Environmental factors regulate soil microbial attributes and their response to drought in rangeland ecosystems

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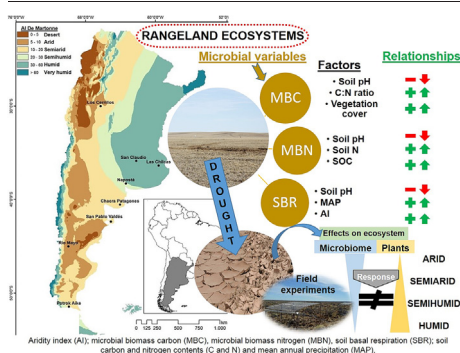[g] CONICET, Argentina
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HIGHLIGHTS

- Microbial biomass and respiration decreased along an aridity gradient, from humid to arid.
- Soil C, N, and vegetation cover positively regulate microbial biomass (C and N).
- Soil pH negatively affected microbial biomass (C and N) and soil basal respiration.
- Differential responses of microbial biomass and soil basal respiration depended upon aridity index.
- Soil microbial variables showed a close relationships with vegetation cover under drought.

GRAPHICAL ABSTRACT

Aridity index (AI); microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), soil basal respiration (SBR); soil carbon and nitrogen contents (C and N) and mean annual precipitation (MAP).

ARTICLE INFO

ABSTRACT

In ecosystems, soil microbial variables characterization are used to determine soil biological health and the response of soils to environmental stress. Although there are strong associations between plants and soil microorganisms, they may respond asynchronously to environmental factors and severe droughts. We aimed to: I) evaluate the special variation of soil microbiome such as microbial biomass carbon (MBC) and nitrogen (MBN), soil basal respiration (SBR) and microbial indexes in eight rangeland sites located across an aridity gradient (distributed from arid to mesic climates); II) analyze the relative importance of main environmental factors (climate, soils, and plants) and their relationships with microbial variables in the rangelands; and III) assess the effect of drought on microbial and plant variables in field-based manipulative experiments. First, we found significant changes of microbial variables along a precipitation and temperature gradient. The responses of MBC and MBN were strongly dependent on soil pH, soil nitrogen (N), soil organic carbon (SOC), C:N ratio and vegetation cover. In contrast, SBR was influenced by the aridity index (AI), the mean annual precipitation (MAP), the soil pH and vegetation cover. MBC, MBN and SBR were negatively related with soil pH

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compared to the other factors (C, N, C:N, vegetation cover, MAP and AI) that had a positive relationship. Second, we found a stronger soil microbial variables response to drought in arid sites compared to humid rangelands. Third, the responses of MBC, MBN, and SBR to drought showed positive relationships with vegetation cover and aboveground biomass, but with different regression slopes, this suggest that plant and microbial communities responded differently to drought. The results from this study improve our understanding about the microbial response to drought in different rangelands, and may facilitate the development of predictive models on responses of soil microorganisms in carbon cycle under global change scenarios.

1. Introduction

Rangelands are among the most widely distributed terrestrial biomes, covering around 52.5 million km^2 (40.5 % of the global land area), and located predominantly in arid and semiarid regions (Sala et al., 2017). Rangeland ecosystems provide multiple goods (e.g., livestock production) and services, and play an important role in global carbon (C) cycling, containing more than one-third of above and belowground C stocks (Havstad et al., 2007; Yahdjian et al., 2015; Zhao et al., 2020; Peri et al., 2021; Jaman et al., 2022). In these and other terrestrial ecosystems, active soil living microorganisms represents only 0.1–2 % of the total soil volume (Blagodatskaya and Kuzyakov, 2013), but are involved in 90 % of soil ecosystem functions (Nannipieri et al., 2003). Characterization of soil microbial variables is being increasingly used to determine soil biological health, including response of soils to environmental stress such as severe droughts, anthropogenic disturbances, and as an indicator of ecosystem resilience (Marcos and Olivera, 2016; Li et al., 2018; Fierer et al., 2021).

Several studies have investigated the biogeographic patterns of the soil microbial variables across precipitation and temperature gradients (Bachar et al., 2010; Maestre et al., 2015; Delgado-Baquerizo et al., 2016; Yao et al., 2017; Ochoa-Hueso et al., 2018; Wang et al., 2021). However, mechanisms by which edaphic, vegetation, and climatic factors interact to shape local microbial communities are not yet fully understood (Waldrop et al., 2017; Sun et al., 2020a; Deng et al., 2021). This is critical for improving our understanding of the major environmental drivers of soil microbial communities and their roles in ecosystem functioning (Saccá et al., 2017; Jansson and Hofmockel, 2020), especially in vulnerable rangelands facing climate change. Moreover, the response of the microbial biomass, activity, and community structure to environmental drivers may depend on each site's location across to aridity gradients (Bachar et al., 2010; Stomeo et al., 2013; Waldrop et al., 2017; Wang et al., 2021; Ding and Eldridge, 2022).

Current climate change scenario are impacting the hydrological cycle by altering precipitation patterns and increasing the frequency of extreme dry events (Trenberth et al., 2014; Bonan and Doney, 2018; IPCC, 2022). In recent years, droughts are increasing in magnitude, frequency and duration, especially in arid and semiarid rangelands (Yahdjian and Sala, 2008; Hoover and Rogers, 2016; Canarini et al., 2017; Zhao et al., 2021), which may lead to land degradation and desertification (Lin et al., 2015; Huang et al., 2016; Middleton, 2018), jeopardizing sustainable livestock production worldwide (Yahdjian and Sala, 2008; Gaitán et al., 2018; Oñatibia et al., 2020; Bondaruk et al., 2022). In addition, the magnitude of change in precipitation (amount, intensity, and frequency) affects processes that control soil organic carbon pools and dynamics in terrestrial biomes as ecosystem responses are largely dependent on the belowground microbial communities (Bardgett et al., 2008; Canarini et al., 2017; Ren et al., 2017; Fuchslueger et al., 2019; Sun et al., 2020b; Deng et al., 2021). Changes in soil microbial variables have subsequent interactive feedbacks on numerous soil functions, such as nutrient cycling and carbon sequestration (Six et al., 2006; Bardgett et al., 2008; Canarini et al., 2017; Deng et al., 2021). Thus, identifying the microbial community responses to change in precipitations can greatly improve our understanding of the ability of ecosystems to deal with future global climate change (Bardgett et al., 2008; Beier et al., 2012; Liang et al., 2017, 2019).

Given the importance of drought, manipulated precipitation experiments have been increasingly used in ecological studies over the past decade (Beier et al., 2012; Nielsen and Ball, 2015; Homyak et al., 2017;

Zhou et al., 2018; Xu et al., 2020). However, results have been diverse and there is still substantial uncertainty in describing microbial community responses to rainfall reductions at regional scales (Shen et al., 2015; Ochoa-Hueso et al., 2018; Xu et al., 2020; Deng et al., 2021). Therefore, more studies of soil microbial response to rainfall reductions are urgently needed to improve predictions of global change feedback on the terrestrial carbon cycle.

Ochoa-Hueso et al. (2018) and Ren et al. (2018) found that rainfall reductions modified soil microbial biomass by reducing soil water and altering plant net primary productivity. Rainfall reductions also decrease the mobility of soil solutes and litter inputs, and limit substrate supply by changing rhizodepositions (Sanaullah et al., 2011; Fuchslueger et al., 2019). In addition, reductions in aboveground net primary production due to reduced rainfall can led to decline in carbon and nitrogen from detritus entering the soil, thus reducing microbial biomass (Sanaullah et al., 2011; Zhang and Xi, 2021; Jaman et al., 2022) through inhibited microbial growth and activity (Bardgett et al., 2008; Dijkstra et al., 2015; Zhao et al., 2021). Therefore, rainfall reductions could have differential responses on soil microbial biomass and activity depending on the aridity of rangelands. Despite an increasing number of studies testing above and belowground ecosystems responses to changes in precipitation (Knapp et al., 2015, 2017; Bondaruk et al., 2022; Jaman et al., 2022), a critical knowledge gap is the combined responses of plants and soil microbes to changes in precipitation. This gap could lead to a biased understanding of rangeland function and the ecosystem services they provide under climate change as soil microorganisms play a key role in carbon cycling processes, such as litter decomposition and CO_2 emissions (Six et al., 2006; Bardgett et al., 2008; Benner, 2011; Liang et al., 2017). Although, there are strong associations between plants and soil microbes through exchanges at root-soil interfaces, plants and microbes may respond asynchronously to soil resource availability due to contrasting life history strategies (Thakur et al., 2015; Sun et al., 2020a; Zhang and Xi, 2021). Soil microorganisms can adapt to changes in soil moisture more rapidly than plants due to their fast growth, considerable capacity for osmotic adjustment under fluctuating soil moisture and community composition shifts (Schimel et al., 2007; Lau and Lennon, 2011; Fuchslueger et al., 2016; Karlowsky et al., 2018b). The asynchrony between plant and microbial biomass may have significant implications for the competitive balance between plants and soil microbes, as well as for the regulation of biogeochemical cycles (Karlowsky et al., 2018b; Williams and de Vries, 2020).

Argentina has an extensive territory covering broad ecological zones, with distinct climates and rangelands (Oyarzabal et al., 2018), accounting for more than two thirds of the total continental area (Anderson et al., 2011). Given their contrasting ecological conditions, these rangelands are expected to respond differently to environmental pressures. Thus, these rangelands are ideal for evaluating ecosystem services and resilience because they vary across climate gradients (Yahdjian and Sala, 2008; Verón et al., 2018; Bondaruk et al., 2022), and are likely to be unevenly affected by forecasted droughts (González et al., 2017). In Argentinean rangelands, soil microbial variables have been rarely studied (Montecchia et al., 2011; Prieto et al., 2011; Olivera et al., 2016; Toledo et al., 2021; Viruel et al., 2022). Therefore, an improved understanding of soil microbial carbon cycling, as well as its interaction with environmental factors, is urgently needed to accurately represent soil microbial feedbacks in ecosystem models to improve predictions of rangeland responses to projected climate change scenarios (IPCC, 2022).

In this work, we built on our former study to investigate the main environmental drivers of soil microbial communities across an aridity gradient in Argentinean rangelands (Bondaruk et al., 2022). As microorganisms play a key role for rangeland carbon cycling, we added the soil component to the previous study focused on vegetation, and we compared the effects of drought on plants and microbes. In this research we used a coordinated manipulative drought experiment in eight Argentinean rangelands to: I) study the variation patterns of soil microbial community attributes such as microbial biomass (C and N), soil basal respiration and microbial indexes along an aridity gradient (arid, semiarid, sub humid and humid); II) analyzed the relative importance of climate, soil and plant factors on microbial variables and the relationships between microbial biomass (C and N) and soil basal respiration with the main environmental factors occurring along the aridity gradient; and III) we further assessed the effects of drought on microbial and plant variables. More importantly, we also assessed the relationships and differential responses to drought of soil microbial variables and vegetation.

2. Materials and methods

2.1. Study sites and aridity gradient descriptions

The sites are part of an international collaborative research network consisting of coordinated drought experiments (Drought Network). Were selected eight rangeland ecosystems across a natural aridity gradient in Argentina, distributed from 29° 57′ to 51°54′ S and 58° 09′ to 70°24′ W (Supplementary Fig. A.1). Based on the meteorological stations data (period 2015–2022), the mean annual temperature ranges from 6.5 to 22 °C, and the mean annual precipitation varies from 137.1 to 1022.3 mm, where 70–80 % of rain events occurs during the growing season (September–March). For each study site, we calculated an aridity index (AI) based on mean annual precipitation (MAP) and mean annual temperature (MAT) as: $AI = MAP/(10 + MAT)$ (De Martonne, 1926). Considering the aridity categories defined by Liu et al. (2016), the eight rangelands were sorted into four ecosystem types: arid ($5 < AI < 10$), semiarid ($10 < AI < 20$), semihumid ($20 < AI < 30$), and humid ($30 < AI < 60$) (Supplementary Fig. A.1; Table 1). Also, the rangelands encompass a great variability in plant composition, plant species diversity and richness, vegetation cover, aboveground net primary productivity (ANPP), and soil physico-chemical properties (Table 1). These natural rangelands mainly sustain extensive livestock production.

2.2. Experimental design

The sites followed a common experimental protocol which allows reliable comparisons among contrasting ecosystems (Knapp et al., 2017) and included experimental rainfall manipulations to understand the ecological drought impact on vegetation (see Bondaruk et al., 2022). The simulation of droughts was induced through a passive well-tested design based on rainout shelters that intercept a fraction of the incoming precipitation (Yahdjian and Sala, 2002). To determine the percentage of precipitation interception, we applied the standardized protocol presented in the precipitation manipulation tool of the Drought Network. This is a software that allows to upload the longest precipitation time series of each site (https://drought-net.colostate.edu/terrestrial-precipitation-analysis-package; Lemoine et al., 2016). Thus, we reduced annual precipitation to ≈50 % in sites. Intercepted precipitation was collected in gutters and directed away by pipes in order to avoid water infiltrating into the experimental drought plots (see Table A.1 supplementary).

The rainout shelters were constructed with transparent plastic tiles, placed above the plant canopy (1.20 to 1.60 m height) in order to minimize impacts on micrometeorological conditions. The rainout-shelter design employed in this study has proven to accomplish the desired reduction in water input and the expected effects on soil moisture on vegetation (Yahdjian and Sala, 2002; Gherardi and Sala, 2013; Bondaruk et al., 2022). The experimental plots (3 × 3 m) were installed at the end of the

growing season in different years (2015 to 2017) following a completely randomized block design that included paired control plots of the same size. At each experimental site, the experiments were established in a block design and generally replicated three times ($n = 3$), although some sites had four replicates ($n = 4$). All experimental sites were fenced to prevent grazing on experimental plots.

2.3. Soil microbial community variables

Soil microbial variables were determined after 5 years of the imposition of drought with rainout shelters, during summer (December–March), which is coincident with the peak of the plant growing season. At each experimental site, eighteen soil samples were taken ($n = 2$ treatments × 3 plots × 3 composite samples). The composite soil samples consisted of 5–7 subsamples from the first 5 cm depth (without plant residues) taken with a metal cylinder (5.6 cm diameter). The samples were placed in a bag and taken to the laboratory, where they were sieved (2 mm) and conditioned to send to Laboratory INTA Río Gallegos (Santa Cruz, Argentina). They were keep refrigerated at 4 °C in the laboratory until the quantification analysis for microbial variables were determined.

The carbon in the microbial biomass (MBC) was estimated using the "chloroform-fumigation extraction" method (Vance et al., 1987). MBC was calculated as: (OCf − OCnf) / kEC; where: OCf = organic carbon extracted from fumigated samples; OCnf = Carbon extracted from non-fumigated samples; and kEC = fumigation efficiency constant = 0.45. MBC was expressed as mg C kg^{-1} dry soil.

The nitrogen in the microbial biomass (MBN) was determined by a modification of the fumigation–incubation method (Joergensen and Mueller, 1996). Liquid chloroform (1 mL) was added directly to 30 g moist soil samples, stirred and left for 20 h in sealed beakers in desiccators. Chloroform was then removed using a vacuum pump. Fumigated and non-fumigated samples were incubated at field capacity for 10 days at 25 °C. After incubation, samples were extracted with 2 M KCl and analyzed for NH_4-N by the Berthelot reaction. MBN was calculated as the difference in N between fumigated and non-fumigated samples, divided by a correction factor. Non-extractable amount of microbial N was compensated for by a correction factor of kN = 0.54. MBN was expressed as mg N kg^{-1} dry soil.

The soil basal respiration (SBR) was estimated by quantifying the carbon dioxide (CO_2) released in the process of microbial respiration during incubation days 1, 7, 14 and 21. This was done by placing 75 g fresh soil (moistened to 60 % of field capacity) into 1.5-L capacity glass containers with hermetic lids, together with a smaller flask containing 20 mL 0.2 M NaOH to capture the released CO_2. The CO_2 was determined by titration with 0.1 M HCl, after precipitation of the barium carbonate formed by adding barium chloride ($BaCl_2$) aqueous solution to the NaOH solution, utilizing phenolphthalein as an indicator (Robertson et al., 1999). The SBR was measured until day 21 of incubation because during that period the samples reached a relatively constant CO_2 production. The mean soil respiration (accumulated SBR/21) during the incubation time was expressed as mg C kg^{-1} soil day^{-1}.

The soil microbial indexes, metabolic quotient (qCO$_2$) was calculated as the C-CO_2 evolution (SBR) per unit MBC and per unit time (Anderson and Domsch, 1990). The MBC/MBN ratio was obtained and the contributions of microbial biomass to SOC (MBC/SOC) were also calculated, expressed as percentage (Anderson and Domsch, 1990).

2.4. Vegetation cover and aboveground biomass

During the experiment, we determined total vegetation cover and aboveground biomass at the peak of the growing season. Cover was determined in 1 m^2 permanent plots located in the center area of each experimental unit. Aboveground biomass was estimated by clipping to the soil surface all aboveground biomass within two frames of 0.2 × 0.5 m from each experimental unit near permanent plots. Then, we dried the samples (60 °C) for 48 h to obtain dry matter plant biomass (total) expressed in g dry matter (DM) m^{-2}. For the Río Mayo (RM) and Chacra Patagones

Table 1

Characterization of the study sites in an aridity gradient in Argentina. Geographic location, description of climatic variables, vegetation, and soil physicochemical characteristics of the eight sites are shown from de most arid to the most humid. Values are mean and standard deviation (± SD). Values of soil variables followed by different lowercase letters in each file indicate significant differences ($p < 0.05$) among sites.

	Río Mayo (RM)	San Pablo Valdes (SPV)	Potrok Aike (PA)	Los Cerrillos (LC)	Chacra Patagones (ChP)	Napostá[a] (N)	Las Chilcas (LCh)	San Claudio (SC)
Coordinates								
Latitude (S)	45°23′51.72″	42°39′12.04″	51°54′57.60″	29°57′01.08″	40°43′23.16″	38°25′26.04″	36° 09′47.52″	35°54′55.44″
Longitude (W)	70°18′21.24″	64°10′17.08″	70°24′26.64″	65°52′24.60″	62°53′56.04″	62°17′16.44″	58° 09′20.16″	61°08′54.24″
Climatic								
MAP (mm yr^{-1})	137.1 ± 44.7	249.3 ± 83.1	186.6 ± 32.7	372.9 ± 71.6	444.2 ± 57.6	579.4 ± 63.4	998.7 ± 152.9	1022.3 ± 233.5
MAT (°C)	9.6 ± 0.3	13.9 ± 0.3	6.5 ± 0.3	22 ± 1	17.4 ± 2	15.4 ± 0.6	15.4 ± 0.4	15.1 ± 0.3
Aridity Index De Martonne (MAP/MAT+10)	7	10.4	11.3	11.7	16.2	22.9	39.3	40.8
Aridity categories	Arid	Semiarid	Semiarid	Semiarid	Semiarid	SemiHumid	Humid	Humid
Vegetation								
Vegetation types	Grass steppe: grasses and dwarf shrubs	Grass steppe: grasses and dwarf shrubs	Grass steppe: grasses and dwarf shrubs	Grass-shrub steppe	Grassland	Grassland	Grassland	Grassland
ANPP (g m^{-2} yr^{-1})	29.01e	160.8cd	45.56e	268.99c	103.80d	347.72c	583.45b	1219.01a
Vegetation cover (%)	35.8c	60.1b	74.7b	94a	71.7b	94.7a	97.8a	96.3a
Species richness (α diversity)	6	11	19	12	5	6	16	4
Dominant species	Mulinum spinosum; *Pappostipa speciosa; Poa ligularis*	*Nassella tenuis; Poa lanuginosa; Sporobolus rigens; Vulpia bromoides*	Carex andina; Nardophyllum bryoides; *Poa spiciformis; Pappostipa speciosa*	*Larrea divaricata; Pappophorum krapovickasii; Aristida mendocina;*	*Nassella longiglumis; Poa ligularis*	*Bromus catharticus;* Nassella nessiana; *Nassella trichotoma*	*Festuca arundinacea; Leersia hexandra; Panicum gouinii; Paspalidium paludivagum;*	*Festuca arundinacea; Sorghum halepense*
Soil								
Soil Taxonomy USDA[b]	Aridisols	Entisols	Aridisols	Aridisols	Entisols	Mollisols	Alfisols	Mollisols
Textural class	Sandy	Sandy	Sandy loam	Sandy loam	Sandy clay loam	Sandy loam	Silt loam	Loam
pH	7.4c	8.0b	6.2d	8.4a	7.6bc	6.0de	5.7e	6.1de
SOC (g kg^{-1})	5.35c	7.37c	24.74b	4.03c	25.37b	35.40a	40.40a	21.71b
N (g kg^{-1})	0.52e	1.13d	3.03b	0.55e	2.83b	3.34ab	3.57a	1.70c
P extractable (ppm)	10.1b	3.5c	28.0a	6.5bc	8.3b	25.0a	24.6a	11.1b
C:N	10.3b	6.5d	8.2c	7.3d	8.9c	10.6b	11.3a	12.8a

[a] Napostá: Campo Experimental Napostá; convenio UNS y MDA-PBA.
[b] Soil Survey Staff (2010).

(ChP) sites, the estimation of aboveground biomass was made nondestructively, through allometric equations that related the relative cover of each plant species present with their aboveground biomass (e.g. Flombaum and Sala, 2007).

2.5. Data analysis

Descriptive analyses of means and standard deviations were realized for climatic, vegetation and soil characteristics. The microbial variables (MBC, MBN, MBC:MBN, SBR, qCO$_2$ and qMC) were analyzed with ANOVA, using the sites (RM, SPV, PA, LC, ChP, N, LCh and SC) and aridity categories (arid, semiarid, semihumid and humid) as factors. Significant differences between means were separated in all cases by Tukey's test with a significance level of $p < 0.05$. Soil biological attributes from all sites (MBC, MBN, MBC:MBN, SBR, qCO$_2$ and qMC) were analyzed using principal component analysis (PCA). We ran random forest (RF) models by means of the *cforest* function in *party* package for R (Hothorn et al., 2008; Strobl et al., 2009), in order to assess relationships between microbial variables (MBC, MBN and SBR) and the climatic, vegetation and soil variables. The variable importance values were determined by using the *varimp* function. To quantify variability in variable importance scores, we developed 100 RF models based on random selections of 80 % of cases, each time using the other 20 % to evaluate model accuracy. RF in *party* package can be used reliably even in situations where the independent variables vary in their scale of measurement. We used main variables obtained of RF model to fit simple linear regressions between climatic, vegetation, soil and soil microbial

community variables. The dependent variables were MBC, MBN and SBR and the independent variables were pH, C, N, C:N, vegetation cover, AI and MAP. The differences induced by experimental drought were tested for significance using one-way ANOVA. Significant differences between means were separated by Tukey's test with a significance level of $p < 0.05$. In addition, we calculated the response ratio (RR) to drought for each microbial variable (MBC, MBN, MBC:MBN, SBR, qCO$_2$ and qMC) in all sites using to the meta-analytical methods (Hedges et al., 1999). Values of RR was calculated as: ln (RR) = ln (Xt) / ln (Xc), where Xt represents the drought treatment and Xc the respective mean values of a particular microbial variable in the control treatment. Significant responses ($p < 0.05$) were determined if the bootstrap confidence interval (CI) did not overlap with zero (Koricheva et al., 2013). Simple regressions were used to examine relationships between the microbial variables' RR (MBC, MBN, MBC:MBN, SBR, and qCO$_2$) and vegetation variables' RR (vegetation cover and aboveground biomass) to drought.

3. Results

3.1. Soil microbial variables along the aridity gradient

Soil microbial variables varied significantly among sites and aridity categories (p < 0.05; Table 2). On the one hand, MBC, MBN and SBR ranged from 85.6 to 613.9, 16.9 to 148.3 and 22.7 to 85.9, respectively, and were significantly higher in LCh site (humid) compared with the other sites. On the other hand, metabolic and microbial indexes such as MBC:

Table 2

Soil biological variables and microbial indexes for the eight sites and sites grouped by aridity in rangelands of Argentina. Mean values and standard deviation (±SD) are shown. Microbial biomass carbon and nitrogen: MBC and MBN (mg kg^{-1} dry soil), MBC:MBN ratio, soil biological respiration: SBR (mg C-CO$_2$ kg^{-1} dry soil d^{-1}), metabolic quotient (qCO$_2$) (μgC-CO$_2$ mg^{-1} MBC d^{-1}) and microbial carbon quotient: qMC (%).Values followed by different letters in each column indicate significant differences (p < 0.05) among aridity categories (uppercase letters) and sites (lowercase letters).

Microbial variables	MBC	MBN	SBR	MBC:MBN	qCO$_2$	qMC
Aridity categories[a]						
Arid	122 ± 35D	22 ± 8C	29 ± 7D	6 ± 2A	0.24 ± 0.03A	2.4 ± 0.7A
Semiarid	252 ± 143C	43 ± 22B	40 ± 12C	6 ± 3A	0.21 ± 0.12A	2.2 ± 0.6A
Semihumid	425 ± 43B	148 ± 37A	50 ± 9B	3 ± 1B	0.12 ± 0.02B	1.3 ± 0.1B
Humid	557 ± 56A	116 ± 49A	74 ± 16A	6 ± 2A	0.13 ± 0.03B	2.0 ± 0.7A
All sites[b]						
RM	122 ± 35e	22 ± 8c	29 ± 7ef	6 ± 2bcd	0.24 ± 0.03a	2.4 ± 0.7ab
SPV	137 ± 45e	17 ± 10c	33 ± 16def	10 ± 4a	0.25 ± 0.09a	1.8 ± 0.6cde
PA	437 ± 36c	70 ± 8b	40 ± 5cde	6 ± 1bc	0.09 ± 0.01c	1.9 ± 0.2 cd
LC	86 ± 37e	24 ± 17c	23 ± 5f	4 ± 3cd	0.27 ± 0.12a	2.1 ± 0.9bc
ChP	295 ± 35d	58 ± 11b	45 ± 9 cd	5 ± 1bcd	0.15 ± 0.03b	2.3 ± 0.3abc
N	425 ± 43c	148 ± 37a	50 ± 9c	3 ± 1d	0.12 ± 0.02bc	1.3 ± 0.1e
LCh	614 ± 63a	148 ± 27a	86 ± 11a	4 ± 1cd	0.14 ± 0.03b	1.5 ± 0.1de
SC	557 ± 46b	72 ± 9b	66 ± 10b	8 ± 1ab	0.12 ± 0.02bc	2.7 ± 0.2a

[a] Sites are depicted as arid (RM), semiarid (SPV, PA, LC, and ChP), semihumid (N), and humid (LCh and SC).

[b] Experimental sites are: Rio Mayo (RM), San Pablo Valdes (SPV), Los Cerrillos (LC), Potrok Aike (PA), Chacra de Patagones (ChP), Naposta (N), San Claudio (SC) and Las Chilcas (LCh).

MBN, qCO$_2$, and qMC decreased along the aridity gradient (p < 0.05 in all cases), except for one humid site (SC) which had high values of MBC:MBN and qMC.

Principal components analysis (PCA; Supplementary Fig. A.2) determined that the first two axes explained 79.3 % of the total variance of the samples (57.7 % and 21.6 % for PC1 and PC2, respectively). In the analysis of axis 1, there was a clear separation between a group containing RM, SPV and LC sites and another with PA, N, LCh and SC sites. This pattern is explained because the first three sites presented higher qCO$_2$ values, while the other sites exhibited higher MBC, MBN and SBR values. In addition, axis 2 separated PA and SC from N and LCh sites, and also SPV site from LC site (Supplementary Fig. A.2).

The Random Forest (RF) model explained 93 % of the variance for MBC, and 86 % for MBN (Supplementary Fig. A.3). The most important variables for predicting MBC and MBN across all sites were soil pH, C:N, vegetation cover, soil N contents and SOC (Fig. 1). For SRB, the RF model explained 73 % of the variance (Supplementary Fig. A.3), and the main explanatory variables were aridity index, MAP, and soil pH. In addition, soil pH was the single most important variable in RF models explaining variability for soil biological variables (Fig. 1).

To better visualize the relationship between soil microbial variables and environmental variables (soil physicochemical characteristics, vegetation, and climate), we analyzed biological correlations by using the most significant variables obtained from RF model. MBC was positively correlated with C:N ratio and vegetation cover (*p* < 0.05; Fig. 2B and C). Similarly, MBN was positively correlated with N and SOC (p < 0.05; Fig. 2E and F), whereas SBR was positively correlated with MAP and the aridity index (p < 0.05; Fig. 2H and I). In contrast, MBC, MBN, and SBR were negatively correlated with the soil pH (p < 0.05; Fig. 2A, D and G).

3.2. Responses of soil microorganisms to drought along the aridity gradient

The effect of drought on soil microbial variables (biomass, activity and microbial indexes) significantly varied among sites (p < 0.05; Supplementary Fig. A.4; Fig. 3). However, drought effects on these variables were not significantly related with the aridity index (*p* > 0.05). Drought decreased the MBC by 22 % and 16 % in RM and LCh, respectively, but it increased these variables in the sites SPV (31 %) and PA (8 %). Drought reduced MBN in RM (32 %), PA (8 %) and N (46 %), but increased it in
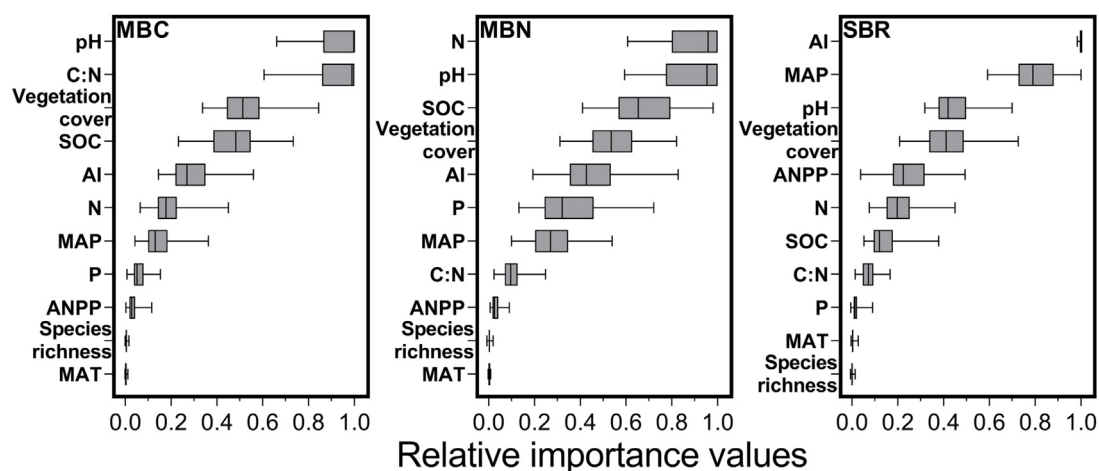

Fig. 1. Relative importance values of independent environmental variables used to characterize the studied rangeland sites in Argentina, resulting from the random forest analysis. Environmental variables representing climate were: mean annual precipitation and temperature (MAP and MAT), and aridity index (AI); the soil: soil pH, soil organic carbon (SOC), nitrogen (N) content, phosphorus (P) content, and C:N ratio; and the vegetation: vegetation cover, aboveground net primary production (ANPP), and plant species richness, for the eight sites and microbial variables microbial biomass carbon (MBC); microbial biomass nitrogen (MBN); and soil biological respiration (SBR).
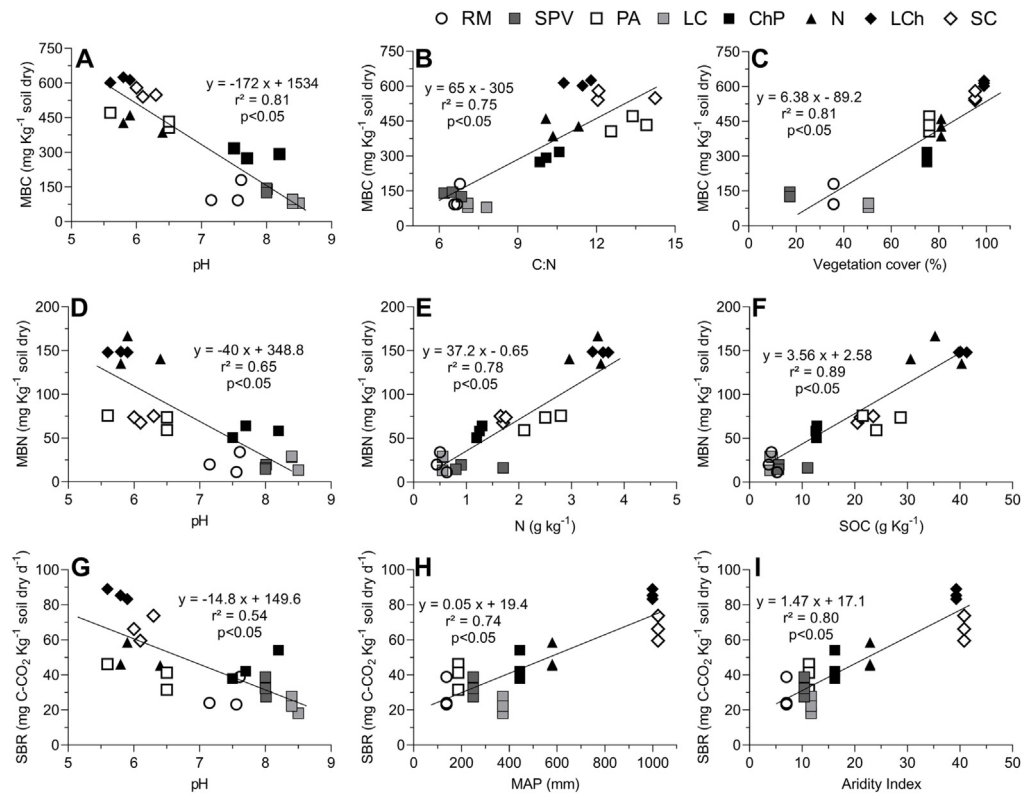
Fig. 2. Relationships between microbial variables and the most important soil, vegetation, and climatic variables selected by the random forest model/analysis, in eight rangelands of Argentina. Microbial biomass carbon (MBC) as a function of A) Soil pH, B) Soil C:N ratio, and C) Vegetation cover. Microbial biomass nitrogen (MBN) as a function of D) soil pH, E) soil N content, and F) SOC. Soil biological respiration (SBR) as a function of G) soil pH, H) mean annual precipitation (MAP), and I) aridity index (AI). Experimental sites were (from arid to humid): Rio Mayo (RM), San Pablo Valdes (SPV), Los Cerrillos (LC), Potrok Aike (PA), Chacra de Patagones (ChP), Naposta (N), San Claudio (SC) and Las Chilcas (LCh). Sites are depicted as arid (circles), semiarid (squares), semihumid (triangles), and humid (rhombuses).

the SPV, LC and LCh sites by 48 %, 40 % and 15 %, respectively. In contrast, drought significantly increased MBC:MBN ratio in RM (13 %), PA (17 %) and N (43 %), but decreased it in SPV (16 %), LC (24 %) and LCh (31 %). The SBR significantly increased under drought by 60 %, 42 % and 11 % in SPV, LC and N, respectively, and it decreased in RM (31 %) and SC (13 %). Finally, the qCO_2 decreased under drought conditions in RM (12 %) and SC (9 %), while it increased in SPV (28 %), LC (25 %), N (13 %) and LCh (15 %) (Supplementary Fig. A.4; Fig. 3).

3.3. Responses of plants and soil microorganisms to drought

Along the aridity gradient, the vegetation cover increased from 35.7 ± 4.1 % to 100 ± 0 % (Table A.2 supplementary). In addition, the aboveground biomass increased along the aridity gradient from 25.5 ± 3.6 g DM m^{-2} in the most arid site (RM) to 769.3 ± 130.1 g DM m^{-2} in the most humid site (SC; Table A.2 supplementary). Drought differently impacted on vegetation cover and aboveground biomass among the sites (Table A.2 supplementary). Vegetation cover and aboveground biomass were significantly reduced by drought in RM (66 and 64 % respectively), and N (37 and 63 %). However, in SPV, vegetation cover and aboveground biomass significantly increased by 30 and 49 %, respectively in response to the drought (Table A.2 supplementary).

Drought impact on vegetation cover estimated by the response ratio (RR) was positively correlated with the effect of drought on MBC, MBN, and SBR, and negatively correlated with the effect of drought on the MBC:MBN (Fig. 4). Similar results were found between responses to drought of aboveground biomass and microbial variables (MBC, MBN, MBC:MBN, and SBR) (Supplementary Fig. A.5). Finally, we found that the drought effects on microbial variables (MBC, MBN, SBR, and qCO_2) were positively correlated (Supplementary Fig. A.6).

4. Discussion

Soil microbial biomass and activity response to aridity gradient mainly was determined by biotic and soil factors, and at a lower extent by climatic variables. When manipulating precipitation (drought) at a site scale, microbial responses varied depending on vegetation cover rather than aridity index.

4.1. Soil microbial variables along the aridity gradient

Our findings provided new insights regarding the impact of environmental factors (soil, vegetation and climate) that drive the changes of soil microbial variables along an aridity gradient in rangeland ecosystems. We found that the responses of MBC and MBN were strongly dependent on soil pH, soil N and SOC, C:N ratio and vegetation cover. In contrast, SBR was influenced by the AI, MAP, pH and vegetation cover. Soil pH showed a negative relationship with MBC, MBN, and SBR compared with other factors that had a positive relationship. Regional scale patterns of microbial community (biomass and activity) were related to the biotic, edaphic and climatic factors such as plant composition and productivity, soil nitrogen, carbon, pH, precipitation and temperature (Yao et al., 2017; Ren et al., 2018; Deng et al., 2021; Wang et al., 2021). This is consistent with our study where soil microbial response varied depending on rangeland characteristics. From arid to humid, these sites differ in their biotic and abiotic factors such as aridity index, MAP, MAT, vegetation types and soil physico-chemical properties. Several studies suggested that the regional climate determines vegetation types and soil characteristics, and therefore, directly and/or indirectly affects soil microbial variables (Chen et al., 2015; Maestre et al., 2015). In our study we found that the biomass and basal respiration of soil microorganisms increased with the aridity index
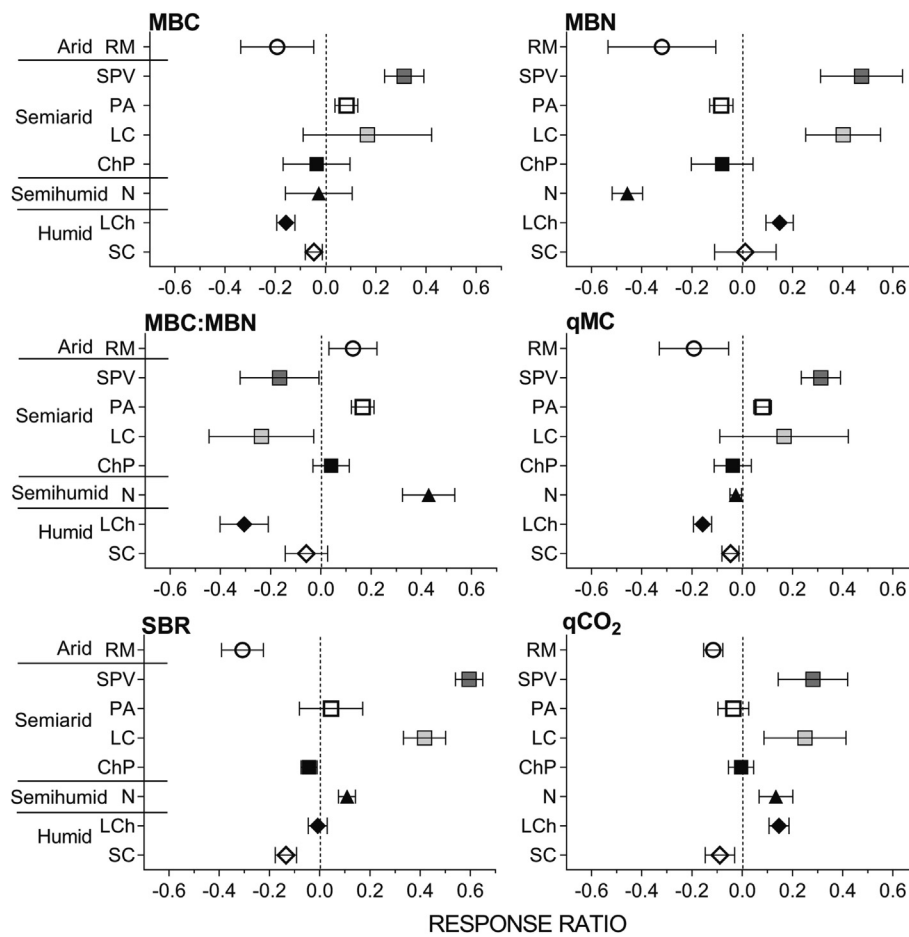
Fig. 3. Drought effects (estimated by the Response Ratio; RR) on soil microbial variables (biomass, activity, and microbial indexes) in eight rangelands of Argentina. The lines/whiskers indicated the 95 % confidence interval (CI). Significant treatment effects were found when the error bars did not overlap with zero. Sites were Rio Mayo (RM), San Pablo Valdes (SPV), Potrok Aike (PA), Chacra de Patagones (ChP), Los Cerrillos (LC), Naposta (N), Las Chilcas (LCh), and San Claudio (SC). Circles represent arid sites, squares semiarid sites, triangles semihumid sites, and rhombuses humid sites.

(arid < semiarid < semihumid < humid). Many studies showed that microbial biomass (C and N) or activity (SBR) were higher with increasing MAP and MAT in rangelands, forests and other biomes (Bachar et al., 2010; Griffiths et al., 2011; Delgado-Baquerizo et al., 2016; Ochoa-Hueso et al., 2018). In our study, random forest analysis indicated that soil and vegetation factors affected microbial biomass, with pH, C:N ratio, N content, SOC and vegetation cover being the most important factors explaining both MBC and MBN (Figs. 1 and 2). This contrasts with previous studies that have identified climate variables such as MAT (Nielsen and Ball, 2015; Yao et al., 2017; Fuchslueger et al., 2019; Yang et al., 2021) and MAP (Ma et al., 2015) as the most important factors regulating growth and activity of soil microbial communities. However, some other studies found results similar to ours, finding that soil microbial community was mainly explained by soil factors (soil pH, soil N content, SOC and C:N), followed by vegetation factors (vegetation cover, plant productivity and species richness) and finally by climatic factors (Lauber et al., 2008; Fierer et al., 2009; Chen et al., 2016; Takriti et al., 2018). In our study, soil microbial response may be the result of climate-plant-soil-microorganisms' interactions, where rangelands with higher rainfall (humid) and vegetation cover or ANPP (Table 1), may increase organic matter mineralization (confirmed with high SBR values), and favor a higher microbial growth (MBC and MBN). This is consistent with previous study, where microbial biomass (bacterial and fungal) increased with SOC and soil N (Fierer et al., 2009; Wang et al., 2021).

In particular, soil pH lead to reduced soil microbial biomass and activity as soil pH tends to become alkaline (from 5.7 to 8.4). Several studies have identified soil pH as a key environmental variable driving soil microbial

communities (Fierer and Jackson, 2006; Sinsabaugh et al., 2008; Liu et al., 2022), where soil microbial biomass decreased with increasing soil pH (6–9) at both regional and continental scales (Fierer and Jackson, 2006; Lauber et al., 2008; Rousk et al., 2010; Liu et al., 2022). In our rangelands, differences in soil pH (see, Table 1) can arise from many factors, including vegetation type, soil characteristics, and climatic variables, which agrees with previous studies (Rengel, 2011; Liu et al., 2022). Thus, pH may serve as an integrating variable representing the physicochemical characteristics of a particular soil (Lauber et al., 2008). Regardless of the mechanism, our results demonstrated that pH was a reasonably good predictor of soil microbial variables (MBC, MBN, and SBR) at the regional scale (Fierer and Jackson, 2006; Hermans et al., 2020; Pan et al., 2023).

Moreover, our study showed the SBR was mainly explained by climatic factors (AI and MAP), followed by soil pH and vegetation cover. Zhou et al. (2013) and Chen et al. (2014) found that microbial activity increased with precipitation, soil N content and low pH associated with bacterial-dominated microbial communities. Differences in MBC:MBN ratio indicates shifts of microbial community composition (Cleveland and Liptzin, 2007). Jansson and Hofmockel (2020) reported that the shifts in the fungi:bacteria ratio was correlated with the MBC:MBN. For instance, in our humid sites, we determined lower values of MBC:MBN, which would suggest a dominance of bacteria in the soil. Conversely, increased MBC:MBN in the arid sites may result in fungal dominance (Sun et al., 2020b). Thus, soils with fungal networks are more stable under water limitations (e.g. arid and semiarid ecosystems) than bacterial communities (Fierer and Jackson, 2006; Barnard et al., 2015; Maestre et al., 2015; de Vries et al., 2018). In addition, results showed that the variation of soil microbial biomass and basal
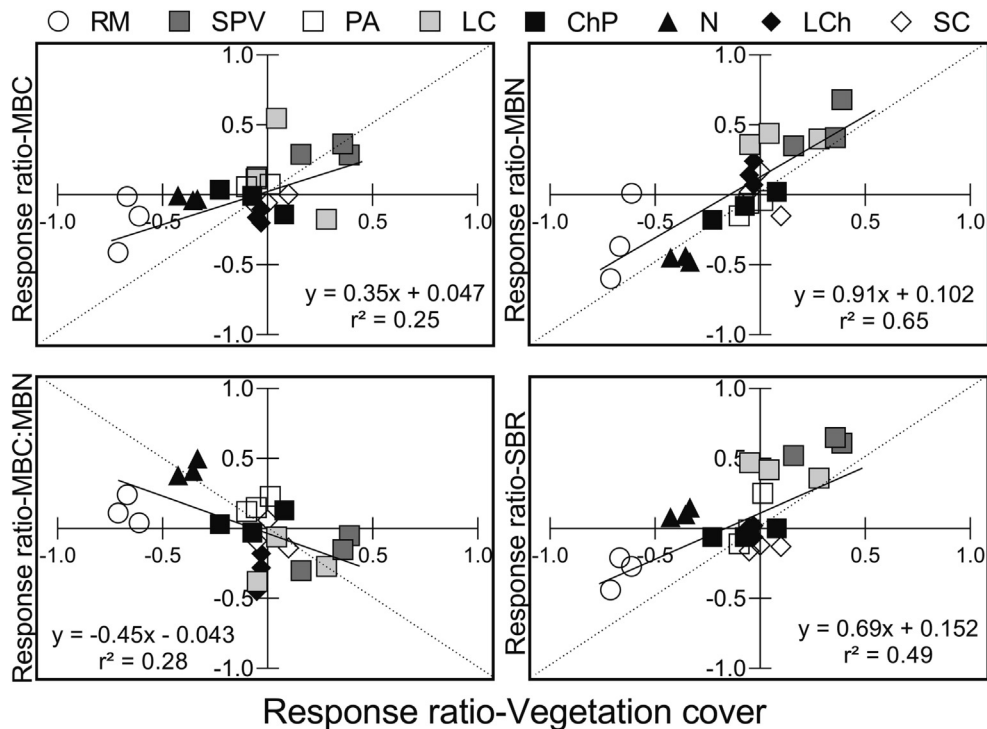
Fig. 4. Relationships between drought response ratio of total vegetation cover and microbial variables: A) microbial biomass carbon (MBC), B) microbial biomass nitrogen (MBN), C) MBC:MBN ratio, and D) soil biological respiration (SBR). Experimental sites are (from arid to humid): Rio Mayo (RM), San Pablo Valdes (SPV), Los Cerrillos (LC), Potrok Aike (PA), Chacra de Patagones (ChP), Naposta (N), Las Chilcas (LCh), and San Claudio (SC). Sites are depicted as arid (circles), semiarid (squares), semihumid (triangles), and humid (rhombuses).

respiration along an aridity gradient in rangelands depends on particular microbial populations adapted to resource availability (soil nutrients and plant input) and habitat conditions (climate and other soil properties) (Fierer and Jackson, 2006; Bachar et al., 2010; Yao et al., 2017; Ding and Eldridge, 2022).

4.2. Responses of soil microorganisms to drought along the aridity gradient

In our study, the effects of drought on soil microbial community showed variable responses. While several studies reported that drought increased or decreased the soil microbial abundance and activity (Fuchslueger et al., 2014, 2016; Ochoa-Hueso et al., 2018), other studies determined no effect (Rousk et al., 2013; McHugh and Schwartz, 2015; Canarini et al., 2016; Hoover and Rogers, 2016). In the present work, we found at a regional level (considering eight rangeland sites) that MBC, MBN and MBC:MBN in the natural rangelands of Argentina were not affected by long-term (5 years) drought under field manipulative experiments. Nonetheless, an increase in SBR and qCO_2 was observed under drought plots. The direction and magnitude of soil microbial differential responses to drought might depend on environmental factors in each site (Ren et al., 2017; Schimel et al., 2007). This was demonstrated in our study (Fig. 4), where in the arid site (RM) microbial biomass (C and N) and SBR significantly decreased (20–30 %) with drought, while MBC:MBN increased. In addition, our results showed that drought modified the efficiency of microorganisms in these arid rangelands (determined with low qCO_2 values). These changes in microbial community could influence C use efficiency used by microbes for growth (Manzoni et al., 2012, 2014; Dijkstra et al., 2015). Thus, drought could directly inhibit microbial growth due to soil water reduction and indirectly by modifying plant and soil resources, as it was reported in other studies (Bardgett et al., 2008; Sanaullah et al., 2011; Manzoni et al., 2012; Ren et al., 2018). In addition, the reductions in aboveground biomass due to decreased rainfall can cause a decline in microbial biomass and activity through reductions in C and N from detritus entering the soil (Nielsen and Ball, 2015; Schrama and Bardgett, 2016; Canarini et al.,

2017; Deng et al., 2021). This was supported in our study, where plants' response to drought was negative in the arid site (Table A.2 supplementary).

In our subhumid and humid sites (AI De Martonne ≥ 22) the responses of biomass and SBR to drought were less consistent. This may indicate that soil microbial community in humid ecosystems are less sensitive to drought (Manzoni et al., 2012; Ren et al., 2017, 2018; Zhou et al., 2018; Xu et al., 2020). Particularly, in the N site (subhumid) the response of microbial biomass to drought was variable; C remained constant, N decreased and C:N increased with drought (Fig. 3). Conversely, we found that drought had negative effects on MBC and MBC:MBN ratio in humid rangelands. Additionally, drought did not generate significant changes on SBR in our sites (Figs. 3 and A.4). The responses of soil microbiome to drought in these rangelands is possibly buffered by complex interactions with environmental factors. Thus, these interactions may enhance the responsiveness of microbial (C and N) turnover in soil under drought (Ren et al., 2017; Deng et al., 2021). Indeed, this response was supported by the regression analysis that indicated a positive relationship between SBR, MCB, MBN and qCO_2 in our rangelands (Supplementary Fig. A.6).

The decreased precipitation tended to increase or maintain the microbial biomass in semiarid sites compared to the other three rangeland ecosystems (arid, semihumid and humid). In contrast, drought stimulated a greater SBR in the semiarid sites (most evident in SPV and LC). Several studies have documented that responses to drought in semiarid ecosystems are very different and depend on the environment (Yang et al., 2021; Zhao et al., 2021). In our study, a possible explanation for this response in semiarid sites could be related to changes in the microorganism communities, as it was found in MBC:MBN (Figs. 3 and A.4). In the semiarid rangelands (PA and ChP sites), high microbial MBC:MBN may indicate fungal dominated soil microbiome (Cleveland and Liptzin, 2007, Sun et al., 2020a), therefore, community structure change drive to better adaptation of soil microorganisms to drought.

Unexpectedly, the microbial biomass exhibited positive trends with drought in the sites SPV and LC (Fig. 3). This may reduce competition for nutrients from plants under drought, leading to higher soil nutrients and

increased N and C availability for soil microorganisms (Dijkstra et al., 2015; Fuchslueger et al., 2016; Karlowsky et al., 2018a; Jaman et al., 2022). Drought RR analyses of aboveground biomass at these study sites may confirm these responses (Table A.2 supplementary). Further, higher microbial biomass (C and N) under drought (Figs. 3 and A.4) might have contributed to N and C resorption, which is considered as an essential strategy of nutrient conservation under stressed conditions (Six et al., 2006; Benner, 2011; Karlowsky et al., 2018b; Sun et al., 2020a).

Main results suggested that in humid rangelands, might lead to less soil microbial response to drought. However, in arid sites (AI < 7) reduced precipitation exerted a negative impact on the soil microbial community. On the other hand, drought impacts on semiarid sites (AI from 10 to 17) are more variable on microbial attributes but could be very vulnerable if droughts intensify in duration and frequency during the next years due to climate change.

Further studies are needed to better explain the specific mechanisms linking plant biomass to microbial community abundance and activity related to above and below ground substrate availability (litter quantity and quality, root biomass or rhizopedosition) (Zhang et al., 2018; Zhang and Xi, 2021; Jaman et al., 2022). The results from this study will improve our understanding of what the main environmental factors that drive the response microbial to drought in different types of rangelands and facilitate the development of predictive models on responses of soil microorganisms in C cycles and vegetation shifts in rangelands across regional scales under global change scenarios.

4.3. Differential responses of plants and soil microorganisms to drought

Positive relationships between plants and soil microbial (biomass and activity) have widely been reported for several natural ecosystems (Paterson, 2003; Van Der Heijden et al., 2008; Sanaullah et al., 2011; Fuchslueger et al., 2016), indicating a close coupling between plants and microorganisms (Bardgett et al., 2005; Fierer et al., 2009; Karlowsky et al., 2018b). Our study showed clear evidence that SBR, MBC and MBN positively correlated with vegetation cover (Fig. 4) and aboveground biomass (Supplementary Fig. A.5) after 5 years of drought treatments in contrasting rangelands. However, the impacts of drought on microorganisms and plants responded differently. Our findings revealed a trend of decoupling of plants and soil microbial community under precipitation reductions.

In the evaluated rangelands drought caused significant decrease in vegetation cover and aboveground biomass in most sites (Table A.2 supplementary; and Fig. 4). Under drought stress plant growth is limited due to stomata closure (Pirasteh-Anosheh et al., 2016; Jaman et al., 2022) and often results in larger root systems and frequently increased C allocation to the roots (Liu et al., 2004; Karlowsky et al., 2018b) facilitating water and nutrient uptake (Huang and Gao, 2000; Liu and Li, 2005). Drought can also alter the quantity and quality of root exudates due to changes in plant species composition (Canarini et al., 2019), and legacy effects have been shown to cause a reduction of belowground C inputs (Fuchslueger et al., 2016). Although root biomass or plant C input were not the focus of this study, plant community dynamics and associated belowground C inputs are likely an important player in the response of microbial communities to drought. However, the response between plant and microorganisms under drought is bi-directional, where plants can shape the soil community (de Vries et al., 2019) and in turn the soil microorganisms can have important consequences for the plant diversity, community composition and survival (Teste et al., 2017; Zhang and Xi, 2021). Therefore, it is not possible to conclude to which extent effects on the plant community could determine responses in soil microbial community or reciprocally.

Certainly, in our study we found that responses to drought in rangelands (arid, semiarid, semihumid, and humid) between microbial and vegetation variables (cover or aboveground biomass) differed in their magnitude (Figs. 3 and A.5). This suggests that plant and microbial communities may respond differently to drought along aridity gradients. This highlights the importance of plant–microbial interactions under climate change

scenarios due to a potential decoupling in the response of both groups. Recently, two meta-analyses found that the asymmetric responses of plant biomass and soil microbial to precipitation change varied with climate conditions (Liu et al., 2016; Wilcox et al., 2017). In our study, we found that the microbial growth and activity showed a higher percentage change in response to drought in arid or semiarid sites, and the opposite trend in humid sites. The asymmetric responses and different change magnitudes between plants and microorganisms under drought stress are possibly related to the root biomass (e.g. exudation, rhizopedosition) that buffered for the growth and activity of microorganisms under drought conditions (Rasse et al., 2005; Dijkstra and Cheng, 2007; Henry et al., 2007; Karlowsky et al., 2018a; Canarini et al., 2019; Williams and de Vries, 2020).

In addition, changing microbial activities in soils experiencing drought may indicate a faster microbial turnover given that drought might also have contributed to higher substrate inputs (labile microbial nutrients), generating a buffer effect that is compensated by the feedback of the microorganisms that die and those that remain active under drought. In our study, the microbial community exposed to drought showed faster growth and respiration rates and lower qCO_2 values. A recent study found a large shift in the microbial community (bacteria, archaea and fungi), after 10 years of recurrent drought as an adaptation mechanism under water stress (Canarini et al., 2021). Previous studies have shown that microbial communities acclimatized to drought by enhancing osmolyte production, synthesis of capsules and exopolymeric substances to retain water, dormancy and sporulation (Sleator and Hill, 2002; Warren, 2014; Canarini et al., 2021), which may determine a more drought tolerant or resilient microbial community compared with plants responses.

Thus, long-term or more frequent exposure to drought events due to climate change can select a more tolerant soil microbial community that may influence the plant-microorganism interactions, as it was reported in other studies (Canarini et al., 2016; Sihi et al., 2018; Zhou et al., 2018; Zhang and Xi, 2021). The results of the present work can be used for improving the modelling of ecosystem C cycling and climate change impact on rangelands by incorporating microbial community variables into ecosystem process models (Luo et al., 2017; Deng et al., 2021).

5. Conclusion

Our findings provided new insights regarding the effect of main environmental factors (soil, vegetation and climate) on soil microbial response (biomass and basal respiration) in rangelands of South America. This study clearly demonstrated that soil microbial variables decreased in the aridity gradient from humid to arid. In this rangeland ecosystems, SOC and soil N contents and vegetation cover are the most important factors that regulate MBC and MBN. In addition, climate (MAP and aridity index) is the main variable which influences SBR. Moreover, the increase of soil pH negatively influences soil microbial variables in this rangeland ecosystems. Our results suggest that plant and microbial variables respond differently to drought along aridity gradients, and reveal a trend towards a decoupling between plants and soil microorganisms to reduced precipitation. Therefore, our findings improve our understanding of the microorganism's response to the main environmental factors in different rangelands, and contributes to the inclusion of microbial variables in the predictive models of the carbon cycle under global change scenarios.

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CRediT authorship contribution statement

Toledo, S.: Investigation; Methodology and performed the soil property analyses; Performed the data analyses; Writing original draft.

Bondaruk, V. F.: Collected the soil samples in the field; Writing-review and editing.

Yahdjian, L.: Conceptualization; Designed the experiments and coordinated the Project (Drought Net Argentina); Writing-review and editing.

Oñatibia, G R.: Collected the soil samples in the field; Writing-review and editing.

Loydi, A.: Collected the soil samples in the field; Writing-review and editing.

Alberti, J.: Collected the soil samples in the field; Writing-review and editing.

Bruschetti, M.: Collected the soil samples in the field; Writing-review and editing.

Pascual, J.: Collected the soil samples in the field; Writing-review and editing.

Peter, G.: Collected the soil samples in the field; Writing-review and editing.

Agüero, W. D.: Collected the soil samples in the field; Writing-review and editing.

Namur, P. R.: Collected the soil samples in the field; Writing-review and editing.

Blanco, L.: Collected the soil samples in the field; Writing-review and editing.

Peri, P. L.: Conceptualization; Investigation, Resources; Writing-review and editing.

T.S.; B.V.F.; Y.L.; O.G.R.; L.A.; A.J.; B.M.; P.J.; P.G.; A.W.D.; N.P.R.; B. L.; P.P.L.: Drafted the manuscript, and all authors were involved in critical revision and approval of the final version.

Data availability statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declaration of competing interest

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

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