

Soil fertility level is the main modulator of prokaryotic communities in a meta-analysis of 197 soil samples from the Americas and Europe

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Review

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Soil fertility level is the main modulator of prokaryotic communities in a meta-analysis of 197 soil samples from the Americas and Europe



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ABSTRACT

Soil is one of the most essential life-supporting environments. The processes that define these environments' structures over time and space are still poorly understood. In order to contribute to elucidating the dynamics of microbial communities in soil with different fertility levels, this study analyzes 197 rhizosphere microbiome samples obtained from different soil types, available in six articles. Data from amplicon sequencing analyses were extracted from the articles and 15 main prokaryotic phyla were identified. Soil physical and chemical characteristics enabled to classify soils as poor, medium, and rich. The SIMPER test showed that prokaryotic communities presented approximately 40 % of dissimilarities when comparing three levels of soil fertility. Proteobacteria, Acidobacteria, and Actinobacteria were the dominant phyla, accounting for 58 % of total OTUs in poor, 54 % in medium, and 47 % in rich soils. However, Verrucomicrobia, Gemmatimonadetes, and Elusimicrobia phyla that seem to present a central importance in the microbial distributions. The relative abundance profile of the main phyla was better separated according to soil fertility level than plant host. Clay, organic matter, pH, K, and P availability show significant linear correlations with some phyla studied. In conclusion, soil physical and chemical characteristics are the main influencers of relative abundance of some prokaryotic phylum. The high diversity of prokaryotic communities present in the plant rhizosphere systems seems to be shifted mainly by soil characteristics.

1. Introduction

Soil is one of the most essential life-supporting environments (Mills, 2003). By definition, a healthy soil has the ability to sustain productivity, diversity, and environmental services of terrestrial ecosystems (Doran and Zeiss, 2000). Thus, soil is expected to keep a suitable functioning of ecosystem services, such as nutrient cycling. However, human activities have intensified the pressure on land resources, resulting in soil quality degradation (Legaz et al., 2017). The soil quality report published by the Food and Agriculture Organization of the United Nations (FAO, 2021) showed that most soils in the world are polluted and are found in poor or very poor conditions (FAO, 2015). Such soils are frequently affected by erosion, acidification, and nutrient lixiviation, leading to crop, animal, and environmental losses (Legaz et al., 2017).

Knowledge about soil structures, evaluation of their stability, stress resilience, biological diversity, and potential of cycling nutrients is essential to identify areas more sensitive to degradation processes.

The soil structure comprises a high variety of mineral particles, organic compounds, and microorganisms. Clay, organic matter, and silt particles form the soil matrix, and soil microorganisms are firmly adhered to the soil (Daniel, 2005). The diversity of belowground microorganisms, community structures, and associations are important soil quality indicators. Although the microbial community structure present in different types of soil has been extensively studied, it continues to be poorly understood due to the sheer number and high complexity of microbes in living soils. It is estimated that 1 g of soil contains up to 1 billion bacterial cells (most of them with an unclear taxonomy position), meters of fungal hyphae, and a wide variety of mites, nematodes,

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Table 1

Rhizospheric soil samples studied.

Geographic coordinates	Number of samples	Host plant	Soil classification	Reference
29°29′11.03″S and 55°27′43.93″W	9	Grassland	Poor	Granada et al., 2019
29°35′31.96″S and 55°22′6.01″W	9	Grassland	Poor	Granada et al., 2019
29°30′41.93″S and 55° 7′13.70″W	9	Grassland	Poor	Granada et al., 2019
30°13'25" S and 52°56'28" W	12	Rice	Medium	de Souza et al., 2021
29°57'00" S and 51°07'11" W	12	Rice	Medium	de Souza et al., 2021
29°05′5″ S and 51°33′15″ W	6	Grapevine	Rich	Unpublished
30°13'42" S and 54°43'47" W	3	Grassland	Poor	Unpublished
31°17'40" S and 53°54'55" W	3	Grassland	Poor	Unpublished
30°05'00" S and 51°40'00" W	14	Pasture	Poor	Beneduzi et al., 2019
30°50'52" S and 51°38'08" W	18	Wheat	Medium	Campos et al., 2016
53°15′43″ N and 6°10′19″E	34	Rice	Rich	da Costa et al., 2020
53°06′59.5″ N and 6°38′49″E	32	Rice	Poor	da Costa et al., 2020
25°00'50" S and 50°09'18" W	12	Maize	Medium	da Costa et al., 2018
24°33'24" S and 54°03'24" W	12	Maize	Medium	da Costa et al., 2018
23°17'34" S and 51°10'24" W	12	Maize	Medium	da Costa et al., 2018

earthworms, and arthropods (Joergensen and Wichern, 2008; Wagg et al., 2014). Across world biomes, soil microbial diversity is directly related to several environmental functions, such as nutrient cycling, organic matter decomposition, heavy metal contamination, and plant productivity (Sokol et al., 2022). Prokaryotic cells are the most numerous in soil biomass, and some studies focusing on the structure of their communities and on environmental factors that affect microbial resilience have been conducted (Granada et al., 2019; Sokol et al., 2022). As a result, there are two well-accepted theories relating soil characteristics to microbial communities: (1) the plant species and its root system directly affect the diversity and structure of prokaryotic communities by changing soil properties (Bakker et al., 2018; Hu et al., 2018), and (2) soil fertility and its physical characteristics are the main influencers of microbial diversity (Daniel, 2005; Chaparro et al., 2012; Hartman and Tringe, 2019).

Intensive agricultural practices use chemical fertilizers and pesticides to increase crop productivity, resulting in an irreplaceable loss of functional biodiversity (Dubey et al., 2019). In a sustainable agriculture framework, plants, soil, and microbes work together to mediate soil health and contribute to plant health and productivity (Chaparro et al., 2012). Soil microbiota affect soil porosity, aeration, and water retention capacity. However, edaphoclimatic factors and agricultural practices, such as monotype cultivation, nutrient adjustment, and use of fertilizers, shift soil microbiome (Dubey et al., 2019). According to Fierer (2017), the most critical soil biotic and abiotic factors that affect the composition of microbial communities are (in descending order) soil pH, organic carbon quality and quantity, available O2, moisture, nitrogen (N) and phosphorus (P) availability, texture, and structure. Several reports have also identified that each plant species strongly affect belowground communities (Peay et al., 2013; Prober et al., 2015; Pii et al., 2016; Fox et al., 2020). In contrast, other studies have shown plant species exerting few effects (Pathma et al., 2021; Tkacz et al., 2020, da Costa et al., 2022).

According to the Naliukhin et al. (2018), soil microorganisms can be divided in three groups: The first group present microorganismsApplied Soil Ecology 186 (2023) 104811

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Point scale for soil fertility classifi	ication.
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Soil characteristic	Classification	Pointing	Range
Organic matter	Low	1	$OM \le 2.5$ %
	Medium	2	$OM \leq 5.0 \%$
	High	3	OM > 5.0 %
Clay	Class 4 (low)	1	$Clay \le 20 \%$
-	Class 3 (medium)	2	$Clay \leq 40 \%$
	Class 2 (high)	3	$Clay \leq 60 \%$
	Class 1 (very	4	Clay > 60 %
	high)		5
рH	Verv low	1	pH < 5
1	Low	2	$pH \le 5.4$
	Medium	3	$pH \le 6$
	High	4	pH > 6
Phosphorous	Very low	1	Clav class 1: $P < 2.0 \text{ mg dm}^{-3}$
1 nosphorous	Very low	1	Clay class 2: $P < 3.0 \text{ mg dm}^{-3}$
			Clay class 3: $P \le 4.0 \text{ mg dm}^{-3}$
			Clay class 4: $P < 7.0 \text{ mg dm}^{-3}$
	Low	2	Clay class 4. $P \ge 7.0$ mg um
	LOW	2	$d_{\rm m}^{-3}$
			dm Classical and Dr. D. 1. C. O. stati
			Clay class 2: $P = 3.1-6.0 \text{ mg}$
			dm -
			Clay class 3: $P = 4.1 - 8.0 \text{ mg}$
			dm °
			Clay class 4: $P = 7.1-14 \text{ mg}$
			dm ⁻³
	Medium	3	Clay class 1: $P = 4.1-6.0 \text{ mg}$
			dm ⁻³
			Clay class 2: $P = 6.1-9.0 \text{ mg}$
			dm^{-3}
			Clay class 3: $P = 8.1-12.0 \text{ mg}$
			dm^{-3}
			Clay class 4: P = 14.1–21.0
			mg dm $^{-3}$
	High	4	Clay class 1: $P = 6.1$ –12.0 mg dm ⁻³
			Clay class 2: $P=9.1{-}18.0~\text{mg}$ dm^{-3}
			Clay class 3: $P = 12.1-24.0$ mg dm ⁻³
			Clay class 4: P 21.1–42.0 mg
	Vom bish	-	Class along 1, D > 12,0 mg
	very lingli	5	dm^{-3}
			Clay class 2: $P > 18.0 \text{ mg}$ dm ⁻³
			Clay class 3: P $>$ 24.0 mg dm $^{-3}$
			Clay class 4: $P > 42.0 \text{ mg}$
			dm ⁻³
Potassium	Very low	1	Low CEC*: K $< 15 \text{ mg dm}^{-3}$
			Medium CEC: <20 mg dm ⁻³
			High CEC: $<30 \text{ mg dm}^{-3}$
	Low	2	Low CEC*: K 16–30 mg dm^{-3}
		-	Medium CEC: K 21–40 mg
			dm ⁻³
			High CEC: K 31_60 mg dm ^{-3}
	Medium	3	Low CEC*: K 31_45 mg dm^{-3}
	Medium	5	Medium CEC: V 41 60 mg
			dm ⁻³
			$\frac{1}{100} CEC V 61 00 m c 4m^{-3}$
	Iliah	4	Fign CEC: K 61–90 mg dm $^{-3}$
	High	4	Low CEC*: K 46–90 mg dm ^{-3}
			Medium CEC: 61–120 mg
			dm ⁻³
		_	High CEC: 91–180 mg dm ^{-3}
	Very high	5	Low CEC*: $K > 90 \text{ mg } \text{dm}^{-3}$
			Medium CEC: $>120 \text{ mg dm}^{-3}$
			High CEC: K $>$ 180 mg dm $^{-3}$

indicators of soil acidity (Ellin6075 family from Acidobacteria phylum, and Intrasporangiaceae, Micrococcaceae, and Nocardioidaceae families from Actinobacteria); the second group present microorganisms which increase their population density with the use of fertilizers (families Solibacteraceae, Micromonosporaceae, Chitinophagaceae, Bradyrhizobiace



Rich

Fig. 1. Percentage of dissimilarities among the three soil types studied inferred by SIMPER test. Comparisons were performed two by two and all grouped.

ae, Hyphomicrobiaceae, Oxalobacteraceae, Sinobacteraceae, and Chthoniobacteraceae); and the third group present microorganisms which decrease their relative abundance with fertilizer application (families Gaiellaceae, Patulibacteraceae, Ellin5301, Methylocystaceae, Rhizobiaceae, Sphingomonadaceae, Comamonadaceae, and Xanthomonadaceae). Thus, the composition of prokaryotic soil communities and their abundances may often be predicted according to soil characteristics (Fierer, 2017). Plants may exert a significant effect on soil microbial communities by modulating soil characteristics (Monokrousos et al., 2020). However, predicting microbial taxa according to plant species is difficult since plant associations with microorganisms are context-dependent (Fierer, 2017).

We hypothesized that soil fertility level (evaluated by chemical and physical characteristics) is the main modulator of soil prokaryotic communities. With this purpose, we elaborated a point scale for soil fertility classification in poor, median or rich. This work uses data collected from several studies that brings information about rhizospheric soil characteristicas [organic matter, clay, P and potassium (K) availability, and pH], prokaryotic communities identified by highthroughput sequencing data and host plant. A total of 197 soil samples were analyzed. Our main conclusions are that: 1) soil characteristics and nutrient contents are the main influencers of the relative abundance of each bacterial phylum; and 2) and that the high amount and diversity in prokaryotic communities present in the plant rhizosphere systems are a consequence of changes in soil characteristics modulated by plant roots.

2. Material and methods

2.1. Data collection

Scientific databases were searched and filtered. Articles were manually analyzed aiming to identify works that analyze soil characteristics (organic matter, clay, pH, and P and K availability) and identify microbial communities through independent methods of isolation (highthroughput amplicon sequencing). Data from high-throughput sequencing were used at the phylum level to reduce differences usually found by using different sequencing and sample preparation methodologies. The selected works were Campos et al. (2016); da Costa et al. (2018); Granada et al. (2019); Beneduzi et al. (2019); da Costa et al. (2020), and de Souza et al. (2021). We also used a collection of 12 unpublished samples in our research group (Table 1).

2.2. Soil fertility classification

Data from soil physical and chemical characteristics were collected from the selected articles. These soils were classified according to fertility level as poor, medium, and rich. This classification considered the official fertility levels for the Rio Grande do Sul State, Brazil, concerning soil physical and chemical characteristics [organic matter (OM) and clay percentages, P and K availability, and pH] and adapted them to a point scale (Table 2). Soil samples that accounted for eight points or less were classified as poor fertility, samples that were within a range of 9-13 points were classified as medium fertility, and samples that resulted in 14 points or more were considered rich fertility.



Fig. 2. (A) Relative abundance of the 15 phyla that presented >1 % of total identified OTUs in poor, medium, and rich soils. (B) Beta dispersion analysis identified in prokaryotic communities (C, D and E) interquartile interval and outliers identified in rich, medium, and poor soils, respectively.

2.3. Determination of prokaryotic phyla

Relative abundance of prokaryotic phyla with relative abundance of up to 1 % was extracted from each selected article using the Web-PlotDigitizer software version 4.6 (available at https://automeris.io/ WebPlotDigitizer), which are able to extract numerical data from plots and graph.

2.4. Statistical analysis

Data from OTU tables and soil characteristics of 197 samples were consolidated into a single table. The beta dispersion analysis was performed with the function betadisper of the vegan package v. 2.5-7 in R v. 4.01. Prokaryotic communities were evaluated by SIMPER test, grouped by discriminant analysis (LDA), correlated with soil characteristics by linear Pearson (r) analysis. Microbial community networks were calculated with the Fruchterman-Reingold algorithm based on Bray-Curtis as a similarity index. These analyses were performed using the software PAST3 (Hammer et al., 2001).

3. Results and discussion

3.1. Soil classification and microbial community's composition

A total of 197 rhizospheric soil samples from 15 different sampling points were studied (Table 1). Among these samples, 79 were classified as poor, 78 as medium, and 40 as rich fertility soils. There were identified 15 prokaryotic phyla with a relative abundance higher than 1 %. According to this composition, poor and medium soils presented 43.3 %, medium and rich soils presented 44.4 %, and poor and rich soils presented 42.2 % of dissimilarities (Fig. 1). Considering the three types of soil studied, the samples showed 43.3 % of dissimilarities. The Proteobacteria phylum was the most representative in the three levels of soil fertility, accounting for approximately 36 % of the total OTUs in poor



Fig. 3. Discriminant analysis (LDA) performed with prokaryotic composition separated by (A) soil type and (B) plant species.

and medium soils and 39 % in rich soils (Fig. 2A). As Byss et al. (2008) and Semenov et al. (2020) already showed, the most abundant phyla of soil bacteria (Proteobacteria) developed well in high nutrient content environments. The relative abundance of the phyla Acidobacteria, Actinobacteria, Bacteroidetes, Cyanobacteria, and Verrucomicrobia varied across the three soil fertility levels. Acidobacteria increased from approximately 7 % in rich and medium soils to 12 % in poor soils; Actinobacteria increased from about 1 % in rich soil to 10 % in medium and poor soils; Bacteroidetes accounted for 3 % in poor and medium soils and 14 % in rich soils; Cyanobacteria accounted for <1 % of total OTUs in medium fertile soil and approximately 5 % in rich and poor soils; and Verrucomicrobia presented about 4 % of total OTUs in poor and medium fertile soils and <1 % in rich soils (Fig. 2A).

Liu et al. (2020) showed that the N source (organic or inorganic) affects the relative abundance of the six most abundant phyla identified: Proteobacteria, Acidobacteria, Chlorofexi, Actinobacteria, Planctomycetes, and Nitrospirae. In this context, soil fertilization with manure may significantly increase prokaryotic diversity due to the development of many unidentified taxa (Semenov et al., 2020). Similar as identified in this work, Zhelezova et al. (2019) identified that the phyla Proteobacteria and Acidobacteria were the most abundant in sandy poor soils, and prokaryotic communities at the phylum level were similar in different

vegetation types. According to the Tkacz et al. (2020) the global prokaryotic microbiota is recruited from the soil surrounding roots, and its profile is affected more by the type of root exudates than by soil type or plant species. These authors showed that the relative abundance of Proteobacteria remains stable in unplanted, bulk, and rhizosphere soils and increases strongly when the rhizoplane was analyzed. The phyla Acidobacteria and Actinobacteria also remained stable in unplanted, bulk, and rhizosphere soils; however, they decreased in a rhizoplane.

3.2. Prokaryotic diversity in each type of soil

Beta dispersion analysis showed significant differences (F = 12.1, p > 0.05) between the three different soil groups (Fig. 2B). Rich soils showed a lower dispersion than medium and poor fertility soils, while medium and poor soils presented a similar beta dispersion. This data show less variance in the community structure of rich soils compared to the other groups. The PERMANOVA test shows clear differences between the microbial community structure of the soil groups studied (F = 14.039, p = 0.001), explaining approximately 12.64 % of the variance in Bray-Curtis distances between samples. Pairwise comparisons of these groups showed that the slightest difference is between poor and medium fertility soils (R² = 0.036, p = 0.002), followed by the distance between



Fig. 4. Linear correlation (Pearson) among 15 individual phyla and soil parameters [clay, organic matter (OM), pH, phosphorous (P) and potassium (K)].

poor and rich soils ($R^2 = 0.114$, p = 0.001). The most marked difference is between groups of medium and rich soils ($R^2 = 0.207$, p < 0.001).

The boxplots shown in Fig. 2 (C, D, and E) identify the interquartile interval and outliers of the 15 phyla observed in the three soil fertility levels analyzed. The low number of outliers observed points to the reliability of distributions analyzed in this work. As can be observed, the abundance of the phylum Proteobacteria was higher in all soil conditions, which was already expected since Proteobacteria was the most abundant phylum in soil sequencing analysis (Liu et al., 2020; Semenov et al., 2020; Tkacz et al., 2020). However, the relative abundance of other phyla changes mainly according to soil characteristics (Yokota et al., 2022). Liu et al. (2020) studied rich soils, and the top five dominant phyla were Proteobacteria, Acidobacteria, Chlorofexi, Actinobacteria, and Planctomycetes, which account for approximately 65 % of the identified OTUs. Naliukhin et al. (2018) showed that the dominant phyla in fertilized and non-fertilized soils were Acidobacteria, Actinobacteria, Armatimonadetes, Bacteroidetes, Planctomycetes, Proteobacteria, and Verrucomicrobia. In our samples, the top five phyla of rich soils were Proteobacteria, Bacteroidetes, Acidobacteria, Cyanobacteria, and Firmicutes (68 % of total OTUs). All phyla identified in the top five phyla in Liu et al. (2020) were in our top ten.

Among the 11 main phyla found by Semenov et al. (2020), who studied medium fertile soils, only the archaeal Thaumarchaeota was not present in our list. Vera-Gargallo et al. (2019) studied hypersaline soils; according to our classification, these samples can be considered poor soils. These authors showed that salinity thresholds affect the composition of soil microbiomes. However, soil-specific properties (such as Al, P, organic matter, and water content) are the major influencers in microbial community composition and structure. From the top 12 pro-karyotic phyla identified by them, only the halophilic phylum Balneolaeota and the recently proposed Rhodothermaeota were not on our list. Lauber et al. (2009) studied 88 soils samples from North and South Americas and showed that the five major groups (Acidobacteria, Actinobacteria, Proteobacteria, Bacteroidetes, and Firmicutes) accounted for >90 % the OTUs. In our data, these phyla are also in our top five; however, they account for approximately 60 % of the identified OTUs.

3.3. Influence of soil type in prokaryotic community's

Tkacz et al. (2020) showed that soil type is one of the most important factors that affect microbial communities. A same soil microbiota colonizes all plant species, but plants can shape their structure. The data analysis presented in Fig. 3 corroborates that conclusion as prokaryotic communities present in studied soils are well separated according to the level of soil fertility (Fig. 3A). Host plant did not clearly separate microbial community profiles of the evaluated samples (Fig. 3B). Leff et al. (2015) studied variations in microbial communities associated with grasslands subjected to different soil nutrient levels (25 different grasslands across the world). These authors reported that the bacterial community's composition was affected by N and P levels, and the relative abundance of soil bacterial groups considered strongly copiotrophic, Actinobacteria and Proteobacteria, increased in nutrient-rich soils; the oligotrophic Acidobacteria decreased in this condition. A similar pattern of prokaryotic phylum was also observed in response to the carbon content in the soil (Eilers et al., 2010). Marschner et al. (2004) showed that the bacterial community structure is affected by soil pH and P fertilization (using DGGE analysis). In the same study, these authors showed that plant species did not affect the rhizospheric bacterial communities associated with cucumber and barley. Liu et al. (2014) showed that soil characteristics were critical influencers of microbial communities, although the analysis explained only 37.52 % of the total variability. These authors showed that geographical distance accounts for 14.75 % of total variability, and 47.73 % of the variability found was not explained.

Among the 15 phyla studied, ten were positively correlated with soil clay and organic matter percentages (Fig. 4; p < 0.05). Except for the



Fig. 5. Network analysis (using Bray-Curtis as similarity index and Fruchterman-Reingold as algorithm) of (A) Poor, (B) Medium, and (C) Rich soils, individually. (D) Network analysis of all pooled microorganisms and soil characteristics.

phyla Bacteroidetes and Proteobacteria, which presented a positive correlation with pH, nine other prokaryotic phyla showed an inverse correlation. As identified in this work, Lauber et al. (2009) showed that the relative abundance of Acidobacteria decreased and that Bacteroidetes increased with an increase in soil pH. However, these authors showed that the relative abundance of Actinobacteria OTUs and soil pH were positively correlated. Our results identified a negative correlation. Acidobacteria, Actinobacteria, Cloroflexi, and Verrucomicrobia increase their relative abundance with a decrease in soil P content. Bacteroidetes, Chlamydiae, and Gemmatimonadetes were positively related to soil P content. The RDA and Pearson correlation analyses performed by Jiang et al. (2019) indicated that soil nutrient availability, mainly available P and K, were the key environmental factors that shaped the bacterial community in saline soils cultivated with tomatoes. These authors tested the influence of six soil parameters on microbial communities. Interestingly, organic matter was less important than the available K, P, N, and soil electrical conductivity. Similar as the data presented in this work, Guo et al. (2019) showed that Acidobacteria was positively correlated with organic matter and negatively correlated with available P and K and pH (p < 0.05).

Network analysis of individual prokaryotic phyla in the three soil fertility classes showed that Verrucomicrobia, Gemmatimonadetes, and Elusimicrobia seem to have a central importance in distributions, and Proteobacteria did not present connections in the three analyzed soils (high number of connections; Fig. 5). The phylum Elusimicrobia is enriched in bioremediation of nitrogen polluted sediments; it plays an essential role in nitrogen cycling and contributes considerably to the removal of nitrogen from sediments. Gemmatimonadetes is a phylum closely related to polyphosphate accumulation in soil (Lu et al., 2022). The network formed by the phyla Tenericutes, Firmicutes, and Bacteroidetes in rich soils marks a high nutrient availability. The relation between Firmicutes and Tenericutes was already observed by Laconi et al. (2021) in enriched fertilized soils. Finally, the network among nine

generalist phyla (Planctomycetes, Proteobacteria, Bacteroidetes, Chloroflexi, Acidobacteria, Actinobacteria, Chlorobi, Cyanobacteria, and Verrucomicrobia) can be the key phyla affecting the stability of microbial communities in different types of soil (Jia et al., 2021).

However, Babin et al. (2019) showed that long-term agricultural management also influence microbial communities, but only at lower taxonomic levels. No clear differences were observed at phylum level. Thus, it is also important to consider soil management to understand microbial community changes. It is known, for example, that crop rotation reduces microbial pathogens load and increase soil biodiversity (Tilman et al., 2002). Granzow et al. (2017) showed that, depending on the cropping regime (monoculture, row intercropping, mixed intercropping), different soil microbial communities could be observed. Soil microbial community structure in more novel agricultural management methods, like pixel cropping (Ditzler and Driessen, 2022) are not yet to be reported in the literature.

Thus, this work summarizes and highlights the importance of soil physical and chemical characteristics to maintain the structure of microbial communities and their resilience. In face of an accelerated climate change scenario, it is crucial to understand the soil as a complex environment in which different communities work together to achieve an effective stability and a sustainable life.

4. Conclusion

Fifteen key phyla, which relative abundance up to 1 %, were identified in the 197 soil samples analyzed in this work. These phyla were also identified in several other reports covering soils from around the world. Soil nutrient analyzes enabled to classify soil samples in poor, median or rich. According to this classification, it was possible to identify differences in microbial communities at superior taxonomic levels (phyla), specially in phyla Proteobacteria, Acidobacteria and Actinobacteria. Others reports, that did not use our fertility classification, were unable to identify microbial community structure differences at phyla level. Soil physical and chemical characteristics were strongly related to the relative abundance the 15 prokaryotic phylum studied. Finally, the diversity of microbial communities present in plant rhizospheric systems may be shifted mainly by changes in soil characteristics (physical and chemical), which can be modulated by plant roots.

Declaration of competing interest

None.

Data availability

No data was used for the research described in the article.

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References

- Babin, D., Deubel, A., Jacquiod, S., Sørensen, S.J., Geistlinger, J., Grosch, R., Smalla, K., 2019. Impact of long-term agricultural management practices on soil prokaryotic communities. Soil Biol. Biochem. 129, 17–28. https://doi.org/10.1016/j. soilbio.2018.11.002.
- Bakker, P.A.H.M., Pieterse, C.M.J., de Jonge, R., Berendsen, R.L., 2018. The soil-borne legacy. Cell 172, 1178–1180. https://doi.org/10.1016/j.cell.2018.02.024.
- Beneduzi, A., dos Anjos Borges, L.G., Alvarenga, S.M., Faoro, H., de Souza, E.M., Vargas, L.K., Passaglia, L.M.P., 2019. Distinct grazing pressure loads generate different impacts on bacterial community in a long-term experiment in Pampa biome. App. Soil. Ecol. 137, 167–177. https://doi.org/10.1016/j. apsoil.2019.02.005.
- Byss, M., Elhottová, D., Tříska, J., Baldrian, P., 2008. Fungal bioremediation of the creosote-contaminated soil: influence of pleurotus ostreatus and Irpex lacteus on polycyclic aromatic hydrocarbons removal and soil microbial community composition in the laboratory-scale study. Chemosphere 73, 1518–1523. https://doi. org/10.1016/j.chemosphere.2008.07.030.
- Campos, S.B., Lisboa, B.B., Camargo, F.A.O., Bayer, C., Sczyrba, A., Dirksen, P., Albersmeier, A., Beneduzi, A., Costa, P.B., Maria, L., Passaglia, L.M.P., Vargas, L.K., Wendisch, V.F., 2016. Soil suppressiveness and its relations with the microbial community in a brazilian subtropical agroecosystem under different management systems. Soil Biol. Biochem. 96, 191–197. https://doi.org/10.1016/j. soilbio.2016.02.010.
- Chaparro, J.M., Sheflin, A.M., Manter, D.K., Vivanco, J.M., 2012. Manipulating the soil microbiome to increase soil health and plant fertility. Biol. Fertil. Soils 48, 489–499. https://doi.org/10.1007/s00374-012-0691-4.
- da Costa, P.B., de Campos, S.B., Albersmeier, A., Dirksen, P., Dresseno, A.L.P., dos Santos, O.J.A.P., et al., 2018. Invasion ecology applied to inoculation of plant growth promoting bacteria through a novel SIMPER-PCA approach. Plant Soil 422 (1), 467–478. https://doi.org/10.1007/s11104-017-3492-6.
- da Costa, P.B., van Elsas, J.D., Mallon, C., dos Anjos Borges, L.G., Passaglia, L.M.P., 2020. Efficiency of probiotic traits in plant inoculation is determined by environmental constrains. Soil Biol. Biochem. 148, 107893 https://doi.org/10.1016/j. soilbio.2020.107893.
- da Costa, P.B., Benucci, G.M.N., Chou, M.Y., Van Wyk, J., Chretien, M., Bonito, G., 2022. Soil origin and plant genotype modulate switchgrass aboveground productivity and root microbiome assembly. MBio 13 (2). https://doi.org/10.1128/mbio.00079-22 e00079-22.
- Daniel, R., 2005. The metagenomics of soil. Nat. Rev. Microbiol. 3, 470–478. Ditzler, L., Driessen, C., 2022. Automating agroecology: how to design a farming robot without a monocultural mindset? J. Agric. Environ. Ethic 35 (1), 1–31. https://doi. org/10.1007/s10806-021-09876-x.
- Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Appl. Soil Ecol 15 (1), 3–11. https://doi.org/10.1016/ S0929-1393(00)00067-6.
- Dubey, A., Malla, M.A., Khan, F., Chowdhary, K., Yadav, S., Kumar, A., Sharma, S., Khare, P.K., Khan, M.L., 2019. Soil microbiome: a key player for conservation of soil health under changing climate. Biodivers. Conserv. 28, 2405–2429. https://doi.org/ 10.1007/s10531-019-01760-5.
- Eilers, K.G., Lauber, C.L., Knight, R., Fierer, N., 2010. Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil. Soil Biol. Biochem. 42 (6), 896–903. https://doi.org/10.1016/j.soilbio.2010.02.003.
- FAO, ITPS, 2015. Status of the World's Soil Resources (SWSR) Main Report. Food and Agriculture Organization of the United Nations and Intergovernmental Technical Panel on Soils, Rome, Italy.
- FAO, UNEP, 2021. Global assessment of soil pollution Summary for policy makers. FAO, Rome. https://doi.org/10.4060/cb4827en.

- Fierer, N., 2017. Embracing the unknown: disentangling the complexities of the soil microbiome. Nat. Rev. Microbiol. 15, 579–590. https://doi.org/10.1038/ nrmicro.2017.87.
- Fox, A., Lüscher, A., Widmer, F., 2020. Plant species identity drives soil microbial community structures that persist under a following crop. Ecol. Evol. 10, 8652–8668. https://doi.org/10.1002/ece3.6560.
- Granada, C.E., Vargas, L.K., Lisboa, B.B., Giongo, A., Martinho, C.T., Pereira, L.D.M., de Oliveira, R.R., Bruxel, F., De Freitas, E.M., Passaglia, L.M.P., 2019. Bacterial and archaeal communities change with intensity of vegetation coverage in arenized soils from the pampa biome. Front. Microbiol. 10 https://doi.org/10.3389/ fmicb.2019.00497.
- Granzow, S., Kaiser, K., Wemheuer, B., Pfeiffer, B., Daniel, R., Vidal, S., Wemheuer, F., 2017. The effects of cropping regimes on fungal and bacterial communities of wheat and faba bean in a greenhouse pot experiment differ between plant species and compartment. Front. Microbiol. 8, 902. https://doi.org/10.3389/fmicb.2017.00902.
- Guo, A., Zhao, Z., Zhang, P., Yang, Q., Li, Y., Wang, G., 2019. Linkage between soil nutrient and microbial characteristic in an opencast mine, China. Sci. Total Environ. 671, 905–913. https://doi.org/10.1016/j.scitotenv.2019.03.065.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST-Palaeontological statistics. Paleontol. Elect. 4 (1), 1–9.
- Hartman, K., Tringe, S.G., 2019. Interactions between plants and soil shaping the root microbiome under abiotic stress. Biochem. J. 476, 2705–2724. https://doi.org/ 10.1042/BCJ20180615.
- Hu, L., Robert, C.A.M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., Van Der Heijden, M.G.A., Schlaeppi, K., Erb, M., 2018. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat. Commun. 9, 1–13. https://doi.org/10.1038/s41467-018-05122-7.
- Jia, M., Gao, Z., Gu, H., Zhao, C., Liu, M., Liu, F., Xie, L., Wang, L., Zhang, G., Liu, Y., Han, G., 2021. Effects of precipitation change and nitrogen addition on the composition, diversity, and molecular ecological network of soil bacterial communities in a desert steppe. PLoS ONE 16, 1–18. https://doi.org/10.1371/ journal.pone.0248194.
- Jiang, S.Q., Yu, Y.N., Gao, R.W., Wang, H., Zhang, J., Li, R., Long, X.H., Shen, Q.R., Chen, W., Cai, F., 2019. High-throughput absolute quantification sequencing reveals the effect of different fertilizer applications on bacterial community in a tomato cultivated coastal saline soil. Sci. Total Environ. 687, 601–609. https://doi.org/ 10.1016/j.scitotenv.2019.06.105.
- Joergensen, R.G., Wichern, F., 2008. Quantitative assessment of the fungal contribution to microbial tissue in soil. Soil Biol. Biochem. 40, 2977–2991. https://doi.org/ 10.1016/j.soilbio.2008.08.017.
- Laconi, A., Mughini-Gras, L., Tolosi, R., Grilli, G., Trocino, A., Carraro, L., Di Cesare, F., Cagnardi, P., Piccirillo, A., 2021. Microbial community composition and antimicrobial resistance in agricultural soils fertilized with livestock manure from conventional farming in northern Italy. Sci. Total Environ. 760, 143404 https://doi. org/10.1016/j.scitotenv.2020.143404.
- Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Appl. Environ. Microbiol. 75, 5111–5120. https://doi.org/10.1128/ AEM.00335-09.
- Leff, J.W., Jones, S.E., Prober, S.M., Barberán, A., Borer, E.T., Firn, J.L., Fierer, N., 2015. Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. PNAS 112, 10967–10972. https://doi.org/10.1073/ pnas.1508382112.
- Legaz, B.V., de Souza, D.M., Teixeira, R.F.M., Antón, A., Putman, B., Sala, S., 2017. Soil quality, properties, and functions in life cycle assessment: an evaluation of models. J. Clean. Product. 140. 502–515. https://doi.org/10.1016/i.jclepro.2016.05.077.
- J. Clean. Product. 140, 502–515. https://doi.org/10.1016/j.jclepro.2016.05.077.
 Liu, J., Sui, Y., Yu, Z., Shi, Y., Chu, H., Jin, J., Liu, X., Wang, G., 2014. High throughput sequencing analysis of biogeographical distribution of bacterial communities in the black soils of Northeast China. Soil Biol. Biochem. 70, 113–122. https://doi.org/ 10.1016/j.soilbio.2013.12.014.
- Liu, L., Li, C., Zhu, S., Xu, Y., Li, H., Zheng, X., Shi, R., 2020. Combined application of organic and inorganic nitrogen fertilizers affects soil prokaryotic communities compositions. Agronomy 10. https://doi.org/10.3390/agronomy10010132.
- Lu, S., He, Y.H., Chen, Y.Q., Chen, L.J., Wang, Z.Y., Yuan, J., Wu, L.C., 2022. Co-analysis of rhizosphere metabolomics and bacterial community structures to unfold soil ecosystem health in Camellia oleifera land under long-term cultivation. Appl. Soil Ecol. 171, 104336 https://doi.org/10.1016/j.apsoil.2021.104336.
- Marschner, P., Crowley, D., Yang, C.H., 2004. Development of specific rhizosphere bacterial communities in relation to plant species, nutrition and soil type. Plant Soil 261, 199–208. https://doi.org/10.1023/B:PLS0.0000035569.80747.c5.
- Mills, A.L., 2003. Eeping in touch: microbial life on soil particle surfaces. Adv. Agron. 78, 2–45.
- Monokrousos, N., Papatheodorou, E.M., Orfanoudakis, M., Jones, D.G., Scullion, J., Stamou, G.P., 2020. The effects of plant type, AMF inoculation and water regime on rhizosphere microbial communities. Europ. J. Soil Sci. 71 (2), 265–278. https://doi. org/10.1111/ejss.12882.
- Naliukhin, A.N., Khamitova, S.M., Glinushkin, A.P., Avdeev, Y.M., Snetilova, V.S., Laktionov, Y.V., Surova, V.V., Siluyanovaa, O.V., Belozerov, D.A., 2018. Changes in the metagenome of prokaryotic community as an indicator of fertility of arable soddy-podzolic soils upon fertilizer application. Eurasian Soil Sci. 51 (3), 321–326. https://doi.org/10.1134/S1064229318030092.
- Pathma, J., Debnath, A., Patil, J.B., Bhushan, L.S., 2021. Deciphering and harnessing plant microbiomes: Detangling the patterns and process—a clean, green road to sustainable agriculture. In: Curr Trends Microb Biotech Sustain Agricult. Springer, Singapore, pp. 123–159. https://doi.org/10.1007/978-981-15-6949-4_6.

- Peay, K.G., Baraloto, C., Fine, P.V.A., 2013. Strong coupling of plant and fungal community structure across western amazonian rainforests. ISME J. 7, 1852–1861. https://doi.org/10.1038/ismej.2013.66.
- Pii, Y., Borruso, L., Brusetti, L., Crecchio, C., Cesco, S., Mimmo, T., 2016. The interaction between iron nutrition, plant species and soil type shapes the rhizosphere microbiome. Plant Physiol. Biochem. 99, 39–48. https://doi.org/10.1016/j. plaphy.2015.12.002.
- Prober, S.M., Leff, J.W., Bates, S.T., Borer, E.T., Firn, J., Harpole, W.S., Fierer, N., 2015. Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. Ecol. Lett. 18 (1), 85–95. https://doi.org/10.1111/ele.12381.
- Semenov, M.V., Krasnov, G.S., Semenov, V.M., van Bruggen, A.H.C., 2020. Long-term fertilization rather than plant species shapes rhizosphere and bulk soil prokaryotic communities in agroecosystems. Appl. Soil Ecol. 154, 103641 https://doi.org/ 10.1016/j.apsoil.2020.103641.
- Sokol, N.W., Slessarev, E., Marschmann, G.L., Nicolas, A., Blazewicz, S.J., Brodie, E.L., Pett-Ridge, J., 2022. Life and death in the soil microbiome: how ecological processes influence biogeochemistry. Nature Rev. Microbiol. 0123456789 https://doi.org/ 10.1038/s41579-022-00695-z.
- de Souza, E.M., Lamb, T.I., Lamb, T.A., Silva, S., de Carvalho, F., Nyland, V., Cristina, M., Lopes, B., Grohs, M., Marconatto, L., Gustavo, L., Giongo, A., Granada, C.E., Sperotto, R.A., 2021. Rhizospheric Soil from Rice Paddy presents isolable bacteria

able to induce cold tolerance in Rice plants. J. Soil Sci. Plant Nutr. 21, 1993–2006. https://doi.org/10.1007/s42729-021-00496-y.

- Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418 (6898), 671–677. https://doi.org/10.1038/nature01014.
- Tkacz, A., Bestion, E., Bo, Z., Hortala, M., Poole, P.S., 2020. Influence of plant fraction, soil, and plant species on microbiota: a multikingdom comparison. mBio 11, 1–17. https://doi.org/10.1128/mBio.02785-19.
- Vera-Gargallo, B., Chowdhury, T.R., Brown, J., Fansler, S.J., Durán-Viseras, A., Sánchez-Porro, C., Bailey, V.L., Jansson, J.K., Ventosa, A., 2019. Spatial distribution of prokaryotic communities in hypersaline soils. Sci. Rep. 9, 1–12. https://doi.org/ 10.1038/s41598-018-38339-z.
- Wagg, C., Bender, S.F., Widmer, F., Van Der Heijden, M.G.A., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. PNAS 111, 5266–5270. https://doi.org/10.1073/pnas.1320054111.
- Yokota, M., Guan, Y., Fan, Y., Zhang, X., Yang, W., 2022. Vertical and temporal variations of soil bacterial and archaeal communities in wheat-soybean rotation agroecosystem. PeerJ 10, 1–18. https://doi.org/10.7717/peerj.12868.
- Zhelezova, A., Chernov, T., Tkhakakhova, A., Xenofontova, N., Semenov, M., Kutovaya, O., 2019. Prokaryotic community shifts during soil formation on sands in the tundra zone. PLoS ONE 14, 1–16. https://doi.org/10.1371/journal. pone.0206777.