions was linked to variables that differed between pedological groups (Fig. 4), further indicating that pedological classification is one of the primary drivers of soil microbiome composition.

The effect size in the dbRDAs, which did not consider covariance, showed that soil pH outperformed all other variables for prokaryotic ASVs and for carbon cycling functions, and had the second greatest effect for fungal ASVs, after GDD (Fig. 2). The soil-related variables that emerged as driving microbial composition when taken individually, namely pedological classification, pH, clay content, silt content, phosphorus concentration and C:N, are consistent with the current literature. Indeed, all these variables, except pedological classification, have been reported as significant in biogeographical studies, with prokaryotes being more influenced by soil properties than fungi (Fierer, 2017; Griffiths et al., 2011; Labouyrie et al., 2023). There is limited literature on the biogeography of prokaryotic functional potential associated with carbon cycling. Nevertheless, our results suggest that prokaryotic carbon cycling functional potential follows patterns similar to those of

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prokaryotic ASVs, with soil classification, pH, and texture explaining most of the observed variation, regardless of climatic and farming context.

In contrast to prokaryotic ASVs and carbon-cycling functional potential, which did not respond to climate or farming practices, fungal ASVs showed significant individual variation in both groups (Fig. 3). These results suggest the presence of secondary mechanisms that drive fungal ASV structure beyond soil properties. In the partial dbRDAs, where effect size did not account for covariates, GDD was the sole significant climatic variable and explained by far the most variation in fungal ASVs, while OF type and CDI were the two significant farming practice variables, with moderate effect sizes (Fig. 2). However, the relatively small variance explained by climatic variables alone in the variance partitioning did not reflect the importance of GDD in dbRDA analyses. This suggests that while GDD could serve as an efficient proxy for predicting fungal ASV structure, only a small portion of fungal ASVs may be directly affected by GDD. Considering climate as having limited effects on fungal community structure is contrary to findings from other studies (Labouyrie et al., 2023; Vetrovsky et al., 2019; Tedersoo et al., 2014), but it has already been reported that climate may have only an indirect effect on fungal structure, rather than direct mechanistic effects (Waldrop et al., 2017). Organic fertilizer type and CDI had moderate effects on fungal ASV structure when covariance among explanatory variables was not accounted for. However, variance partitioning revealed that farming practices explained only a small proportion of the unique variation, with much of their explanatory power shared with soil and climatic variables. This pattern is consistent with previous studies suggesting that the effects of organic fertilizers on soil microbial communities are largely mediated through changes in soil physicochemical properties (Francioli et al., 2016). Still, this interpretation does not explain why differential abundance analyses identified so few taxa that differed among organic fertilizer types.

The simultaneous significant effects of GDD, OF type and CDI could point to certain conservation farming systems. In Quebec, more OFs tend to be applied in peripheral regions, where agriculture is mainly oriented towards livestock production and more diversified crop production, due to a colder climate. This hypothesis is further supported by the importance of the shared variance involving climate or farming, as well as by the fact that the number of years with perennials and carbon concentration had moderate effect sizes, even though they were not significant. Indeed, because significance was based on marginal effects, these variables could have been non-significant only due to redundancy with other variables.

Except for OF type and CDI, which significantly contributed to the fungal ASV structure, none of the nine farming variables tested had a significant effect on their own. This result could, in part, be explained by the relatively small dataset, the mode of data collection, an unsupervised survey, and the resolution of the data collected. Indeed, fertilizer use was described only by the OF type, without information on nutrient quantity and quality. Indices such as STIR, compaction risk, and CDI were more detailed, but STIR and compaction risk did not account for soil moisture during field operations. CDI did not consider crop and cover crop implantation success and was imprecise in estimating the number of species in prairies. Furthermore, some studies have found an important interaction between STIR and residue retention (Navarro-Noya et al., 2013), but residue management information was not available in the dataset. Still, the relatively small portion of variance explained by

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agricultural management alone, relative to the total explained variation, is consistent with other research indicating that soil properties more strongly influence community structure than land use (Kuramae et al., 2012).

4.2 Going beyond pH as a master variable

Historically, pH has been identified as a master variable for soil microbial community structure, supported by studies of natural soils (Fierer and Jackson, 2006; Lauber et al., 2009; Griffiths et al., 2011). However, while pH governs proton transfer through acid-base reactions, it may not be the primary mechanism directly regulating community structure. Indeed, authors have suggested that pH may instead indirectly influence soil microbial communities by serving as a proxy for other important soil characteristics (Waldrop et al., 2017; Lauber et al., 2009). Many previous studies considered only a limited set of variables and did not include pedological classification. In contrast, redox potential, which reflects soil oxidation-reduction reactions and electron transfer, has been consistently identified as central in microbial ecology (Lipson et al., 2015; Fierer, 2017), providing a direct mechanism underlying both soil microbial community composition and activity (Husson, 2012). Soil pH and redox potential interact (Van Breemen, 1987), but are not mutual predictors and have been reported to be moderately to weakly correlated in unsaturated soils (Bohrerova et al., 2004; Tano et al., 2020). This relationship may be even weaker in cultivated soils, such as those examined in this study, where topsoil pH is frequently adjusted to meet agronomic requirements.

Here, even if pH was a strong community driver when considered by itself (Fig. 2), our results lead us to propose using soil taxonomic classification rather than pH as a first-level property to distinguish the structures and responses of arable soil microbial communities to anthropogenic drivers. Soil pH has received considerably more attention than redox potential in microbial studies, despite theoretical evidence supporting the importance of redox potential. The limited focus on redox potential has been attributed to its greater variability and lower measurement reliability. Studying redox potential in conjunction with pH is considered necessary for a more complete understanding of soil-plant interactions and soil biogeochemistry (Husson, 2012). Incorporating pedological classification can help address this challenge, as both redox potential and pH are central to soil genesis (Husson, 2012; Gotoh and Patrick Jr., 1974; Chadwick and Chorover, 2001). Indeed, a major part of the pedogenesis of mineral soils is the chemical transformation and the transportation of materials in the soil profile. The major chemical constraints of these transformations are proton activity (pH), dicing acid-driven mineral alterations, and electron availability (redox potential), driving oxidation state, element solubility and the transport of redox-sensitive elements, and the interaction between these two (Ugolini and Sletten, 1991; Chadwick and Chorover, 2001). In this study, soils marked by oxidation-reduction processes, also known as gleying, due to a recurrent, prolonged water presence were classified in the gleysolic order (Bedard-Haughn, 2011). Soils that had developed under lower pH values were predominantly from the podzolic order, where low pH strongly altered the surface horizon mineral and organic matter, transporting the altered mineral in the deeper horizons (Sanborn et al., 2011).

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4.3 Pedological classification as an integrative framework for interpreting soil microbial structure

Given that soil variables explained most of the variance in microbial structure, and that amongst soil variables, pedological classification emerged as a powerful driver, we explored how it could serve as a conceptual and analytical framework for interpreting patterns in soil microbial structure. Pedology provides a robust framework for investigating the microbiome of sites with diverse geographic and edaphic contexts. The primary scientific rationale is that pedological classification serves as a master variable, integrating multiple climatic and edaphic variables that shape soil community structure, including those that are rarely measured. Farming practices, by contrast, exerted a substantially smaller direct influence on the overall microbial community structure. This is complementary to literature showing that the effects of farming practices are often soil-dependent (Degrune et al., 2019). Because such comparatively subtle, context-dependent farming management effects risk being masked by the much larger variance associated with soils of distinct origin, stratifying sites by soil characteristics before evaluating the effects of anthropogenic disturbances should improve the detection of the effects of farming practices on microbial community structures. Direct comparisons of effect sizes between soil and farming practices remain rare, and the present study helps address this gap. Differential abundance analyses of taxonomic families across various OF types further demonstrate that stratifying datasets by pedological classification enhances the understanding of how farming practices affect the soil microbiome. Specific taxonomic families also exhibited distinct responses to OF type within pedological groups, and these groups differed in the number of taxa sensitive to these OF treatments.

Although pedogenetic horizons have been proposed as a central element shaping the ecological functioning of soil microbiota in a theoretical context (Costantini and Mocali, 2022; Food and Agriculture Organization of the United Nations et al., 2020), relatively few soil microbiome studies have explicitly examined the influence of pedological classification on microbial community structure. To our knowledge, only two such studies have investigated this relationship, both in New Zealand's agricultural systems and focusing exclusively on prokaryotic communities. In a first study spanning 24 sites and three agricultural land-use types, prokaryotic assemblages and diversity varied significantly with pH and land use, while soil order provided the best explanation for community structure and diversity within land-use types (Kaminsky et al., 2017). In a second study, Kaminsky et al. (2021) reported that soil order acted as a secondary modifier of prokaryotic community structure across 92 pastures, after pH and geographic region.

Here, we demonstrated in several ways the relevance of including pedological classification. First, by investigating both prokaryotic and fungal communities, as well as inferred carbon cycling functional group potential, we demonstrated that the influence of pedological classification is not limited to prokaryotic community structure. Second, rather than treating pedological classification solely as one explanatory variable among others, we showed that grouping soils by pedological classification provides a powerful analytical framework for disentangling the more subtle, context-dependent effects of agricultural practices. Indeed, stratifying analyses by pedological groups revealed microbial responses to OF type and STIR specific to soil taxonomy. Together, these results suggest that the effects of farming practices on soil microbiome are

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mediated by pedological context, while offering a practical framework for explicitly integrating this reality into the analysis of microbial communities.

The power of the dataset used in this study was limited by the number of sites relative to the diversity of agricultural practices encountered. This prevented us from adequately reaching definitive conclusions relative to the specific effects of soil tillage intensity and OF type, as initially targeted by our second objective. The differential abundance analyses conducted in this paper therefore point to some microbial taxa that could be of interest in further studies on the effect of such agricultural practices in humid continental climates.

5 Conclusion

Here, we present an observational study aiming to decipher the intricate sources of drivers of topsoil microbial composition in Quebec's corn and soybean cash crop fields. This work presents a unique regional-scale biogeographical assessment of arable land, investigating a wide range of soil, climate and farming practices-related variables as potential drivers. Under diversified agricultural conditions, soil microbial ASV structure and carbon-cycling functional potential were predominantly structured by intrinsic soil properties, such as pedological subgroups, rather than by climatic variables or farming practices. Pedological classification emerged not only as a strong explanatory variable but also as a highly relevant framework for distinguishing soils when assessing anthropogenic effects on the structure of their microbial communities. Importantly, our results suggest that the sensitivity of microbial taxa to OF type is intrinsic to the pedological group. By integrating long-term soil-forming processes and intrinsic soil properties, pedological classification likely captures key environmental controls of microbial communities, including variables that are otherwise difficult to measure directly, such as redox conditions, and that modulate soil-specific responses to management practices.

These findings support the use of soil classification as a central framework for interpreting agricultural soil microbiomes. This framework allows for more robust and meaningful comparisons among sites, more consistent monitoring across broad geographic scales, and the detection of soil-specific microbial responses to farming practices. Integrating pedological classification into large scale microbiome studies and soil monitoring frameworks may therefore improve our capacity to assess microbial indicators of soil functioning and health. Although the observed trends were clear, they need to be confirmed by studies with larger sample sizes and other farming systems and pedoclimatic settings. Further examination of these trends using other microbiome study methods, such as metagenomics or metatranscriptomics, could also improve understanding of how they translate into ecosystem functioning. Extending this approach to other agricultural and pedological classification systems will be essential to test the generality and relevance of this framework beyond the scale of the present study. Further developing knowledge of pedological groups' relative responses to diverse anthropogenic perturbations could also improve decision-making by prioritizing agroenvironmental interventions and resources for more sensitive pedological groups, which would benefit more from beneficial management practices. Machine learning

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approaches may further enhance this application of the framework by identifying non-linear interactions and complex microbial signatures associated with farming practices that may remain hidden in linear statistical analyses.

Appendix A

The STIR index was calculated as follows:

$$\mathrm{STIR} = 0.5sp \times 3.25t \times d \times sd \quad \text{(A1)}$$

where *sp* is the operational speed recommended by the manufacturer (mi/h), *t* is the perturbation level associated with tool type (disks, etc.), *d* is the mean working depth recommended by the manufacturer (in), and *sd* is the perturbed soil surface (%).

The compaction risk index was first calculated for each field operation *j* as:

$$C_j = I_p \cdot I_o \cdot I_m \cdot I_{np} \cdot I_{pr} \cdot I_v \cdot I_{gps} \quad \text{(A2)}$$

where I_p, I_o, and I_m are the period, operation, and machinery size indices (Table A1), and I_{np} is the number of passes index calculated as:

$$I_{np} = 1.6666(1 - e^{-1.655 \cdot n_{passes}}) \quad \text{(A3)}$$

with n_{passes} being the total field passes (Botta et al., 2009) and I_{pr}, I_v, and I_{gps} are mitigation factors for radial tires (0.5 vs. 1.0), controlled traffic lanes (0.9 vs. 1.1), and RTK-GPS guidance (0.9 vs. 1.0), respectively.

From the calculation of the compaction risk associated with every field operation, the five-year compaction risk index was calculated as:

$$C_{total} = \sum_{j=1}^{N} C_j \quad \text{(A4)}$$

where *N* is the total number of machinery operations during the five-year survey.

Table A1: Reference indices used in the calculation of the compaction risk index.

Index	Measured metric	Metrix value	Index value
Period index (*Ip*)	Period	Pre-sowing	1.5
		Spring	1.5
		Post-emergence	1
		Growing season	1
		Summer	1
		After the first cut	1
		After the second cut	1
		After the third cut	1
		Post-harvest summer	1

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		Post-harvest	1
		Early fall	1
		Fall	1
		Late fall	1.5
Operation index (*Io*)	Equipement type	Subsoiler	2
		Plow	2
		Chisel	2
		Zone-till or strip-till	1
		Combined tool	2
		Spader	1
		Offset disk	2
		Disk harrow	1
		Cultivator	1
		Rotary tiller	1
		Rotary harrow	1
		Roller	1
		Field cultivator	1
		Spreader	4
		Solid manure	4
		Liquid mineral fertilizer	1
		Broadcast mineral fertilizer	1
		Pesticide	2
		Conventional seeding	1
		Direct seeding	2
		Broadcast seeding with green manure	1
		Mower and tedder	2
		Hay baler	2
		Grazing animals	1
		Windrower	2
		Baler	3
		High-density vegetable seeder	1
		Potato planter	2
		Ridger	1
		Hiller	1
		Root and potato harvester	3
Machinery size (*Im*)	Total axle weight (kg)	7500	1
		10000	2
		15000	3
		30000	4

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Code and data availability

Code and some example data are available in a GitHub repository at https://github.com/JeanneDurivage/microbiome-ESSAQ_article (Durivage et al., 2026). The sequence data for the sites in this study are part of a larger dataset deposited in the NCBI Sequence Read Archive (BioProject PRJNA1210483). The initial data is not available due to legal limitations. Indeed, the organizations responsible for conducting the Quebec 2020 soil health survey have confidentiality agreements with the farmers involved in this study, preventing the publication of the data. The authors have been granted access to an anonymised dataset but are not allowed to publicly share it. The GitHub repository still demonstrates the dataset structure and some summary statistics.

Author contributions

Jeanne Durivage conducted conceptualization, methodology, investigation, data curation, formal analysis, visualization and writing (original draft preparation). Thiago Gumiere and Mary-Cathrine Leewis conducted supervision. Marc-Olivier Gasser, Richard Hogue, and Thomas Jeanne, along with the *Institut de recherche et de développement en agroenvironnement* team, conducted the project administration, provided resources, investigation, data curation, and developed the methodology through the realization of the Quebec 2020 Soil Health Inventory and conducted supervision. Marie-Élise Samson conducted project administration, resource acquisition, funding, and supervision and participated in conceptualization. All authors participated in manuscript writing (review and editing).

Competing interests

The authors declare no conflicts of interest.

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