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Soil microbial community responses to labile organic carbon fractions in relation to soil type and land use along a climate gradient

Paulina B. Ramírez[a], Sebastián Fuentes-Alburquenque[b], Beatriz Díez[b,c], Ignacio Vargas[a,d], Carlos A. Bonilla[a,d,*]

[a] *Departamento de Ingeniería Hidráulica y Ambiental, Pontificia Universidad Católica de Chile, Av. Vicuña Mackenna 4860, Macul, Santiago, 7820436, Chile*
[b] *Departamento Genética Molecular y Microbiología, Pontificia Universidad Católica de Chile, Chile*
[c] *Center for Climate and Resilience Research - CR2, Universidad de Chile, Chile*
[d] *Centro de Desarrollo Urbano Sustentable CONICYT/FONDAP/15110020, El Comendador 1916, Providencia, Santiago, 7520245, Chile*

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ABSTRACT

There has been a growing interest in studying the labile C pool in order to promote the sequestration and stabilization of soil organic carbon (SOC). Although labile SOC fractions have emerged as standardized indicators because of their potential to detect early SOC trends over time, the relationships between microbial attributes and labile SOC remains poorly understood. In this study, we explored the influence of labile SOC fractions on the topsoil bacteria-archaea community across 28 sites with different land use, climate aridity, and soil types across a wide range of SOC content (0.6–12%) in central Chile. We applied Illumina sequencing to the 16S rRNA to examine shifts in the diversity and composition of these soil microbial communities. Additionally, labile SOC fractions such as the permanganate oxidizable carbon (POXC) and light fraction organic matter (LFOM), along with the soil physicochemical properties were analyzed. The results demonstrated that among all of the environmental factors tested, the pH, POXC/SOC ratio and LFOM were key drivers of microbial community structure (β-diversity). The α-diversity metrics exhibited a decreasing trend when aridity increased, and community structure was found to vary, with high POXC/SOC in sites associated with drier conditions. In addition, POXC/SOC ratios and LFOM were clearly related to shifts in the relative abundances of specific taxonomic groups at genera level. When there was high POXC/SOC and low LFOM content, members of Bacteroidetes (*Adhaeribacter*, *Flavisolibacter*, and *Niastella*), Proteobacteria (*Skermanella*, *Ramlibacter*, and *Sphingomonas*), and Archaea (Thaumarchaeota) were found to be the most dominant groups; however, the microbial taxa responded differently to both labile C fraction types. These results have implications for understanding how labile C content can potentially be used to predict shifts in the microbial community, thus facilitating the development of predictive ecosystem models, as well as early warning indicators for soil degradation.

1. Introduction

Microbes play a key role in soil organic matter (SOM) decomposition and processes associated with SOM stabilization (Kallenbach et al., 2016). Changes in microbial communities in response to ecosystem disturbances such as increases in aridity as well as agricultural practices may represent large net changes in soil organic carbon (SOC) dynamics, which are important for soil productivity and sustainability (Dimassi et al., 2014; Farina et al., 2013; Hermle et al., 2008; Ramírez et al., 2019; Six and Paustian, 2014). Although microbial communities may be able to respond rapidly to changing environmental conditions (Cruz-Martínez et al., 2009; Prosser et al., 2007), their influence on SOM in a variety of climates, soil type and vegetation is still unclear. This understanding is particularly important in order to generate more accurate estimates of soil C stock under a future climate scenario.

The chemical composition of SOM as well as the long-term accessibility of stored carbon to decomposers have led to the study of labile SOC fractions in soils as early indicators of SOC changes and soil productivity (Belay-Tedla et al., 2009; Biederbeck et al., 1994; Gregorich et al., 1994; Song et al., 2012). Consequently, a wide range of labile SOC fractions

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* Corresponding author. Departamento de Ingeniería Hidráulica y Ambiental, Pontificia Universidad Católica de Chile, Av. Vicuña Mackenna 4860, Macul, Santiago, 7820436, Chile.
E-mail address: cbonilla@ing.puc.cl (C.A. Bonilla).

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have emerged based on chemical or physical separation methods (Cambardella and Elliott, 1992; Haynes, 2005; Sparling, 1992; Strosser, 2010). The permanganate oxidizable carbon (POXC) fraction, determined by the chemical SOM fractionation method, is one of the most reliable indicators used for soil health assessment, including the evaluation of short- and long-term impacts of soil management (Culman et al., 2012; Hurisso et al., 2016; Morrow et al., 2016; Skjemstad et al., 2006). Light fraction organic matter (LFOM) separated from the soil by density fractionation techniques, is composed of more recently deposited organic matter particles (plant residues), and responds more rapidly to the effects of management practices (Gregorich and Ellert, 1993; Janzen et al., 1992; Spycher et al., 1983; Tan et al., 2007). Although the labile SOC fractions might be more suitable than SOC to trace changes induced by soil management practices or environmental conditions, there are important gaps in the understanding about how the structure and composition of microbial communities respond to changes in soil labile fractions. This is an important issue to address since studies have not accounted for the intrinsic role of soil microorganisms as important factors controlling SOM lability, accessibility, and turnover rates.

Soil C pool dynamics are driven by shifts in microbial community composition and activity (Liang et al., 2017; Ng et al., 2014). However, despite the role of microorganisms within SOC dynamics, bacterial communities are not always entirely controlled by changes in SOC content, which is particular evident when this relationship is evaluated at a regional scale (Delgado-Baquerizo et al., 2018; Maestre et al., 2015; Plassart et al., 2019; Tian et al., 2017). On large geographic scales, climate and soil pH have been documented as primary factors controlling microbial community structure and composition (Delgado-Baquerizo et al., 2016; Maestre et al., 2015; Rousk et al., 2010; Shen et al., 2013). In addition to the influence of these factors, soil physical protection has also been named among the factors controlling the microbial community shifts (Schimel and Schaeffer, 2012). Accordingly, labile sources of carbon, released by a physical or chemical disturbance in our study, may be more responsive to microorganisms than SOC. Therefore, we hypothesize that shifts in soil bacterial-archaeal diversity and composition are primarily explained by labile SOC fractions rather than by SOC on different ecosystems. In that sense, microbial communities associated with the labile SOC fractions might be more suitable as ecological indicators to evaluate SOC changes in response to global warming and agricultural intensification, and this will improve the ability to predict soil degradation induced by SOC decline.

To test our hypothesis, we studied microbial communities across soils with contrasting SOC content and labile SOC fractions under different climate aridity and land use conditions. Sequencing of the 16S rRNA genes together with physicochemical analyses, LFOM, and POXC measurements were used to discern the structure of the soil bacterial and archaeal communities. Therefore, the objectives of this study were: (1) To assess the relationships between soil microbial community diversity and physicochemical factors, (2) To evaluate the relative importance of the labile SOC fraction as a driver of the soil microbial communities in terms of their structure and composition, and (3) To identify the specific taxa that may be linked to increased labile SOC fractions.

2. Materials and methods

2.1. Study area description

A total of 28 sites were sampled over two years in the summer season (January to February) of 2016 and 2017 (Table 1). The sites are located at elevations below 500 m on nearly flat slopes (less than 6%) in two main zones, semiarid and subhumid areas from the Metropolitana to Maule regions (33°00′ S to 36°00′ S), and humid and hyper humid areas in Araucanía region (38°00′ S to 40°00’ S) (Fig. 1).

Semiarid and subhumid areas includes the most productive agricultural land in the country, characterized by irrigation and intensive agriculture practices (Bonilla and Johnson, 2012; Bonilla and Vidal, 2011). These soils have suffered significant periods of water shortages (Álvaro-Fuentes et al., 2008). Here, the mean annual temperature (MAT)

Table 1

Site characteristics and geographic location of the 28 study sites.

Site	Soil order[a]	Climate	Elevation (m)	Latitude (S)	Longitude (W)	Vegetation cover[b]/Land use[c]
AGD	Mollisol	Semiarid	168	33.57°	71.15°	Orchard/WP
LAP	Inceptisol	Semiarid	105	33.84°	71.28°	Cereal crop/C
LGG	Alfisol	Semiarid	186	33.96°	71.52°	Grassland recolonization, tree shrub/NC
PAH	Mollisol	Semiarid	221	33.58°	71.01°	Cereal crop/C
PMR	Mollisol	Semiarid	186	33.49°	71.20°	Crop/C
TRO	Mollisol	Semiarid	143	33.98°	71.40°	Orchard/WP
DAO	Inceptisol	Subhumid	92	35.45°	71.70°	Cereal crop/C
LIU	Inceptisol	Subhumid	108	35.39°	71.59°	Cereal crop/C
TAL	Alfisol	Subhumid	141	35.37°	71.56°	Cereal crop/C
CHO	Inceptisol	Humid	34	38.62°	72.85°	Grassland recolonization/NC
LCH	Inceptisol	Humid	125	38.07°	73.02°	Cereal crop/C
LMO	Inceptisol	Humid	111	38.04°	73.06°	Grassland recolonization/NC
LTA	Inceptisol	Humid	288	38.60°	72.30°	Grassland recolonization/NC
RHO	Inceptisol	Humid	83	38.02°	73.03°	Crop/C
SCS	Inceptisol	Humid	71	38.06°	72.85°	Grassland recolonization, shrub/NC
SSF	Alfisol	Humid	293	38.20°	72.78°	Cereal crop/C
AGF	Inceptisol	Hyper humid	308	38.53°	72.25°	Grassland recolonization/NC
ARC	Ultisol	Hyper humid	56	38.75°	72.85°	Cereal crop/C
CHS	Andisol	Hyper humid	457	39.38°	72.22°	Grassland recolonization/NC
HCE	Inceptisol	Hyper humid	33	38.69°	72.88°	Grassland recolonization/C
LAS	Andisol	Hyper humid	97	39.20°	72.67°	Grassland recolonization/NC
LOC	Andisol	Hyper humid	115	39.38°	72.62°	Pine forest/WP
MAL	Andisol	Hyper humid	150	39.35°	72.57°	Cereal crop/C
PHE	Andisol	Hyper humid	321	38.66°	72.25°	Grassland recolonization/shrub/NC
PQN	Inceptisol	Hyper humid	63	38.79°	73.31°	Grassland recolonization/NC
PUE	Inceptisol	Hyper humid	4	38.77°	73.39°	Grassland recolonization/NC
SPT	Andisol	Hyper humid	400	38.66°	72.11°	Cereal crop/C
SPTN	Andisol	Hyper humid	398	38.65°	72.11°	Native forest/NF

[a] The Soil Order Taxonomy was reported by CIREN according to Soil Survey Staff (2006).

[b] Vegetation cover within the survey area.

[c] Land use was categorized as C: cultivated; NC: non-cultivated; NF: native forest; WP: woody perennial.

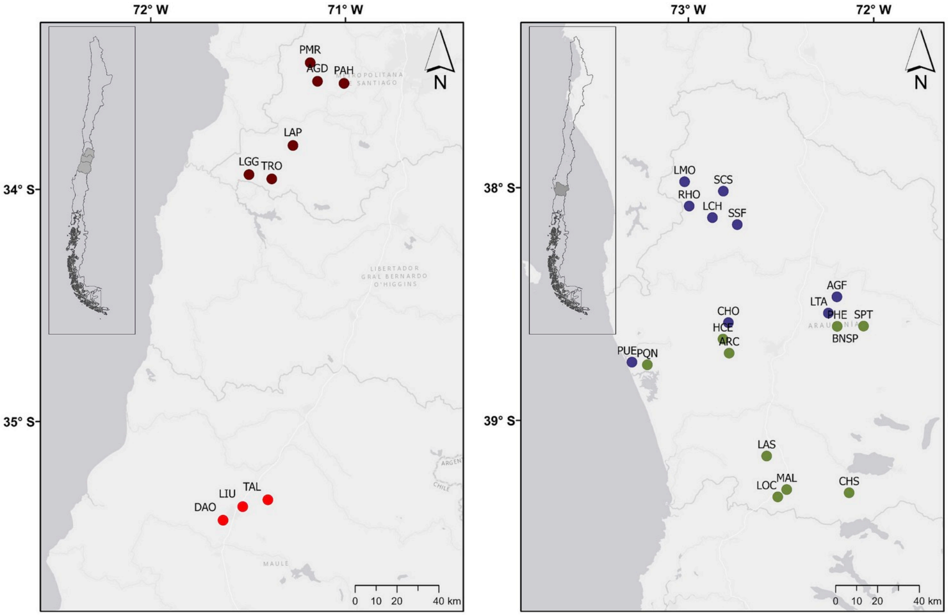

Fig. 1. Soil sampling areas in north-central and south-central Chile. Semiarid sites are shown as brown circles, subhumid as red circles, humid as blue circles, and hyper humid as green circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

reaches 15 °C, the annual evapotranspiration (ET) about 1200 mm, and the mean annual precipitation (MAP) ranges from 400 mm to 635 mm. In contrast, in the humid and hyper humid conditions, the climate is typically rainy cool temperate with an ET of 650 mm, a MAT of 12 °C and a MAP >1200 mm. Agricultural land in the Andean foothills are dominated by volcanic soils (Andisols) characterized by high SOC content and the presence of evergreen forests dominated by *Nothofagus* species (Panichini et al., 2017). Here, soils are commonly used for small-grain crops, pasture, or forest plantations (Stolpe, 2005).

2.2. Climate

The climate data were obtained from two Chilean government agencies, General Directorate of Water (DGA), and National Institute of Agriculture Research (INIA). The aridity at each site was obtained by computing the aridity index (AI) based on the United Nations Environment Programme (UNEP, 1992) as the ratio of MAP to ET. Thus, low AI values in extremely arid regions imply that all precipitation was essentially converted into evapotranspiration. Considering the AI and the dry season duration (UNESCO, 2010), the climate aridity was categorized into four regimes according to water availability: semiarid (AI = 0.20–0.5), subhumid (AI = 0.5–0.65), humid (AI = > 1) with a dry period of 3–4 months, and hyper humid (AI = > 1) with a dry period of 1–2 months.

2.3. Soil sampling and experimental design

The sites were selected to represent a large range of different soil types and C contents, based on the official national soil repository data from the Chilean Natural Resources Information Center (CIREN) (Table 1). The CIREN sites were relocated with GPS in order to have information on the land use history of each site. Initially, all CIREN sites were used for agricultural purposes, however, some of them have changed over the last three decades. Thus, the sampling sites were classified in four land use types: 1) cultivated (C), sites planted with annual crop systems and/or vegetables that were continuously cultivated for at least 20 years, 2) non-cultivated (NC) agricultural sites without agricultural activity or abandoned with natural vegetation due to secondary vegetation succession for at least 5 years, 3) native forest or relatively undisturbed systems (NF, mainly with *Nothofagus obliqua* (Mirb.) Blume, a type of native oak), and 4) woody perennial (WP, fruit orchard and industrial tree planting) for at least 7 years.

The sites were sampled with two replicates randomly assigned at a distance of 100 m. Plant residues and the O horizon were removed, just prior to sampling. In order to determine the physicochemical parameters, soils were collected at a depth of 15 cm using a soil auger (20 cm diameter). For the microbiological analyses, the auger-hole was deepened approximately 30 cm to ensure that the inner walls of the core were scraped in the upper 15 cm of soil. In each replicate, two soil samples (four samples per site) were scraped with sterile 15 mL polypropylene tubes without gravel and plant debris. The samples were transported in an ice-box and stored at −80 °C until the DNA was extracted.

2.4. Soil physicochemical properties

For the physicochemical analyses (Table 2), air-dried soil samples were sieved < 2 mm. The SOC was determined using the Walkley Black method (Walkley and Black, 1934). The soil texture (clay, silt, and sand)

Table 2
Soil physicochemical properties categorized according to aridity regimes. Average values and standard deviations for the studied soils are shown.

Aridity regime	Sand (g 100g^{-1})	Clay (g 100g^{-1})	BD (g cm^{-3})	WSA (%> 0.25 mm)	C/N	pH
Semiarid	50.3 ± 24.3^{a}	24.5 ± 11.4^{a}	1.5 ± 0.1^{c}	66.5 ± 11.6^{a}	19.5 ± 3.9^{a}	7.2 ± 0.6^{c}
Subhumid	32.4 ± 10.7^{a}	26.8 ± 0.7^{a}	1.3 ± 0.1b^{c}	73.0 ± 5.3^{a}	18.0 ± 0.0a	6.5 ± 0.1^{b}
Humid	49.3 ± 13.7^{a}	18.9 ± 6.2^{a}	1.1 ± 0.1^{b}	88.5 ± 9.0^{b}	16.2 ± 0.4a	5.5 ± 0.3^{a}
Hyper humid	37.2 ± 15.6^{a}	24.3 ± 11.8^{a}	0.8 ± 0.3^{a}	89.8 ± 3.3^{b}	16.2 ± 4.4a	5.7 ± 0.3^{a}

Significant pairwise differences ($P < 0.05$) are denoted with different letters. BD: bulk density; WSA: water-stable aggregates. Significant pairwise differences ($P < 0.05$) are denoted with different letters.

was determined using the hydrometer method (Gee and Bauder, 1986). The nitrogen was measured using the Kjeldahl digestion, and the pH was measured in a 1:2.5 soil/water suspension (Sadsawka et al., 2006). The bulk soil density was measured using the gravimetric method with the soil cores oven-dried at 105 °C for 48 h (Blake and Hartge, 1986). The water-stable aggregates were measured by using a wet-sieving apparatus (Eijkelkamp, Giesbeek, Netherlands) and calculated as the proportional mass of stable aggregates in the 1–2 mm range relative to the overall soil as described by Kemper and Rosenau (1986).

2.5. Labile SOC fractions

The POXC was determined using the methodology described by Weil et al. (2003), with slight modifications as explained by Culman et al. (2012). Briefly, 2.5 g sieved soil were added in duplicate into propylene tubes with 18 mL of deionized water and 2 mL of 0.2 M $KMnO_4$. The tubes were shaken vigorously for 2 min at 240 oscillations/min. The tubes were removed from the shaker and allowed to settle for 10 min at room temperature. Then, 0.5 mL of solution was taken from the tube and placed in another tube with 49.5 mL of deionized water, allowing the reaction to end. The absorbance of each sample was measured at 550 nm using a Pocket Colorimeter™ II, Wavelength Specific Model.

The LFOM was measured using a modified Janzen et al. (1992) method. Specifically, 10 g of sieved soil was weighed and 40 mL NaI was added with a density of 1.7 g cm^{-3}. The tubes were shaken and then allowed to settle for 48 h before removing the floating material using a fiberglass filter in a Buchner funnel. The material was washed twice with demineralized water, transferred onto filter papers, dried at 60 °C for 24 h, and weighed. The LFOM was reported as the mass in g kg^{-1} soil because on degraded soils, mostly under semiarid conditions, the amount of LFOM was negligible and not sufficient for the elemental C analysis of LFOM.

2.6. Soil DNA extraction, 16S rRNA gene amplification, and sequencing

DNA was extracted from fresh soils (0.25 g dry weight equivalent) using the Power Soil DNA Isolation Kit (MoBio, Carlsbad, CA, USA) following the manufacturer's instructions. The nucleic acids were quantified using the Qubit DNA probe (Invitrogen) and the quality was assessed by spectrophotometry (A_{260}/A_{280} ratio).

Amplification and sequencing of the 16S rRNA gene was performed according to the Earth Microbiome Project protocols (www.earthmicrobiome.org/protocols-and-standards). The V4–V5 region (16S rRNA) was amplified by PCR with 515F (GTGYCAGCMGCCGCGGTAA) and 926R (CCGYCAATTYMTTTRAGTTT) bacterial-archaeal primer pairs (Walters et al., 2016). The amplification products were multiplexed and sequenced in the Illumina MiSeq platform (250 bp x 2) at Argonne National Laboratory (Lemont, IL, USA) as described previously by Caporaso et al. (2012). The sequences were submitted to the NCBI BioProject database with the project identification number PRJNA509899 and sample accession numbers SAMN10589514 to SAMN10589621.

2.7. Sequenced data processing and taxonomic assessment

Raw sequence processing for the Operational Taxonomic Unit (OTU) were performed using the QIIME2 software package v.2017.10 (Caporaso et al., 2010). The sequences were quality-checked, assembled, and chimera-filtered using the DADA2 algorithm (100% identity) (Callahan et al., 2016). The OTU taxonomy was assigned using the SILVA 128 database (Quast et al., 2013). The 0.98% of the reads that corresponded to chloroplasts and mitochondria were discarded. An OTU table was composed of 1,635,321 reads distributed into 17,541 OTUs across 108 samples (4 samples were discarded for low depth sequencing). The OTU table was rarefied to 6808 reads per sample to compute the diversity metrics. For the phylogenetic metrics, the sequences were aligned with MAFFT (Katoh and Standley, 2013) and the tree was constructed using FastTree (Price et al., 2010).

2.8. Statistical analyses

Normality and homoscedasticity were tested using Shapiro-Wilk and Levene's test, respectively. Because some variables did not pass the test, analysis of variances was conducted using a non-parametric Mann-Whitney *U* test. Fisher's Least Significant Difference (LSD) test was used to determine pairwise differences of means at 95% confidence using Statgraphics plus 5.1 (Manugistics, Inc., Rockville, MD, USA). The α-diversity indices include the OTU richness, Shannon, Pielou's evenness, and Faith's phylogenetic diversity. Replicates were averaged to give a single site value, and Spearman's rank correlation coefficients (ρ) were used to examine the linear relationship between soil physicochemical properties, climate aridity and α-diversity indices in Sigma Plot software (Systat Software, Inc, Point Richmond, CA).

All analyses were performed in R software version 2.5–5 (R Foundation for Statistical Computing, Vienna, Austria) using the R packages vegan (Oksanen et al., 2013). For the calculation of β-diversity, Bray Curtis dissimilarity (1 - similarity) and weighted UniFrac distance, the OTU table was first collapsed by site (i.e. the relative abundance of each OTU was averaged in each of the 28 sites). The Mantel tests were performed to test correlations between community β-diversity and geographical distance matrixes as well as between community β-diversity and Euclidean distances of environmental variables (climate and edaphic factors).

A distance-based redundancy analysis (dbRDA) was conducted to assess the influence of spatial and environmental data on community β-diversity at different sites. We further transformed the geographical latitude and longitude coordinates into a geographical distance matrix measured in meters, using the geosphere R package (Hijmans et al., 2019). The spatial variables were obtained using the distance matrix to determine the Principal Coordinates of Neighbor Matrices (PCNM), which represent linear descriptors of geographical distances that can be included in the same way as any numerical metadata in a multivariate analysis (Borcard et al., 1992). The environmental variables were first examined to reduce the collinearity by excluding predictors with a variance inflation factor (VIF) > 10. We performed a forward selection procedure of the environmental and PCNM variables to select the descriptors that had significant effects on β-diversity (Blanchet et al., 2008). A partial db-RDA was performed on the data set to partition the variance explained by each variable (Peres-Neto and Legendre, 2010) The results of variation partitioning were based on adjusted fractions of variation (Peres-Neto et al., 2006), using the RsquareAdj function implemented in R package vegan.

2.9. Differential abundance across different levels of labile SOC fractions

The identification of the microbial genera that were differentially abundant across the POXC/SOC levels was performed by analyzing the community composition (ANCOM, Mandal et al., 2015) implemented in QIIME2. The non-rarefied OTU table was collapsed to the genus level. Low abundance genera ($<0.01\%$ of the total reads and present in <3 of the 108 samples) were filtered out because no comparisons among the groups could be computed with these values. ANCOM was applied to find the differences in the mean abundances for each genus across 5 groups defined by increasing the POXC/SOC ratio levels (%) to 0.5–1.0, 1.0–1.5, 1.5–2.0, 2.0–3.0, and >3.0. The 62 genera with significant different mean abundances were filtered into a new table and each one was correlated with the three main environmental descriptors in the metadata, namely, the POXC/SOC, LFOM, and pH. After the multiple Spearman's correlations, genera passing the following four criteria were kept: 1) $\rho < -0.6$ (strong negative correlation), 2) $\rho > 0.6$ (strong positive correlation), 3) p-value < 0.0001 (significant correlation), and 4) $|\rho_{POXC/SOC}| > |\rho_{LightFraction}|$, $|\rho_{POXC/SOC}| > |\rho_{pH}|$ (the correlation with the

POXC/SOC was stronger than the correlation with the other two variables). The same procedure was applied for the LFOM, where the 5 groups were defined by the increased LFOM content (g kg^{-1} soil): 2–5, 5–10, 10–25, 30–60, and >100. The 25 genera with significant different mean abundances were filtered using the same criteria, except for the fourth that was: $|\rho_{LightFraction}| > |\rho_{POXC/SOC}|$, $|\rho_{LightFraction}| > |\rho_{pH}|$.

3. Results

3.1. Soil physicochemical properties

The highest SOC content were mainly observed in hyper humid conditions (71.4 g kg^{-1}) and the lowest SOC content was found in semiarid conditions (10.9 g kg^{-1}) (Table 3). POXC and LFOM exhibited similar trends to those found in SOC, showing significant differences along the aridity gradient. POXC accounted for a high proportion of the SOC (POCX/SOC) in drier climates, from 3.0% for semiarid conditions to 1.2% in hyper humid conditions. LFOM increased in the range of 3.3–4.4 g kg^{-1} of soil in the drier areas to 41.0 g kg^{-1} of soil for hyper humid areas (Table 3). Across all 28 sites, the results showed that the aridity index had significant effects on SOC content ($\rho = 0.94$, $P < 0.05$) (Table 4).

3.2. Bacterial-archaeal diversity associated with the environmental factors

The relationships between the common α-diversity indices were also explored (Table 4). Analysis of the correlations among the diversity measures showed that the Shannon index was significantly correlated with each one of the other diversity metrics. In addition, the Shannon diversity showed significant correlations ($P < 0.05$) with the aridity regime ($\rho = 0.54$), SOC ($\rho = 0.54$), POXC ($\rho = 0.47$), LFOM ($\rho = 0.38$) and POXC/SOC ($\rho = -0.42$). The OTU richness showed a significant ($P < 0.05$) increase with aridity index ($\rho = 0.49$), SOC content ($\rho = 0.48$), POXC ($\rho = 0.46$), and a decrease with bulk density ($\rho = -0.44$) and the POXC/SOC ratio ($\rho = -0.34$). The phylogenetic diversity increased significantly with increasing pH ($\rho = 0.52$), water-stable aggregates ($\rho = 0.52$) and C/N ($\rho = 0.41$).

The microbial community clustering based on the Bray-Curtis dissimilarity distributed the samples into two main groups (Fig. 2). The first group contained all 19 sites from the south, which are found in areas with low POXC/SOC and low pH under decreasing aridity (AI > 1). The second group contained all 9 sites from the north, which are found in areas with high POXC/SOC and high pH under increasing aridity (AI < 1). Since the community similarities decreased with geographical distance (Fig. S1), we investigated whether the community differences were correlated to the geographical distance or the environment. Mantel tests showed that the Bray-Curtis community distance matrix was significantly correlated with both the geographic (Mantel's $r = 0.702$, $P = 0.001$) and environmental (Mantel's $r = 0.208$, $P = 0.036$) distance matrices. On the other hand, the matrix of the pairwise phylogenetic distances (weighted UniFrac) was significantly correlated (Mantel's $r = 0.691$, $P = 0.001$) with only the geographic distance matrix, but not with the environmental distance matrix (Mantel's $r = 0.054$, $P = 0.277$).

Table 3
Mean values ± standard deviation for soil organic carbon and labile fractions observed in different aridity regimes.

Aridity regime	SOC (g kg^{-1} soil)	POXC (g kg^{-1} soil)	POXC/SOC (%)	LFOM (g kg^{-1} soil)
Semiarid	10.7 ± 3.8^{a}	0.32 ± 0.12^{a}	3.0 ± 0.5^{a}	4.0 ± 1.1^{a}
Subhumid	16.3 ± 3.2^{a}	0.46 ± 0.10^{a}	2.8 ± 0.1^{a}	3.3 ± 0.5^{ab}
Humid	26.5 ± 6.1^{a}	0.40 ± 0.08^{a}	1.5 ± 0.2^{b}	8.2 ± 1.9^{ab}
Hyper humid	71.4 ± 35.4^{b}	0.77 ± 0.27^{b}	1.2 ± 0.3^{b}	41.0 ± 45.0^{b}

Significant pairwise differences ($P < 0.05$) are denoted with different letters. SOC: soil organic carbon; POXC: permanganate oxidizable carbon; POXC/SOC: POXC to SOC ratio; LFOM: light fraction organic matter.

The effects of environmental and spatial variables on the bacterial-archaeal communities were assessed by db-RDA according to the OTU-based Bray-Curtis dissimilarity (Fig. 3). A forward selection of the explanatory variables only retained pH, POXC/SOC, and LFOM as significant environmental variables. PCNM variables were not maintained as significant spatial descriptors. The environmental variables SOC, POXC, C/N, texture, bulk density, soil taxonomic order, aridity and land use were not significant descriptors and were thus excluded from further analyses. The db-RDA plot shows a cluster with high values of pH and POXC/SOC associated with semiarid and subhumid conditions, whereas a second cluster was closely related to LFOM content under hyper humid areas (Fig. 3). A partial db-RDA analysis showed that a total of 16.7% of the community variations was explained by pH, POXC/SOC and LFOM (Table 5). The influence of these variables independently accounted for 9.1%, 9.8% and 4.1% of the explained variance, whereas the mixed effects accounted for 6.1% (i.e. the total explained variation minus the exclusive contribution of each three variable). In addition, for each variable, the exclusive importance of pH, POXC/SOC, LFOM accounted for less than 4% of the total variance. The analysis of phylogenetic β-diversity (weighted UniFrac) exhibited a clustering pattern similar to the one found in the Bray-Curtis analysis (Fig. S2).

3.3. Linking the soil bacterial-archaeal structure to the labile SOC fractions

After determining the importance of both the POXC/SOC ratio and the LFOM for explaining the microbial community, the samples were grouped into five POXC/SOC ratio ranges (%): 0.5–1.0, 1.0–1.5, 1.5–2.0, 2.0–3.0, and >3.0. Genera that correlated with these different labile carbon content ranges were identified across the samples. The soil pH was excluded from further taxa analyses because it has been widely described in the literature. A total of 62 genera were significantly different in abundance between the five POXC/SOC ratio ranges. Consistent shifts in the microbial community composition were observed across the larger POXC/SOC ratios and the relative abundance of specific bacterial genera became more dominant when the POXC/SOC values were higher than 2%. Three genera, *Adhaeribacter* (Bacteroidetes), *Skermanella* (Alphaproteobacteria), and an unidentified member of the genus Acidobacteria subgroup 7 increased with the POXC/SOC (Spearman's $\rho > 0.6$, $P < 0.0001$), accounting for 0.14–0.20% of the total sequences. Five other unidentified genera were found to decrease with the POXC/SOC (Spearman's $\rho < -0.6$, $P < 0.0001$), namely, one each assigned to the Acidobacteria subgroup 2, the Chloroflexi JG37-AG-4 group, the Planctomyceteceae family, and two members of the Solirubrobacterales (Actinobacteria), accounting for 0.4–1.5% of the total sequences (Fig. 4a).

For the LFOM content (g kg^{-1} soil), the same analysis was performed by grouping the samples into five ranges: 2–5, 5–10, 10–25, 30–60, and >100. A total of 25 bacterial genera were found to have significantly different abundances across the five LFOM content ranges. Two genera, *Edaphobacter* (Acidobacteria) and Candidate *Xiphinematobacter* (Verrucomicrobia) were found to increase with the LFOM (Spearman's $\rho > 0.6$, $P < 0.0001$), accounting for roughly 0.2% of the total sequences. Five genera (0.3–1.5% of the total), *Flavisolibacter* (Bacteroidetes), *Niastella* (Bacteroidetes), *Ramlibacter* (Betaproteobacteria), *Sphingomonas* (Alphaproteobacteria) and an uncultured soil Thaumarchaeota, decreased with the LFOM content (Spearman's $\rho < -0.6$, $P < 0.0001$).

4. Discussion

The interaction between soil microbial community and labile organic fractions has been largely unexplored. Here, we provide evidence that microbial community structure and composition were primarily controlled by labile SOC fractions rather than by SOC content under changes in climates aridity, soil types, and land use record. Our data

Table 4
Correlation coefficients (Spearman's ρ) between the soil physicochemical properties, climate, and α-diversity indices.

	PD	Richness	Evenness	SOC	POXC	POXC/SOC	WSA	LFOM	Sand	Silt	Clay	C/N	pH	BD	AI
Shannon	0.42	0.93	0.72	0.54	0.47	−0.42	NS	0.38	−0.39	0.44	NS	NS	NS	−0.51	0.54
PD		0.51	NS	NS	NS	NS	−0.48	NS	NS	NS	NS	0.41	0.52	NS	NS
Richness			0.49	0.48	0.46	−0.34	NS	NS	NS	NS	NS	NS	NS	−0.44	0.49
Evenness				0.49	NS	−0.49	NS	NS	−0.38	0.46	NS	NS	NS	−0.44	0.50
SOC					0.84	−0.91	0.57	0.82	NS	0.42	NS	NS	−0.59	−0.94	0.94
POXC						−0.58	NS	0.71	−0.42	0.50	NS	NS	−0.33	−0.79	0.75
POXC/SOC							−0.57	−0.74	NS	NS	NS	NS	0.64	0.87	−0.89
WSA								0.48	NS	NS	NS	NS	−0.82	−0.58	0.55
LFOM									NS	NS	NS	NS	−0.65	−0.84	0.83
Sand										−0.85	NS	NS	NS	NS	NS
Silt											NS	NS	NS	NS	0.39
Clay												NS	NS	NS	NS
C/N													NS	NS	NS
pH														0.65	−0.62
BD															−0.90

N.S. = $P > 0.05$, non-significant relationship between the two variables.
PD: phylogenetic diversity; SOC: soil organic carbon, POXC: permanganate oxidizable carbon; POXC/SOC: POXC to SOC ratio; WSA: water-stable aggregates; LFOM: light fraction organic matter; BD: bulk density; AI: aridity index.

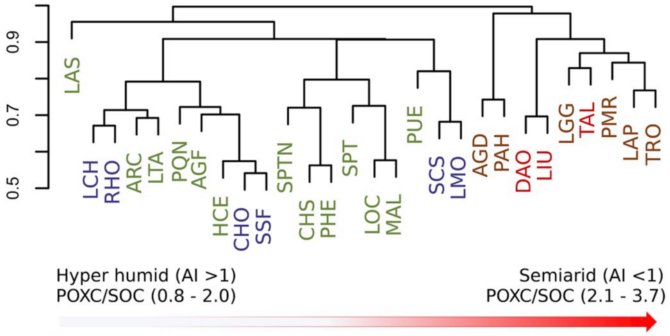

Fig. 2. Cluster analysis of the microbial communities based on the Bray–Curtis dissimilarity matrix.

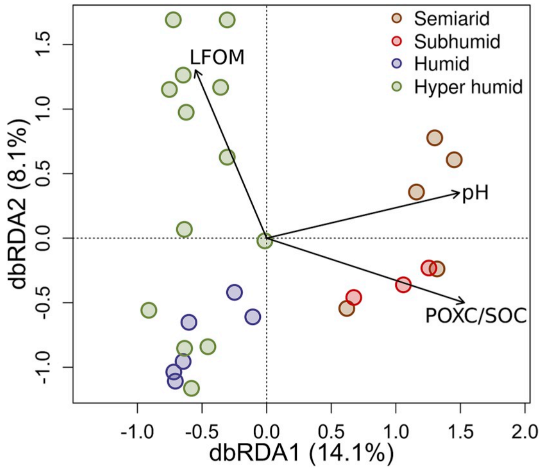

Fig. 3. Distance-based redundancy analysis (db-RDA) of the community beta-diversity (Bray-Curtis dissimilarity), soil physicochemical properties, and spatial variables. Variables and physicochemical vector correlation plots showing strengths and directions of the relationships between the physicochemical variables. Axis legends represent the percentages of variation explained by the axis.

further demonstrate that POXC and LFOM regulated changes in microbial communities, which were supported by variations in α-diversity, most importantly in Shannon and OTU richness, as well as in β-diversity. Such differential responses were represented by a community-wide response, and variations in the microbial composition and in the abundances of certain microbial taxa.

4.1. Effects of soil physicochemical properties on bacterial-archaeal communities

Although our findings provide evidence that the SOC content was not a significant predictor of the community β-diversity, a positive correlation was found between SOC and certain α-diversity metrics (Shannon index, OTU richness, and evenness). Similarly, previous studies have also identified a significant relationship between the α-diversity and the SOC content (Maestre et al., 2015; Ren et al., 2018b). In addition, previous studies (Delgado-Baquerizo et al., 2016; Maestre et al., 2015; Wieder et al., 2014) have reported SOC as the strongest bacterial community predictor in SOC content under 40 g kg^{-1} soil. In the present study, the C content ranged from 6 to 121 g kg^{-1} soil, suggesting that SOC has a larger influence in the communities when the SOC content is low. In addition, soil variables such as soil pH, POXC/SOC, LFOM were key environmental drivers of the community β-diversity. We found that soil pH was the main descriptor of phylogenetic (alpha) diversity and β-diversity. This is in accordance with results of Siciliano et al. (2014), who reported that soil pH plays a larger role in determining phylogenetic structure and composition of bacterial communities. Therefore, once again this highlights the importance of soil pH driving changes in microbial community under different ecosystem, particularly in southern hemisphere (Delgado-Baquerizo et al., 2018, 2016; Fierer and R. B. Jackson, 2006; Rousk et al., 2010).

Our analysis showed negative effects of increasing bulk density on the Shannon diversity, OTU richness, and evenness. Low values of bulk density reflect an improvement in the soil structure, and it is correlated with high water infiltration and low rates of surface runoff and erosion (Xiao et al., 2017). It has already been shown that this parameter affects

Table 5
Total and exclusive variation of β-diversity explained by the significant environmental variables.

Explanatory variable	Bray-Curtis	
	Variation explained (%)	
	Total	Exclusive
pH	9.1	3.9
POXC/SOC	9.8	3.3
LFOM	4.1	3.4
Total explained	16.7	–
Unexplained	83.3	–

POXC/SOC: POXC to SOC ratio; LFOM: light Fraction organic matter.

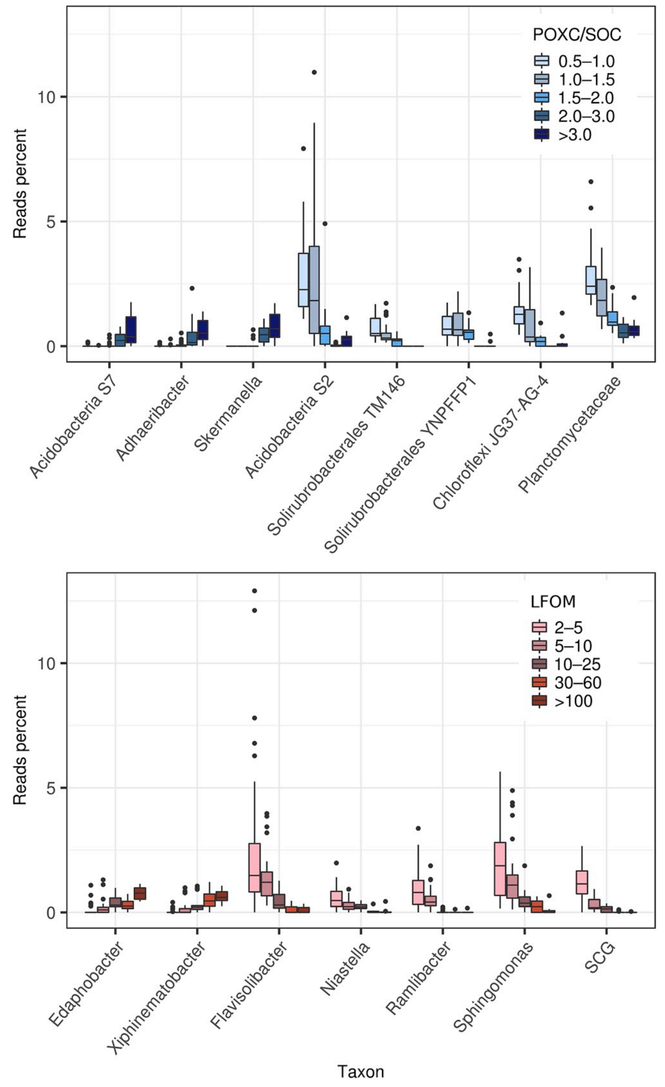

Fig. 4. Changes in the relative abundances of the bacterial-archaeal genera at different intervals of A) POXC/SOC ratio, and B) LFOM. Only those genera significantly correlated are shown, genera with Spearman's $\rho > 0.60$ were positively correlated, and $\rho < -0.6$ were negatively correlated. SCG: Soil Crenarchaeotic Group.

soil microbial activity and microbial biomass (Liu et al., 2018a,b; Torbert and Wood, 1992). Moreover, high bulk density is typically associated with soil compaction and reduced O_2 concentration resulting in a decrease in bacterial abundance, and microbial respiration (Chao et al., 2019; Li et al., 2002), which might explain the decline in the α-diversity observed in our samples. Additionally, physical protection of the SOM by aggregates is an important mechanism for C stabilization, which form complex niches that harbor various bacterial species (Bach et al., 2018; Sánchez-Marañón et al., 2017; Wiesmeier et al., 2019). Phylogenetic diversity was positively correlated with the water-stable aggregates, indicating that the soil aggregation may be supported by a wide range of phylogenetically distant community members.

4.2. *Effects of climate aridity on soil bacterial-archaeal communities*

Both climate aridity and microbial community α-diversity (Shannon index, OTU richness and evenness) exhibited significant relationships across all sites. This inverse relationship indicates that rising aridity levels, typically represented by a low aridity index, might lead to a decline in soil diversity resulting from low water availability. Some studies have reported that aridity is a major factor that decreases the abundance of soil bacteria, even more so than soil management history (Acosta-Martínez et al., 2014; Delgado-Baquerizo et al., 2018; Gosling et al., 2013; Maestre et al., 2015; Ren et al., 2018a). This is because access to nutrients becomes more limited as the water film thickness is reduced by drought (Barnard et al., 2013; Fierer et al., 2003; Stark and Firestone, 1995). In this study, climate aridity was not a significant predictor of the microbial community β-diversity. However, the cluster analysis clearly divided the microbial community structure into two different groups according to the level of the POXC/SOC ratio under warmer and colder climates. In warmer climate conditions, as long as the water availability is not a limiting factor, the organic matter decomposition and the release of nutrients is accelerated (Jobbágy and Jackson, 2000), and thus, these areas are especially susceptible to C depletion (FAO, 2004; Lal, 2001; Ramírez et al., 2019). Consistently, a community structure divergence was observed indicating the role of climate aridity as relevant environmental filters in the decomposition.

4.3. *POXC/SOC ratio as a driver for the soil bacterial-archaeal communities*

POXC represents a labile organic matter pool detected by a mild oxidizing agent $KMnO_4$, which has been applied to several studies for representing microbial oxidation (Blair et al., 1995; Conteh et al., 1999; Loginow et al., 1987). Two genera categorized as copiotrophic and as initial metabolizers of labile C, *Adhaeribacter* (Bacteroidetes; Cytophagaceae) and *Skermanella* (Alphaproteobacteria; Rhodospirillaceae), increased their relative abundance under higher POXC/SOC ratios (Fierer et al., 2007; Padmanabhan et al., 2003; Tian et al., 2017). Previous studies have indicated that POXC reflects a more processed and stabilized pool that promotes organic matter formation (Hurisso et al., 2016; Romero et al., 2018; Tirol-Padre and Ladha, 2004). However, POXC is highly influenced by climate (Duval et al., 2018), therefore, it is possible that under more arid conditions, the POXC accumulation relative to SOC might be strongly accelerated by a lower transformation of organic debris to organic matter, which is reflected by a higher ratio of POXC/SOC. Such conditions might selectively increase the abundance of specific bacterial taxa related to sites where SOM formation is markedly decreased as a result of a reduced precipitation and low net primary productivity (Duval et al., 2013). Particularly, Proteobacteria and Bacteroidetes have been primarily related to high soil respiration rates under climate change and land use intensification scenarios through shifts in soil microbial community composition (Kuramae et al., 2012; Liu et al., 2018a,b; Xiao et al., 2017). Altogether, these findings suggest that these genera could potentially be affected by changes induced by organic matter inputs, which might be occurring for C mineralization or degradation of soil organic matter, and may be suitable indicators of soil health in agroecosystems.

In the soils studied here, Acidobacteria subdivision 7 increased with the POXC/SOC ratio, whereas an inverse trend was observed in Acidobacteria subdivision 2 with the same ratio. Nevertheless, caution should be taken when interpreting these relationships because Acidobacteria members are highly susceptible to changes in soil pH (Sait et al., 2006). For example, members of subdivision 7 may respond to increases in the soil pH containing high levels of Ca, Mg, Mn, and B (Kielak et al., 2016; Rousk et al., 2010), and this is consistent with the calcareous and alkaline properties of northern central Chilean soils (Casanova et al., 2013). Low content of POXC to SOC selectively modifies the relative abundance of two unidentified genera belonging to *Solirubrobacterales* (Actinobacteria; Class Thermoleophilia), one belonging to Chloroflexi (JG37-AG-4), and the other belonging to the Planctomyceteceae family, which was found to increase with low POXC/SOC. These results also are in agreement with Grządziel and Gałązka (2018), which observed a negative effect in *Solirubrobacter* in degraded soils in comparison to healthy ones. Furthermore, Trivedi et al. (2016) observed a higher relative abundance of Chloroflexi in agricultural soils as compared to non-cultivated soils, consistent with our results where most of studied soils were previously disturbed by agriculture. Taken together, this finding supports the fact that microbial processing involves not only consumption and degradation, and they are now also recognized as dominant agents of soil C formation or by microbial transformation involved in the stabilization of fresh plant material into soil organic matter (Bradford et al., 2016; Roth et al., 2019). The differences in the relative abundances of dominant soil bacterial genera could provide insights into the interplay between soil microorganisms and POXC.

4.4. LFOM as a driver of soil bacterial-archaeal communities

Influenced by the quantity and the characteristics of plant C inputs, agricultural practices, and climate, the LFOM accumulation is a useful predictor of soil respiration and N mineralization (Cambardella and Elliott, 1992; Gosling et al., 2013; Hassink, 1995; Janzen et al., 1992). Indeed, a high LFOM content should reflect the slower decomposition of root and plant fragments (Rui et al., 2016; Song et al., 2012). However, in our study, LFOM content explains less than 10% of the β-diversity variation. Consistent effects were found by Cookson et al. (2005), who found non-significant relationships between the LFOM and the microbial community structure using phospholipid fatty acid patterns (PLFA). These results suggest that the accumulation of LFOM might selectively increase or decrease the abundance of specific bacterial and fungal taxa while having a small impact on the microbial species diversity. Thus, we identified some specific taxa in soils with higher LFOM content that included *Edaphobacter* (Acidobacteria; Acidobacteriaceae) and the Candidatus *Xiphinematobacter* (Verrucomicrobia; Chthoniobacterales). Acidobacteria and Verrucomicrobia have been described as opportunistic bacterial towards short-term changes in water availability, with rapid declines in ribosomal synthesis during drought (Barnard et al., 2013; Maestre et al., 2015). Razanamalala et al. (2018), found a clear relationship between the light fraction organic C (LFOC) and the occurrence of Acidobacteria and Verrucomicrobia members ($R^2 = 0.88$, both cases). Additionally, some of the genera found in our study have been previously described as ecologically important indicators used to assess soil quality. For example, strictly aerobic *Edaphobacter* (Dedysh et al., 2012), has been associated with acidic soils with good quality (Grządziel and Gałązka, 2018). Further, Sun et al. (2017) determined that during long-term restoration of reclaimed mine soils, an increase in the Candidatus *Xiphinematobacter* was also related to the nematode populations and the potential development of higher trophic levels in the soil.

In contrast, as the LFOM content decreased, the microbial community appeared to shift from strictly oligotrophic to oligotrophic/copiotrophic, with an increase in Bacteroidetes (*Flavisolibacter and Niastella),* and members of Proteobacteria such as *Ramlibacter* and *Sphingomonas*. These shifts can be explained by a decrease in the labile C and N substrates and the increase of nutrient-poor and recalcitrant C compounds (Schimel and Schaeffer, 2012). Members of the family *Sphingomonadaceae* and the genus *Ramlibacter* (Burkholderiales) have been recommended as sensitive indicators of arable soil fatigue (Wolińska et al., 2018). Furthermore, it has been reported that some members of the genus *Ramlibacter* have the ability to divide using desiccation-tolerant mechanisms in arid environments (de Luca et al., 2011). Additionally, our results showed that decreases in the LFOM induce Thaumarchaeota growth that result as a consequence of lower water availability starvation conditions (Meisner et al., 2018). Consistently, Thaumarchaeota have been described as ammonia-oxidizing archaea abundant in terrestrial high-temperature habitats with a history of drought and dessert soils (Daebeler et al., 2018; Meisner et al., 2018; Tripathi et al., 2015).

5. Conclusion

In this study we examined the factors controlling major shifts in the soil bacterial-archaeal communities and identifies taxa that might respond to changes in labile SOC fractions. The findings demonstrate that microbial diversity and composition are highly controlled by labile SOC fractions across a wide range of environmental combinations. The POXC/SOC ratio and the LFOM were found to be more involved as descriptors of the community structure than other commonly used descriptors such as SOC, C/N, and land use. Along with soil pH, labile SOC fractions were found to promote changes in soil microbial diversity and composition. Such responses were demonstrated by variations in both α- and β-diversity, and also by changes in the abundances of specific microbial taxa. Although we considered the impact of different land use systems, there was a non-significant influence of soil management practices in microbial communities across a climate gradient. In addition, we found that aridity had a greater impact on labile SOC fractions than land use when soils were analyzed on a larger scale. Climate aridity affected α-diversity, and differentiated patterns of the community structure were found under more arid conditions with higher POXC content relative to SOC. These results provide a better understanding of the link between soil microbial communities and labile SOC fractions, and additional insights into the prediction of microbial responses under future climate change.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.107692.

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