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Precipitation Controls on Soil Biogeochemical and Microbial Community Composition in Rainfed Agricultural Systems in Tropical Drylands

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Abstract: The current and expected expansion of agriculture in the drylands of Mexico, together with the decrease in precipitation occurring in the country, likely affect ecosystem processes and will bring great challenges for the suitability of rainfed agriculture for smallholder farmers. Here, we assessed metrics of the soil C, N, and P cycles, as well as soil microbial diversity, under rainfed maize and common bean cropping in arid and semiarid regions of central Mexico. The soil enzymatic vector angles of cultivated plots in both regions were above 45°, suggesting P limitation for microbial growth and crop productivity. Although changes were not observed in the intensity of this P-limitation with aridity, we found a negative effect of drought increase on the concentration of soil organic C and total N, with consequences for the C, N, and P balance in soils. Increasing aridity leads to the homogenization of microbial diversity. Considering a scenario in which decreases in mean annual precipitation would uncouple the biogeochemical cycles and homogenize soil biodiversity, the ecological implications could be an increase in the vulnerability of agricultural ecosystems to drought, with negative consequences for the suitability of rainfed agriculture in the drylands of central Mexico.

Keywords: climate change; drought; enzyme stoichiometry; smallholder farming; soil biogeochemistry

1. Introduction

Nearly 75% of the agricultural production in rural Mexico is rainfed. This type of agriculture has seen rapid growth since the late 1980s [1], especially due to the expansion of maize and common bean cropping in the semiarid and arid regions of the country. Given its reliance on precipitation, this kind of agriculture is highly vulnerable to climate variability and climate change [2,3]. Substantial precipitation decreases in Mexican semiarid lands have been observed over the past 30 years [4], putting this agriculture under severe threat. Precipitation variability does not only affect plant growth in the current year; it may also have a strong effect on long-term food yields, considering the central role of precipitation in biogeochemical cycling and carbon (C) sequestration in agricultural soils [5,6]. Although many measures have been suggested to reduce the vulnerability of smallholder farmers to climate change at a global scale [7], regional diagnoses of the effect of changes in

precipitation patterns on soil fertility are still lacking and are crucial for adaptation to climate change in rainfed agricultural fields [8,9].

While rainfed agriculture is widespread in the tropics, there are few reports on how soil function in agroecosystems changes as drought intensity and frequency increase [10–12], and none of these reports is focused on maize and common bean rainfed agroecosystems. Moreover, the effects of aridity on soil bacterial and fungi diversity and community composition in rainfed agriculture are not well documented in semiarid and arid tropical regions, despite the crucial role of microbes in reducing the impact of drought on plant performance and crop yields [12,13]. Thus, understanding the effects of drought on soil function, in combination with soil microbial activity, is crucial for better management of agricultural soils and for designing adaptive strategies to climate change. Climate models predict that by the end of the 21st century, central Mexico will experience long-term precipitation decreases of around 25% [14], and this precipitation shift could have significant effects on the biogeochemistry of rainfed agriculture, especially in arid and semiarid regions. Given this difficult scenario, in this study, we aimed to identify differences in soil biogeochemistry in arid areas under rainfed agriculture. For this purpose, we selected two arid areas with different amounts of mean annual precipitation (554 and 416 mm of mean annual precipitation; MAP) that are representative of the agricultural areas in Mexico.

The reduction of soil fertility is one of the most acute problems that tropical rainfed agriculture faces. This loss is closely associated with the disturbance of natural biogeochemical cycles in soils. Although limitations of net primary productivity in terrestrial ecosystems are multielement in nature [15], phosphorus (P) often limits plant growth in tropical regions [16], including agricultural ones [17]. This limitation is the result of low amounts of total P in the system, or because P is present in forms that are not available to plants. Phosphorus limitation is pervasive in tropical areas with drought [18,19], as well as in semiarid and arid regions, due to reduced diffusion of nutrients into the soil solution [20]. Moreover, the export of P due to harvesting tends to increase soil P limitation in agricultural ecosystems, with 30% of the global crop area showing a P deficit [21]. Phosphorus deficit also impacts agricultural soils through its negative effect on the growth of soil microbial biomass, i.e., one of the main drivers of soil function [22]. Different studies have been conducted on the effects of P limitation on microorganisms in native [23,24] and agricultural tropical soils [25]. Direct evidence indicates that P addition causes an increase in soil microbial nutrient immobilization, but also a decrease in soil phosphatase activity [24,26]. Therefore, as is also the case for plants, the level of a single nutrient can be the rate-limiting factor for microbial processes at the ecosystem scale [27,28].

Microbial nutrient limitations can be investigated by measuring potential exoenzymatic activity. This efficient method has been proposed as a means of inferring nutrient limitations for heterotrophic soil microorganisms [29]. Enzymes are considered to be particularly relevant, as they catalyze the rate-limiting step of decomposition and nutrient mineralization [30,31]. It is suggested that the production of enzymes targeting different nutrient resources reflects the metabolic and stoichiometric requirements of soil microorganisms [29]. However, microbial biomass carbon:nitrogen:phosphorus (C:N:P) ratios are relatively invariant across ecosystems [30], differences in microorganisms' efforts to acquire C, N, and P should be expected among ecosystems that differ in nutrient quantity as well as quality, for microorganisms to maintain homeostasis. Therefore, high enzyme activity targeting a particular resource is thought to indicate nutrient limitation by that resource, and ratios of C-, N-, and P-acquiring enzyme activity to the activity of enzymes targeting other resources should reflect relative nutrient availability and, thus, limiting factors for microorganisms [29].

Here, we examine the diversity and composition of soil microbial communities in traditional cropping systems with maize and common bean, two staple crops for human diet and nutrition worldwide [32], with the goal of contributing to a better understanding of the relationship between microbial communities, soil nutrient cycling, and drought. We carried out these analyses in maize-bean agroecosystems in an arid and a semiarid

region in Mexico. The semiarid region has precipitation rates similar to those of many parts of Mexico [4], and the arid region has precipitation rates comparable to those projected to occur over the next century [33]. Based on measurements of organic C and total N and P soil concentrations, enzymes used to infer growth-limiting nutrients, and soil microorganism DNA was examined to assess how aridity alters belowground processes controlling soil microbial composition and biogeochemical heterogeneity. Specifically, we explored: (i) the links between soil and crop characteristics across regions, (ii) the potential nutrient and/or carbon limitation of microbial activity, and (iii) the relationships among precipitation regime, soil characteristics, and microbial composition. Finally, using data of plant productivity and leaf and root nutrient concentrations in studied crops we discussed the variation in soil-plant relationship across regions. One advantage of this study system was that potential differences in soil biogeochemical cycles and microbial community composition due to air temperature, chemical fertilization, and cropping systems were excluded, as the selected plots of the two regions have minimal differences in these climatic characteristics and crop management.

2. Materials and Methods

2.1. Study Sites

The study sites are located in the central highlands of Mexico in the state of Guanajuato. Two locations were selected to provide data on an arid region and a semiarid region, as per aridity indices [34]. The arid sites are in the municipality of *San Felipe* (21°29'00" N, 101°13'00" W) and the semiarid ones are in *Guarapo* (20°23'03" N, 101°24'38" W). Multiple representative sites of rainfed maize (*Zea mays* L., Mexican landrace) ($n = 5$) and common bean (*Phaseolus vulgaris* L., 'Flor de junio' cultivar) ($n = 4$) cropping were selected. The two locations are 140 km apart from each other. Despite their similar precipitation distributions throughout the year (i.e., with a rainy season from June to September that concentrates ~ 60% of total annual precipitation; [35]), they differ in rainfall regimen and aridity (by 33% in the case of mean annual precipitation; and by 67% in the case of aridity) (Table 1). The soils generally fall into two groups, Inceptisols, and Entisols, and vary from medium to shallow depths. The time of cropping (ranging from 30 to 40 years) does not vary across regions, and the range of the annual fertilization rates is similar at arid and semiarid locations (40–50 kg of N and 5 to 7 kg of P per hectare). Dry fertilizers (urea, consisting of $(\text{NH}_2)_2\text{CO}$, or triple superphosphate, consisting of $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$) are applied by hand, as appropriate. The sowing and harvest dates for both crops are May and November, respectively, in the case of maize, and May and September in the case of common bean; the sowing of both crops is two weeks before in the semiarid site than in the arid counterpart. Despite the differences in precipitation regimen between locations, the yields of both maize and common bean do not vary between regions (Table 1).

Maize crops cover 7.76 million hectares of Mexico and represent 14.5% of the national agriculture gross domestic product (GDP) [36]. On the other hand, the common bean covers 1.63 million hectares and represents 1.93% of the national agriculture GDP in the country [37]. The yield of both crops should increase in the period 2016 to 2030 (by 4.0% per year in the case of maize, and by 5.7% per year in the case of common bean) to satisfy the expected increase in demand [36,37].

The state of Guanajuato is one of the largest producers of maize and common bean in the country. The southern half of the state contains extensive and fertile plains of the *El Bajío* ecoregion (semiarid climate), located in the trans-volcanic Mexican belt, and the northern plain is part of the *Sierras y Altiplanicie de Mesa Central* ecoregion (arid climate), located in drylands of central Mexico. Despite its importance for the Mexican agricultural sector, the current and expected expansion of rainfed agriculture, together with the expected decrease in precipitation amount, are likely to have strong effects on soil processes and will bring great challenges for the suitability of rainfed agriculture in these regions.

Table 1. General characteristics of arid and semiarid sites and crops.

Site Characteristics	Arid Region	Semiarid Region
Climate [†]		
Mean annual precipitation (MAP, mm yr ⁻¹)	416	554
Mean annual temperature (MAT, °C)	18.1	18.9
Potential evapotranspiration (PE, mm yr ⁻¹)	2350	1832
Aridity index (MAP/PE ratio)	0.18	0.30
Mean monthly precipitation during the growing season of maize (mm month ⁻¹)	52 ± 10	72 ± 20
Mean monthly precipitation during the growing season of common bean (mm month ⁻¹)	65 ± 8	94 ± 12
Mean monthly temperature during the growing season of maize (°C month ⁻¹)	19.4 ± 1.0	20.1 ± 1.2
Mean monthly temperature during the growing season of common bean (°C month ⁻¹)	20.3 ± 0.5	20.9 ± 0.4
Crop characteristics [‡]		
Grain yield (Mg ha ⁻¹)		
Maize	1.17 ± 0.17	1.50 ± 0.50
Common bean	0.28 ± 0.06	0.33 ± 0.22
Root biomass (g plant ⁻¹)		
Maize	24.7 ± 3.3	24.9 ± 2.9
Common bean	1.54 ± 0.2	0.77 ± 0.16
Leaf N (mg g ⁻¹)		
Maize	17.9 ± 2.4	22.8 ± 0.8
Common bean	39.5 ± 1.5	40.4 ± 1.9
Leaf P (mg g ⁻¹)		
Maize	2.3 ± 0.5	1.8 ± 0.1
Common bean	2.7 ± 0.2	2.1 ± 0.1
Root N (mg g ⁻¹)		
Maize	6.6 ± 0.8	9.3 ± 0.2
Common bean	16.8 ± 2.2	15.6 ± 1.2
Root P (mg g ⁻¹)		
Maize	0.5 ± 0.1	0.5 ± 0.04
Common bean	1.9 ± 0.2	1.2 ± 0.2

Note. Values are mean ± 1 SE. [†] Long-term climatic data (1980–2015) from National Commission of Water (CONAGUA) personal communication; [‡] Julieta A. Rosell (unpublished data).

2.2. Soil Sampling and Measurements

Soil samples were collected in the middle of the rainy season (in August) to determine the effects of precipitation regimen on soil microbial diversity and community composition, and on soil pH, organic C, total N, and total P in the 0–20 cm horizon. At each plot, three equidistant lines (separated by 20 m) were drawn and three soil cores, 7.5 cm in diameter and 20 cm deep, were taken from three equidistant points (separated by 20 m) along each line. The nine cores (3 samples × 3 lines) were combined into one composite sample per plot. In agricultural soils, nutrient availability and root uptake decline substantially below the plow layer [38] as a consequence of the upper 20 cm of soil containing a significant proportion of crop roots [39]. On the other hand, long-term trials have shown that fertilizers mainly affect nutrient availability in the plow layer, with very little impact on deeper soil layers [40]. At the study sites, the upper 20 cm of the soil profile in both regions concentrates soil organic matter, fine roots (<1 mm in diameter), and nutrients (V́ctor Peña, unpublished data).

The composite soil sample from each plot was sieved through a 2 mm mesh to remove plants, roots, and gravel and minimize the influence of plant residues on physical, chemical, and microorganism analyses. Samples were kept at −20 °C prior to analysis. Soil pH was determined in a 1:2.5 soil to deionized water ratio using a glass electrode. Soil organic C (OC) was analyzed in an automated C-analyzer after grinding a 5-g air-dried subsample was passed through a 100-mesh screen. Concentrations of total N (TN) and total P (TP) were

determined using acid digestion in concentrated H_2SO_4 and analyzed in an automated NP-analyzer.

2.3. Enzyme Analyses

We measured the indicator enzymes most commonly used to infer growth-limiting nutrients, i.e., β -1,4-glucosidase (BG; enzyme commission number: EC 3.2.1.21) and polyphenol oxidase (POX; EC 1.10.3.1) to infer C-acquiring enzymes, leucine aminopeptidase (LAP; EC 3.4.11.1), β -1,4-N-acetylglucosaminidase (NAG; EC 3.2.1.14) to infer N-acquiring enzymes [29], following the method proposed by Jackson et al. [41]. The enzyme assays were incubated at 25 °C for 2 h and their absorbance was recorded using a microplate reader at 410 nm for BG, LAP, NAG, and AP activities, and at 460 nm for POX activity. The concentration of pNP (or tyrosine, for POX) detected in the soil sample was corrected by subtracting the sum of absorption from the sample and substrate control wells, and enzyme activities were calculated as follows:

$$EA = (\text{final absorbance}) / (C \times \text{incubation time} \times \text{soil dry mass});$$

where EA is the enzyme activity expressed in μmol of pNP (or tyrosine, for polyphenol oxidase) released per gram of soil per hour ($\mu\text{mol g}^{-1} \text{hour}^{-1}$); and C is the conversion factor that relates absorbance to μmol of pNP (or tyrosine, for polyphenol oxidase) in each enzyme activity.

The relationships between relative enzyme activities for C vs. N, (BG + POX/LAP + NAG), C vs. P (BG + POX/AP), and N vs. P (LAP + NAG/AP) were calculated [29]. Moreover, a quantitative method to interpret simultaneous microbial C, N, and P acquisition through the activities of these key extracellular enzymes was applied, as proposed by Moorhead et al. [42]. The method is based on the calculation of two vector components, length and angle, created by plotting the proportional C:N vs. C:P ratios of enzyme activity, to quantify relative investments in C vs. nutrient (i.e., N or P) acquisition (vector length) and P vs. N acquisition (vector angle).

2.4. DNA Extraction and Sequencing

Microbial DNA was extracted from 0.5 g of soil from each plot by triplicate, using the MoBio Power Soil DNA commercial kit (MoBio Laboratories, Solana Beach, CA, USA) in accordance with the manufacturer's instructions. The bacterial 16S rRNA gene (V1-V2 hypervariable regions) and fungal ITS regions were amplified and sequenced with 27F/388R primers [43] and ITS1F/ITS2aR primers [44,45], respectively, using an Illumina MiSeq at the Research and Testing Laboratory (Lubbock, TX, USA).

2.5. Data Analysis

Mean values per region and per cropping system were calculated for soil clay content, pH, organic C, total N, total P, enzyme data (the activity of β -glucosidase, polyphenol oxidase, β -1,4-N-acetylglucosaminidase, leucine aminopeptidase and phosphatase, and enzyme activity ratios), and microbial diversity data (Shannon and Simpson indexes), and these values were used for statistical analyses. To investigate crop changes in soil element concentrations and enzymes activities under crops over both regions, a least-squares linear model was adjusted and a two-way analysis of variance (ANOVA) was performed considering crop and region, and their interaction. The residuals were explored for normality and variance homogeneity using the Shapiro–Wilk's test and Levene's test, respectively. Data were transformed logarithmically when the assumptions of normality and homoscedasticity did not occur. Principal component analysis and Pearson correlation coefficients were performed to examine the relationships among soil biogeochemical and microbiological metrics in both regions.

Illumina raw sequences were processed using the Quantitative Insights into Microbial Ecology 2 pipeline (QIIME2) [46] with default arguments, except on the quality filter, where sequences with more than 2 N's were removed [47]. Operational Taxonomic Units (OTUs)

were clustered with a 97% similarity cutoff using VSEARCH [48]. Taxonomic assignment of representative OTUs was performed with the Greengenes DataBase (v 13.8); [49] for the 16s RNA gene, and with the UNITE DataBase for the ITS region. Shannon and Simpson diversity indices were calculated to estimate diversity from the OTU derived using the bioinformatic procedure of the “phyloseq” R package [50]. Relative abundance of microbial groups was estimated for each crop in each region and a generalized linear model (GLM) was adjusted with a binomial distribution, a two-way Analysis of Deviance (ANODEV) was performed considering crop and region and their interaction, and the inferences were made based on the Wald’s test, following the standard procedures presented by McCullagh and Nelder [51]. The summary of the variance components can be found in the supplementary information (Tables S1–S6). All statistical analyses were performed using the R Version 3.6.1 [52] and the “emmeans” package [53].

3. Results

3.1. Soil pH and Biogeochemical Properties

The soil pH did not change across regions or crops ($p > 0.05$) (6.4 ± 0.16 ; mean \pm 1 SE for all samples). Consistently, soil organic C and total N concentrations decreased with a decrease in precipitation amount (Table 2; $p < 0.01$, for organic C, and $p = 0.04$, for total N, Table S1). However, differences in soil total P between regions were low and non-significant ($p = 0.55$, Table S1). Soil C:N ratios were low (ranging from 6 to 10), reflecting N accumulation in the soil by fertilization and decreased with aridity (from 8.2 on average in the case of the semiarid region to 6.4 in the case of the arid region). Similarly, C:P and N:P ratios showed an abrupt decrease with aridity (from 51 to 34 and 6.5 to 5.2 for the C:P and N:P ratios, respectively). Soil organic C and, total N and P concentrations did not vary between crops (i.e., maize and common bean crops) (Table 2; $p = 0.05$ to 0.60, Table S1).

Table 2. Organic carbon, total nitrogen, and total phosphorus concentrations in topsoil (0–20 cm in depth) under different cropping systems in arid and semiarid regions.

Crop	Region	Organic C	Total N	Total P
			(mg g ⁻¹)	(μg g ⁻¹)
Maize	Arid	11.70 Ba \pm 0.52	1.65 Aa \pm 0.36	340 Aa \pm 73
	Semiarid	22.23 Aa \pm 0.75	2.27 Aa \pm 0.57	415 Aa \pm 93
Common bean	Arid	11.48 Ba \pm 0.61	1.99 Ba \pm 0.40	330 Aa \pm 81
	Semiarid	19.37 Ab \pm 0.91	2.97 Aa \pm 0.71	396 Aa \pm 98

Note. Values are means \pm 1 SE ($n = 5$ for maize and $n = 4$ for common bean crops). Different capital letters indicate means are significantly different ($p < 0.05$), when testing for differences between regions within a crop. Different lowercase letters indicate means are significantly different ($p < 0.05$), when testing for differences between crops within a region.

Extracellular enzyme activity in soils under maize crop and common bean crop is shown in Table 3. We found an increasing gradient of enzyme activity in the direction of NAG < LAP < POX ~ BG < AP. The corresponding ANOVA indicated that at least one enzymatic level differs from the rest ($p < 0.001$) and paired comparisons using the Tukey–Kramer HSD test showed that enzymes of the N cycle sustained lower levels of activity ($p < 0.05$ in all cases), while those of the P cycle were the most active ($p < 0.05$ in all cases). Enzymes of the C cycle had intermediate levels of activity ($p > 0.05$).

Table 3. β -1,4-glucosidase, polyphenol oxidase, leucine aminopeptidase, β -1,4-N-acetylglucosaminidase and acid phosphatase activities in topsoil (0–20 cm in depth) under different cropping systems in arid and semiarid regions.

Crop	Region	BG	POX	LAP	NAG	AP
		($\mu\text{mol pNP}$)	($\mu\text{mol tyrosine}$)	($\mu\text{mol pNP g soil}^{-1} \text{ hour}^{-1}$)	($\text{g soil}^{-1} \text{ hour}^{-1}$)	($\text{g soil}^{-1} \text{ hour}^{-1}$)
Maize	Arid	0.339 Aa \pm 0.014	0.295 Aa \pm 0.021	0.168 Aa \pm 0.008	0.158 Aa \pm 0.014	0.679 Aa \pm 0.077
	Semiarid	0.373 Aa \pm 0.019	0.318 Aa \pm 0.022	0.139 Aa \pm 0.009	0.129 Aa \pm 0.017	0.701 Aa \pm 0.074
Common bean	Arid	0.342 Aa \pm 0.017	0.322 Aa \pm 0.025	0.214 Aa \pm 0.009	0.138 Aa \pm 0.015	0.638 Aa \pm 0.050
	Semiarid	0.251 Aa \pm 0.021	0.237 Aa \pm 0.026	0.184 Aa \pm 0.011	0.126 Aa \pm 0.017	0.580 Aa \pm 0.078

Note. Values are means \pm 1 SE ($n = 5$ for maize and $n = 4$ for common bean crops). Abbreviations: AP, acid phosphatase; BG, β -1,4-glucosidase; LAP, leucine aminopeptidase; NAG, β -1,4-N-acetylglucosaminidase; POX, polyphenol oxidase. Different capital letters indicate means are significantly different ($p < 0.05$) when testing for differences between regions within a crop. Different lowercase letters indicate means are significantly different ($p < 0.05$) when testing for differences between crops within a region.

No significant changes in β -1,4-glucosidase and soil N and P enzyme activities were detected between regions or crops (Table 3; region effect, $p = 0.10$ to 0.35 ; crop effect, $p = 0.55$ to 0.89 , Table S2). In contrast, the activity of POX across crops varied as a function of region (crop*region effect, $p = 0.04$, Table S2). In addition, there were no significant regional or crop effects on C:P and N:P enzyme activity ratios in soils (Table 4; region effect, $p = 0.74$ and 0.64 , respectively; crop effect, $p = 0.89$ and 0.68 , respectively, Table S3). In contrast, the enzyme activity ratio for C:N under each crop varied as function of region (crop*region effect, $p = 0.03$, Table S3).

Table 4. Enzymatic stoichiometry displayed as enzymatic (BG + POX): (LAP + NAG), (BG + POX): AP, and (LAP + NAG): AP activity ratios in topsoil (0–20 cm in depth) under different cropping systems in arid and semiarid regions.

Crop	Region	(BG + POX): (LAP + NAG)	(BG + POX): AP	(LAP + NAG): AP
Maize	Arid	1.99 Ba \pm 0.11	0.94 Aa \pm 0.11	0.43 Aa \pm 0.03
	Semiarid	2.69 Aa \pm 0.14	1.11 Aa \pm 0.12	0.49 Aa \pm 0.07
Common bean	Arid	1.93 Aa \pm 0.16	1.18 Aa \pm 0.12	0.63 Aa \pm 0.05
	Semiarid	1.66 Aa \pm 0.17	1.12 Aa \pm 0.14	0.83 Aa \pm 0.10

Note. Values are means \pm 1 SE ($n = 5$ for maize and $n = 4$ for common bean crops). Abbreviations: AP, acid phosphatase; BG, β -1,4-glucosidase; LAP, leucine aminopeptidase; NAG, β -1,4-N-acetylglucosaminidase; POX, polyphenol oxidase. Different capital letters indicate means are significantly different ($p < 0.05$) when testing for differences between regions within a crop. Different lowercase letters indicate means are significantly different ($p < 0.05$) when testing for differences between crops within a region.

The enzymatic vectors (length and angle) for soils under maize and common bean crops are shown in Figure 1. Generally, the soil from both regions showed enzymatic vector angles above 45° , suggesting a general P limitation for microorganism growth. Paired comparisons of angles using the Tukey-Kramer HSD test indicated that inter-region variation was statistically indistinguishable ($p > 0.05$). In addition, the paired comparisons of lengths, also using the Tukey-Kramer HSD test, showed that the soils of the common bean plots have smaller vector lengths than the soils of their maize counterpart ($p < 0.05$), possibly indicating higher levels of C limitation for the activity of soil microorganisms, regardless of region ($p < 0.01$).

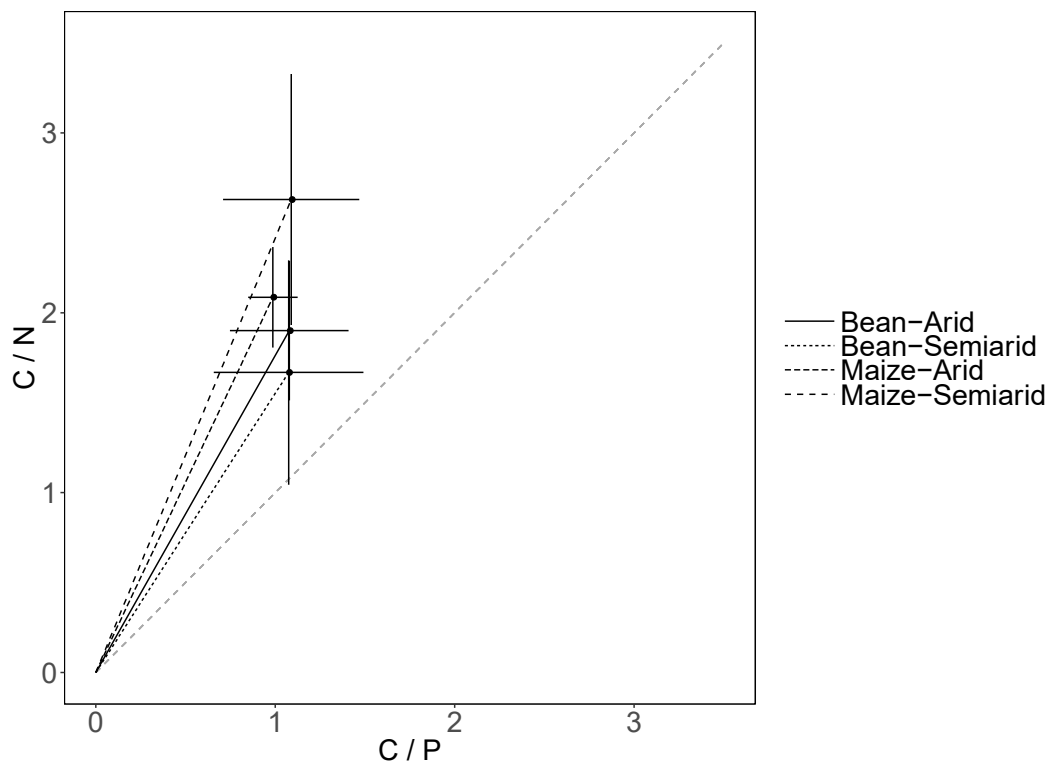


Figure 1. Vectors of enzymatic stoichiometry carbon: nitrogen and carbon: phosphorus activity ratios in soils under maize and common bean cropping in arid and semiarid regions.

3.2. Soil Microbial Community Composition and Diversity

Decreasing precipitation had a significant impact on soil bacterial phylogenetic diversity. It was found that the number of bacterial and fungal OTUs was higher in the arid region (351 ± 5.4 and 822 ± 8.7 , respectively; mean ± 1 SE) than in the semiarid one (272 ± 4.0 and 764 ± 7.0 , respectively) ($p < 0.01$). The fungi-to-bacteria abundance ratio varied from 2.2 to 3.5 and decreased with a decrease in precipitation amount ($p < 0.05$). The Shannon and Simpson indices indicated that soil bacterial diversity increased with decrease precipitation amount (Table 5; $p < 0.001$ and $p = 0.002$, respectively, Table S4). Additionally, there was a reduction in bacterial diversity under maize crop relative to its diversity under common bean crop ($p = 0.01$ in the case of Shannon index, and $p = 0.02$ in the case of the Simpson index). In contrast, there were no significant differences in fungi diversity whether comparing regions or crops (Table 5; $p = 0.28$ to 0.94 , Table S4).

Table 5. Shannon and Simpson diversity indices for bacteria and fungi communities in topsoil (0–20 cm in depth) under different cropping systems in arid and semiarid regions.

Crop	Region	Shannon Index (<i>H</i>)		Simpson Index (<i>D</i>)	
		Bacteria	Fungi	Bacteria	Fungi
Maize	Arid	5.44 Aa \pm 0.04	4.19 Aa \pm 0.12	0.991 Aa \pm 0.0005	0.936 Aa \pm 0.0098
	Semiarid	4.97 Bb \pm 0.04	4.11 Aa \pm 0.12	0.987 Bb \pm 0.0006	0.948 Aa \pm 0.0089
Common bean	Arid	5.51 Aa \pm 0.05	4.31 Aa \pm 0.13	0.992 Aa \pm 0.0005	0.941 Aa \pm 0.0106
	Semiarid	5.27 Ba \pm 0.05	3.84 Aa \pm 0.13	0.990 Aa \pm 0.0006	0.923 Aa \pm 0.0111

Note. Values are means ± 1 SE ($n = 5$ for maize and $n = 4$ for common bean crops). Different capital letters indicate means are significantly different ($p < 0.05$) when testing for differences between regions within a crop. Different lowercase letters indicate means are significantly different ($p < 0.05$) when testing for differences between crops within a region.

Dominant groups in the bacterial community were very consistent across regions within each of the crops. The most abundant groups were *Proteobacteria*, *Actinobacteria*, and *Acidobacteria* in all soils, with an average of 76% of the total bacterial sequences (Figure 2a). On the other hand, *Ascomycota* phylum dominated the fungal community (accounted for 69% of the total fungal sequences), followed by *Basidiomycota* (6%); approximately 23% of the fungal OTUs could not be classified (Figure 2b). Although *Proteobacteria* and *Actinobacteria* consistently were the most abundant species, their abundances were sensitive to precipitation regimen increasing with decrease in precipitation amount ($p < 0.001$, Table S5). *Acidobacteria* abundance across regions varied as a function of crop (crop*region effect, $p < 0.001$). In contrast, there was no regional pattern in abundances of the dominant fungal group *Ascomycota* ($p = 0.97$, Table S6). Regional patterns in *Basidiomycota* abundances varied as a function of crop system (crop*region effect, $p < 0.001$). The effect of region on *Basidiomycota* abundances was much stronger under maize crops (its abundance increased by a factor of 2 with a decrease in rainfall amount), than it was under the common bean crops (abundances increased by 17% with an increase in rainfall amount).

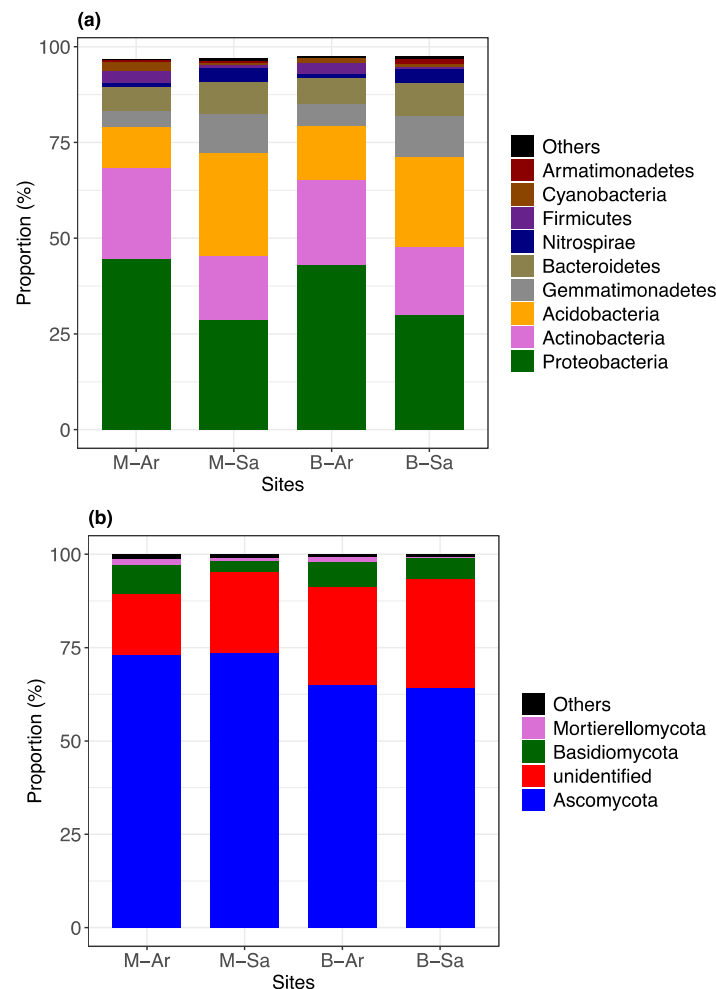


Figure 2. Bacterial (a) and fungal (b) community compositions at the phylum level in soils under maize (M) and common bean (B) cropping in arid (Ar) and semiarid (Sa) regions.

The pattern of abundances across regions detected in the dominant groups of soil bacteria and fungi was not consistent in the less common phyla. In these less common phyla, only *Firmicutes* (range of variation in the relative abundance of 1–4%) showed significant variation with a comparable response to that exhibited by dominant groups (i.e., they were more abundant in soils from the arid region; $p < 0.001$, Table S5). In contrast, the relative abundance of *Bacteroidetes* (6–9%) and *Nitrospirae* (4–10%) increased with an increase in

precipitation amount ($p < 0.001$, in both cases). Abundances of *Gemmatimonadetes* (4–10%), *Cyanobacteria* (0.6–1.8%), and *Armatimonadetes* (0.2–1.2%), as well as of *Mortierellomycota* (0.4–2%) across regions varied as a function of crop (region*crop effect, $p = 0.01$ to 0.002, Tables S5 and S6).

3.3. Multivariate Analysis and Soil Metric Relationships

The first two principal component (PC) axes together explained 58% of the variance of soil data and showed a clear distinction between regions in terms of soil biogeochemical and microbial community composition (Figure 3). Specifically, the plots of the semiarid region showed greater dispersion within biplots (by a factor of 6) compared to those of the arid region ($p < 0.001$), indicating a decrease in soil heterogeneity with a decrease in precipitation. The first PC axis (PC1) clearly separated the study plots considering the precipitation regimen. Soil organic C, total P, and total N, and *Acidobacteria*, *Nitrospirae*, *Gemmatimonadetes*, *Bacteroidetes*, and *Armatimonadetes*, loaded strongly in the same direction on PC1, which explained 40% of the variation among soil metrics (Figure 3, Table 6). In contrast to this direction, *Proteobacteria*, *Actinobacteria*, *Firmicutes*, and *Cyanobacteria* were loaded on the same first PC axis and related to arid plots, indicating that bacterial groups were more sensitive than fungi to water stress. The second PC axis (PC2) explained 18% of the variance and represented a soil enzyme-activity axis, which was positively correlated with P (acid phosphatase), N (β -1,4-N-acetylglucosaminidase), and C (polyphenol oxidase and β -1,4-glucosidase) enzymes, but negatively correlated with leucine aminopeptidase. In addition to the decrease in biogeochemical and microbial heterogeneity observed with the increase of drought, the number of significant correlations between soil metrics decreased by ~50% with the decrease in precipitation amount (from 33 in the semiarid site to 16 in the arid counterpart) (Table S7).

Table 6. Eigenvalues, cumulative percent variation, and eigenvectors of the first three principal components (PCs) for the top-soil (0–20 cm in depth) characteristics that best predicted the soil biogeochemical and soil microbial composition spectrums.

	PC1	PC2	PC3
Eigenvalue	7.929	3.625	2.546
Cumulative percent variation	39.65	57.77	70.5
Eigenvectors			
Soil organic carbon (OC)	−0.96 ***	0.17	−0.02
Soil total nitrogen (TN)	−0.64 **	0.16	−0.12
Soil total phosphorus (TP)	−0.75 ***	0.42	0.15
β -1,4-glucosidase (Bg)	−0.19	0.80 ***	0.15
Polyphenol oxidase (Pox)	0.05	0.73 ***	0.21
Leucine aminopeptidase (Lap)	0.40	−0.77 ***	−0.19
β -1,4-N-acetylglucosaminidase (Nag)	0.28	0.72 ***	−0.05
Acid phosphatase (Ap)	0.03	0.89 ***	0.03
Acidobacteria (1)	−0.95 ***	−0.11	0.02
Actinobacteria (2)	0.82 ***	0.01	0.34
Armatimonadetes (3)	−0.58 *	−0.20	0.47
Ascomycota (4)	0.09	−0.06	−0.60 **
Bacteroidetes (5)	−0.58 *	−0.08	−0.36
Basidiomycota (6)	0.56 *	−0.25	0.55 *
Cyanobacteria (7)	0.62 **	−0.04	0.48 *
Firmicutes (8)	0.62 **	0.14	−0.64 **
Gemmatimonadetes (9)	−0.80 ***	−0.08	−0.16
Mortierellomycota (10)	0.44	0.23	−0.79 ***
Nitrospirae (11)	−0.90 ***	−0.31	−0.01
Proteobacteria (12)	0.89 ***	0.16	−0.02

Note. Significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

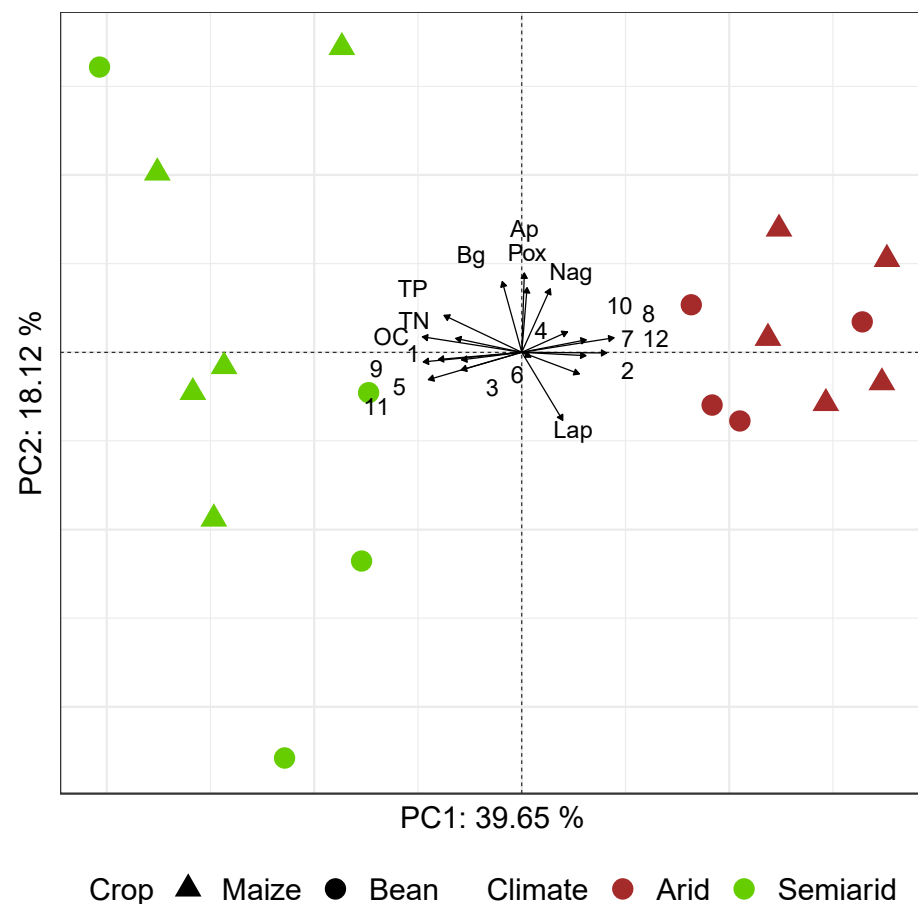


Figure 3. Principal components (PC) analyses biplots of the soil data under maize and common bean cropping in arid and semiarid regions. OC, organic carbon; TN, total nitrogen; TP, total phosphorus Ap, acid phosphatase; Bg, β -1,4-glucosidase; Lap, leucine aminopeptidase; Nag, β -1,4-N-acetylglucosaminidase; Pox, polyphenol oxidase; 1, *Acidobacteria*; 2, *Actinobacteria*; 3, *Armatimonadetes*; 4, *Ascomycota*; 5, *Bacteroidetes*; 6, *Basidiomycota*; 7, *Cyanobacteria*; 8, *Firmicutes*; 9, *Gemmatimonadetes*; 10, *Mortierellomycota*; 11, *Nitrospirae*; 12, *Proteobacteria*.

4. Discussion

It is expected that many tropical semiarid regions will suffer droughts with increasing frequency and intensity over this century [14]; since this change in climate will likely alter the functions of tropical agricultural ecosystems and the yield of major crops [54], we sought to contribute to the understanding of how soil biogeochemistry and microbial diversity in rainfed agriculture may be sensitive to differences in precipitation regimes.

4.1. Differences in Soil-Plant Relationships with Changes in Precipitation Regime

Climate impacts on food security will involve negative impacts on crop yields. However, unlike other studies [55–57], we were not able to detect a substantial change in yield variability (for both common bean and maize) across regions despite the variation in precipitation regimes (Table 1). Nevertheless, aridity had different impacts on nutrient cycling. For example, low precipitation amounts can drive a decrease in soil total N without consequences for leaf and fine root N concentrations in common bean plants. In contrast, although soil total P concentration did not vary with increased aridity in bean agroecosystems, its concentration in leaves and roots did increase with increased aridity. Thus, this evidence suggests that, under arid conditions, this legume would have greater P concentrations in leaves to compensate for the expected lower photosynthetic rates induced by reduced stomatal conductance [58]. This would also happen in roots, enhancing root

metabolism and growth for the uptake of soil nutrients and water [59]. Moreover, it was observed that beans in the arid region allocated more resources to roots (root biomass increases by a factor of 2 with a decrease MAP; Table 1). Thus, the data indicated differences in resource investment strategies for common bean plants under increased aridity, as would be expected under an 'optimal partitioning theory' [60]. On the other hand, in maize, the observed decrease in soil total N with increased aridity had consequences for leaf and fine root N concentrations. However, in maize, P concentrations in leaves and roots and root biomass were insensitive to more extended and frequent precipitation shortages, probably reflecting better adaptation to aridity in this C₄ species.

These results show a striking contrast in the consequences of increased aridity in rainfed agriculture between biological N-fixation species and species without this capacity. Overall, our results support the conclusion that increased aridity results in N depletion in maize, and more efficient P cycling in beans. The scarcer and more seasonal precipitation in the arid region, as compared to its semiarid counterpart, possibly leads to a mismatch between the time when most of the N is mineralized by soil microbes and the time of greatest N uptake by plants [61], something that needs to be taken into account in management practices of rainfed agriculture in drylands worldwide under climate change.

4.2. Nutrient Limitation in Agricultural Ecosystems in Tropical Arid Lands

Despite P fertilization, P limitation may occur in the studied soils, and the deficit in soil P may lead to a loss of attainable yield of both crops (see the low yield in maize and bean crops in both regions in Table 1). Our results indicate that agricultural soils in both regions had elevated phosphatase activity (a sensitive indicator of limited P supply for ecosystem demand; [62]). This nutrient limitation was also revealed by enzymatic vector angles above 45° in agricultural soils, which are often related to an increase in microbial investment in P acquisition under low P supply [42,63]. These results are consistent with other studies showing that soil microorganisms are P-limited in native [23,64,65] and agricultural ecosystems [17,25]. Furthermore, we saw no differences in vector angles across regions (following the proposal to use indicator enzymes to reflect P-acquiring effort; [29]), as could be expected due to the limited mobility and dissolution of P in dry tropical soils. This condition would be exaggerated in our drier sites. We cannot determine whether such lack of expected responses to increased aridity resulted from chemical P fertilization (i.e., an indirect consequence of an increase in P supply) or whether it reflects highly efficient use of this extra anthropogenic P input by crops (as suggested by the observed increase in P concentrations in leaves and roots of common bean plants in the arid region), or both. In contrast, the N cycle seems to be sustained by the chemical fertilization, and to large extent by atmospheric and biological processes, the latter of which may be augmented by abundant microbial N fixation in tropical soils [66,67].

In contrast to other studies that indicate that microorganisms in tropical soils are primarily limited by C and secondarily limited by P [23,68], our data suggest that P limitation is generalized in these arid and semiarid soils, affecting the relative microbial investments in P-acquiring enzymes that may be related to common (e.g., *Actinobacteria*) and rare (e.g., *Firmicutes*) bacterial abundances, water-stress tolerant organisms with the capacity to release unavailable P [69–71]. On the other hand, our analyses suggest that C limitation is common for bean systems in both regions, despite that generally the precipitation stimulates the mineralization of soil organic C [72]. The C limitation for soil microbial function in the common bean soils could be related to bacterial demand, due to the fact that fungi often exhibit a more flexible C:N:P stoichiometry and are better at using crop litter resources than bacteria [73,74].

4.3. Soil Biogeochemistry and Microbial Community Composition Are Sensitive to Drought Increase

We found that the precipitation regime was linked to clear differences in soil biogeochemistry and microbial community composition, as indicated by our multivariate analysis. In particular, the lower dispersion of arid plots showed in the PCA indicate that increased

aridity reduces soil biogeochemical heterogeneity [75], while higher intra-annual variability in precipitation leads to lower coordination in the soil functioning as was evidenced by the Pearson correlation analysis, which could affect the food security [5].

Predicted increases in aridity are expected to lead to severe nutrient depletion, particularly in the most arid sites [76]. Our results show that despite inorganic fertilization decreased the concentration of N (and also of C), it did not increase the concentration of P (as expected by the low P mobility in the soil), hence affecting soil C, N, and P balance in the arid region. Thus, we observed an abrupt decrease in the C:P and N:P ratios from semiarid to arid regions. These abrupt changes indicate that biologically controlled C and N cycles seem to become uncoupled from P biogeochemically controlled cycles in response to increasing aridity, with negative consequences for the reduced crop yields.

In turn, the soil microbial community composition was less variable within the arid region than within its semiarid counterpart, as indicated by a decrease in bacterial α -diversity with increased aridity. The observed uncoupling of α - and β -diversity suggests the homogenization of soil microbial community composition and a net loss of its biodiversity in the soil with increased aridity as was observed in other studies [77,78]. This lower microbial taxonomic diversity suggests a lower soil functional capacity [79,80] with aridity.

Our results, particularly the increase in the fungi to bacterial abundance ratio with aridity, are consistent with previous reports showing that fungi are more resistant to drought than bacteria [81,82]. Although the precipitation regime has a legacy effect on the composition of the fungal community [83], fungi can be more tolerant to extreme drought than bacteria. Furthermore, fungi diversity displayed no regional trends. Our study also indicated that bacterial community composition remained stable under drier conditions, possibly due to attenuation of bacteria as a result of extended drought exposure [84] and/or altered functionality to build up resilience [85]. Despite this resilience in community composition, variance in the responses of more abundant gram-positive bacteria was observed and could be explained in terms of distinct classes within this group [86]. For example, the abundance of gram-negative bacteria, such as *Proteobacteria*, increased with aridity. Meanwhile, the abundance of other gram-negative bacteria, such as *Acidobacteria*, decreased in the function of the crop system, thus reflecting that these taxa are not universally linked to aridity and showing varying trends in response to changes in water stress [87,88]. The differences between both groups in response to drought increase could be related to changes in soil organic C composition and bacterial C metabolizing patterns [80], since *Proteobacteria* abundance increases with higher C mineralization rates, and *Acidobacteria* abundance increases with lower C mineralization rates, which is driven by the stronger water pulses effects on soil organic matter decomposition with aridity [89]. Additionally, a higher abundance of gram-positive bacteria, such as *Actinobacteria*, found in the arid region, may indicate that the bacterial community composition in these agricultural ecosystems shifts due to osmotic stress. Gram-positive bacteria are known to be more drought tolerant (stronger cell wall and drought avoidance strategies such as spore formation) than gram-negative bacteria [90,91]. Thus, we speculate that these microbial taxonomic shifts were likely due to osmotic stress caused by the lower precipitation amount in the arid region. This is consistent with other evidence [83,92,93] that found similar relationships between drought and soil bacterial community responses, reflecting the opportunistic strategy of typical copiotrophs with high growth rates (e.g., *Proteobacteria*; [94]).

We also observed a decrease in the abundance of rare bacterial taxa with an increase in aridity. Rare soil microorganisms can be highly active and diverse [95], contributing to processes in the soil even with low abundance [96]. Moreover, the growth rates of rare microbes are not necessarily different from abundant ones [97]. As such, drought intensification may potentially lead to altered composition of the microbial community through effects on rare members of the community, with negative consequences for ecosystem stability and functioning [98] in view of the strong links between rare taxa and soil ecosystem processes [95].

The analysis of enzyme activity, a proxy of the microbial nutrient demand, indicates similar activity for all enzymes (i.e., C-, N- and P-acquiring enzymes) across regions despite changes in aridity and the observed greater substrate accumulation when xeric condition increase (Table 2). Similar enzyme activity across regions could be due to reduced competition with plants under increasing drought, given that the levels at which microbes become water-limited are typically much lower than those for plants [99], and/or too large organic matter inputs from the death of more abundant root biomass (Table 1). The lack of changes in enzyme activities across regions is also possible due in part to the interplay of two factors whose relative contributions are difficult to quantify: the shift in microbial community composition along these regions and increasing efficiency within microbial species as they respond to reduced nutrient availability or water stress [100].

Aside from the soil microbial diversity and biogeochemical patterns observed, our study on the consequences of the regional variation in precipitation regimen in drylands of Mexico, allows us to identify that the effect of drought intensification on *Basidiomycota* (a fungal group including mycorrhizal species and pathogens of bean and maize crops [101,102]) abundance in these agroecosystems will vary, depending on the details of the identity of crop species. Given the potential for crop system sustainability in response to the massive impact of climate change on rainfed agricultural systems in tropical drylands, the topic of the present study warrants subsequent investigation.

5. Conclusions

The future of rainfed agriculture in tropical regions is uncertain; particularly, the regulation of major biogeochemical cycles is expected to be modified by changes in the precipitation regime. Our data suggest that there is a phosphorus limitation for microbial growth in soils across the studied regions. This generalized limitation of microbial activity by phosphorus supply may have profound effects on crop productivity in semiarid and arid regions. Although the intensity of this P-limitation was not sensitive to aridity increase, our findings suggest that the predicted precipitation reduction in arid lands will disrupt carbon, nitrogen, and phosphorus balance in soils, and will alter both the composition of soil microbial communities and the resource investment strategies of maize and common bean plants. In a scenario in which decreases in mean annual precipitation uncouple biogeochemical cycles and homogenizes soil microbial biodiversity, the vulnerability of rainfed agricultural ecosystems would increase with severe consequences for the livelihoods of the people in the drylands of central Mexico.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/su132111848/s1>, Table S1: Analysis of variance (ANOVA) for soil organic carbon, total nitrogen and total phosphorus concentrations considering the main effects (crop and region) and their interaction (crop*region), Table S2: Analysis of variance (ANOVA) for enzyme activities considering the main effects (crop and region) and their interaction (crop*region). Table S3: Analysis of variance (ANOVA) for enzyme stoichiometry activity ratios considering the main effects (crop and region) and their interaction (crop*region). Table S4: Analysis of variance (ANOVA) of soil microbial diversity considering the main effects (crop and region) and their interaction (crop*region). Table S5: Analysis of deviance (ANODEV) of soil bacterial abundance considering the main effects (crop and region) and their interaction (crop*region). Table S6: Analysis of deviance (ANODEV) of soil fungi abundance considering the main effects (crop and region) and their interaction (crop*region).

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