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Potato cultivation and livestock effects on microorganism functional groups in soils from the neotropical high Andean *Páramo*

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ABSTRACT: *Páramo* ecosystems are of great importance because they are considered hotspots within the Tropical Andes. They are also very important for their role as producers and regulators of water processes in the Neotropic. However, the human occupation of the Colombian *Páramo*s has generated conflict between environmental benefits and productive land uses, specifically the potato cultivation and livestock. To assess possible changes associated with potato cultivation (*Solanum tuberosum* L.) and livestock on the microbial communities of *Páramo* soils, the objective of this research was to evaluate the possible effects of potato cultivation and livestock farming on the soil microorganisms associated with different functional groups (nitrogen fixers, phosphate solubilizers and cellulolytic) in the *Páramo* of Nevados National Natural Park (Nevados NNP), Colombia. Samples were collected from soils under potato cultivation, livestock, and *Páramo* conservation areas over two climatic seasons (rainy and dry) in three farms at different elevations (3769, 3590, and 3432 m a.s.l.). The microorganisms were isolated using selective culture media for each functional group and identified using molecular markers; microbial diversity was analyzed using multivariate statistical tools. Changes were dependent on land use, elevation, and climate and were statistically significant in the rainy season on all three farms and one of the farms during the dry season. Similarly, the results indicated that climate has a greater impact on the evaluated microbial communities than land use does; the changes were significantly different between the soil under potato cultivation and in conserved *Páramo* sites at most of the evaluated locations and between soil subjected to livestock farming and *Páramo* in certain locations. However, the differences between potato cultivation and livestock farming were smaller. This study showed for the first time that the microbial structure (abundance and composition) of microorganism functional groups was different as a result of potato cultivation and livestock farming on *Páramo* soils, although these changes were dependent on farm elevation and climate.

Keywords: land use impact, microbial diversity, microbial soil ecology, protected areas, strategic ecosystems.

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INTRODUCTION

*Páramo*s are Neotropical ecosystems that cover large areas between the high-Andean treeline (3,000 to 3,800 m a.s.l. and the snowline (4,400 to 4,800 m a.s.l.) in the northern Andes (Luteyn, 1999; Hofstede, 2008) and are most extensive in Ecuador, Venezuela, Costa Rica, and Colombia (Hofstede, 2003). *Páramo*s are considered strategic ecosystems because of their high potential for hydrological regulations and carbon storage, and most of the water that comprises the complex hydrological network of different Andean regions is produced and originates in the *Páramo*s. Thus, these ecosystems provide significant environmental services for rural and urban communities (Cleef et al., 1983; Hofstede, 1995; Estupiñán et al., 2009). Furthermore, they are important for carbon storage and ecotourism development due to their beauty and cultural value (Lotero et al., 2007).

*Páramo*s and arctic ecosystems are very similar in their cold conditions, slow organic matter decomposition, and vegetation structure (Billings, 1973; Smith and Young, 1987). However, *Páramo*s exhibit daytime temperatures of up to 25 °C and nighttime temperatures as low as 0 °C, and they are subject to lower atmospheric pressure than lower-elevation ecosystems, which explains the extreme conditions in these ecosystems (Hofstede, 1995). *Páramos* are considered a biodiversity hotspot because of their location within the Andes mountain range (Myers et al., 2000; Madriñán et al., 2013), and their high biodiversity and endemism are at high risk.

Although *Páramo* ecosystems are environmentally significant, they are subject to various threats, including agricultural practices associated with potato cultivation and livestock farming that remove natural vegetation and have mechanical and chemical impacts on soils through cattle trampling and the application of agrochemicals (cultivation). However, the effects of these practices on the diversity of the microorganisms in *Páramo* soils are still unclear.

Edaphic microbial diversity is essential for maintaining proper ecosystem functioning (Bissett et al., 2007; Brussaard et al., 2007; Zhang et al., 2013) because soil microorganisms contribute to biogeochemical cycles as well as organic matter decomposition and energy flow bai. Protecting soil microbial diversity contributes to the sustainability of ecosystems and reduces their risk of degradation (Wasaki et al., 2005; Zhang et al., 2013). Microbial communities are sensitive to changes resulting from agricultural practices, such as cultivation systems, tillage, irrigation, fertilization (Doran and Zeiss, 2000; Chaparro et al., 2012; Shi et al., 2013; Zhou et al., 2014), pesticide application, production intensity, system homogeneity, and environmental factors (Nazih et al., 2001).

Thus, edaphic microorganism functional groups such as nitrogen (N) fixers, phosphate solubilizers, and cellulolytic organisms are important, and free-living, nitrogen-fixing prokaryotes have been estimated to contribute 60 kg ha^{-1} yr^{-1} N to the soil (60 %) (Burns, 1982). Therefore, biological nitrogen fixation provides the most significant external source of N for different ecosystems (Poly et al., 2001; Mantilla-Paredes et al., 2009). Phosphorous is the second-most limiting macronutrient for plant growth after nitrogen (Yadav and Dadarwal, 1997), which is why microbial solubilization of fixed phosphate in the soil is particularly important (Nesme et al., 2014). Similarly, cellulose is one of the critical components of plant structures, and its decomposition provides carbon, which improves soil fertility and ecological balance (Yang et al., 2014). Therefore, cellulolytic microorganisms play an important role in transforming cellulosic wastes into energy (Talia et al., 2012; Yang et al., 2014).

Furthermore, additional research into the functional diversity of microbial communities and the impacts of agricultural practices on soil microorganisms are necessary to promote greater sustainability in agricultural systems (Bainard et al., 2013). Different investigations have suggested that the cultivation-dependent strategy is a valid indicator for detecting impacts to soils, reporting that analyzing the main functional groups of soil microorganisms is appropriate for detecting changes caused by productive practices, xenobiotics, and land use (Wang et al., 2010; Zhang et al., 2010; Wang et al., 2012; López-Piñeiro et al., 2013).

In spite of the importance of *Páramo* ecosystems, research on the effects of potato cultivation and livestock on *Páramo* soils, especially on microorganisms, is limited. Thus, this study aimed to evaluate the possible changes related to potato cultivation and livestock farming on the diversity of culturable microorganism functional groups related to nitrogen fixation, phosphate solubilization and cellulose degradation in the *Páramo* soils of Nevados National Natural Park (Nevados NNP). It was hypothesized that the sites with potato cultivation and livestock farming would exhibit significant changes in microorganism functional groups of soil compared with *Páramo* sites that have been conserved without agricultural activities.

MATERIALS AND METHODS

Description of the research area

Nevados NNP is located on the eastern and western slopes of the Colombian Cordillera Central at elevations between 2,600 and 5,321 m a.s.l. (Lotero et al., 2007). It is a region of high interest both in Colombia and around the world. The park contains diverse ecosystems that include areas of perpetual snow cover, *superpáramo*s, *Páramo*s, and high-Andean and sub-Andean forests between 400 and 5,300 m a.s.l., with the *Páramo* and *superpáramo* ecosystems being the most representative of the area (Fandiño and Wyngaarden, 2002).

This research was conducted in El Bosque Village of Nevados NNP, Colombia, where samples of rhizospheric soil were collected under the following three land-use systems: potato cultivation, livestock farming, and conserved *Páramo*, which was subject to the least anthropogenic influence. These land-use systems were evaluated in three agroecosystem locations: Buenos Aires (N 04° 44’ 58.3” - W 75° 26’ 40.4”; 3769 m a.s.l.), El Edén (N 4° 44’ 32.3” - W 75° 26’ 37.9”; 3590 m a.s.l.) and La Secreta (N 4° 44’ 08.5” - W 75° 26’ 34.7"; 3432 m a.s.l.). The Buenos Aires agroecosystem has a pluvial cold climate, is located near Otun Lake between 3,600 and 4,000 m a.s.l., and has average daily temperatures of 6 to 9 °C and average annual precipitation between 2,000 and 4,000 mm. In this region, microclimates are created by the intense circulation of local winds resulting from proximity to the Santa Isabel volcano (IGAC, 2004). The El Edén and La Secreta, agroecosystems have a cold and humid climate, altitudes between 3,000 and 3,600 m a.s.l., average daily temperatures between 9 to 12 °C and average annual precipitation between 1,000 and 2,000 mm. According with USDA (Soil Survey Staff, 2014), the soils belong to the order Andisol, with Typic Haplocryands found at the Buenos Aires farm and Thaptic Hapludands found at the La Secreta and El Edén farms (Avellaneda-Torres et al., 2014a, 2018). In the evaluated agroecosystems, the potato crop is tilled in rotation with pastures (livestock) in biannual cycles and with fallow longer than seven years. The potato cultivation is performed using conventional techniques in combination with practices adopted from the Green Revolution such as the application of agrochemicals, including carbofuran, parathion, methamidophos, chlorpyrifos, profenofos, mancozeb, propineb, mefenoxam, phenothrin, and nitrogen:phosphorus:potassium fertilizers (Avellaneda-Torres et al., 2014b, 2018). The typical fodder growing in the livestock area includes orchard grass (Orchoro - *Dactylis glomerata sp.*), ryegrass (*Lolium sp.*), and *Lachemilla sp.* The *Páramo* areas with the least human interference were selected as control locations, and these areas exhibited the typical vegetation of the ecosystem, including *Cortaderia selloana*, *Pernettya prostrata*, *Buddleja* sp., *Lupinus albus* sp., *Dendropanax* sp., and *Chusquea* sp. Although the three types of land use are within the *Páramo* ecosystem, we use *Páramo* to refer to the area with the least possible human influence.

Sampling design

This research predicts that land use (potato cultivation and livestock farming) changes the diversity of microorganisms belonging to the functional groups related to different biogeochemical cycles (carbon, nitrogen, and phosphorus) in unperturbed soils. In this sense, the null hypothesis is of there is no difference in the soil microorganism diversity independently of the land use. This null hypothesis was evaluated on three farms located at different elevations. At each, the three types of land use (i.e., potato cultivation, livestock farming, and conserved *Páramo*) were sampled, each one with three random 10 × 10-m observation windows (quadrats) distanced apart by 30-40 m within each quadrat, ten subsamples were collected and used to form a compound sample. To evaluate the temporal generality of the null hypothesis, this sampling design was implemented twice at each farm: once during the dry season and once during the rainy season. In the end, there were a total of 54 samples of soil.

Isolation, culturing, and determination of the abundance of culturable microorganisms belonging to soil functional groups

For each of the soil samples, the colony-forming units (CFU g^{-1} of soil) were determined using the serial dilution method and plated for the following groups of microorganisms: total bacteria and fungi, biological nitrogen fixers, phosphate solubilizers, and cellulolytic organisms. Nutrient agar was used to count the total bacteria, and dextrose potato agar with 50 mg L^{-1} chloramphenicol was used to count the total fungi. The soils were before passed through a 2-mm sieve.

The nitrogen-fixing microorganisms were counted and isolated using selective medium lacking nitrogen (Rennie, 1981) with the following modifications: 5 g mannitol, 5 g malic acid, 0.5 mL sodium lactate (600 mL L^{-1}), 0.8 g K_2HPO_4, 0.2 g KH_2PO_4, 0.2 g $MgSO_4$ $7H_2O$, 0.06 g $CaCl_2$, 0.1 g NaCl, 0.001 g yeast extract, 0.0025 g Na_2MoO_4 $2H_2O$, 0.0024 g Na_2EDTA, 0.0018 g $FeSO_4$, 5 µg biotin, 10 µg p-aminobenzoic acid, 18 g agar, and 2.0 mL bromothymol blue (0.5 g kg^{-1} in 950 mL L^{-1} ethanol) in 1 L distilled water and adjusted to a pH of 7. The phosphate-solubilising microorganisms were counted and isolated using the medium proposed by Sundara and Sinha (1963) with the following modifications: 0.5 g $(NH_4)_2SO_4$, 0.2 g KCl, 0.3 g $MgSO_4$ $7H_2O$, 0.004 g $MnSO_4$, 0.002 g $FeSO_4$ $7H_2O$, 0.2 g NaCl, 10 g glucose, 0.5 g yeast extract, 0.1 g bromocresol purple, 5.0 g $Ca_3(PO_4)_2$, and 15 g agar in 1 L distilled water adjusted to pH 7.2. The cellulolytic microorganisms were counted and isolated using carboxymethyl cellulose medium (CMC) at 10 g kg^{-1} as the only carbon source, 0.5 g KH_2PO_4, 0.2 g $MgSO_4$ $7H_2O$, 0.1 g NH_4NO_3, 0.02 g $FeSO_4$ $7H_2O$, 0.05 g $Ca(NO_3)_2$ $4H_2O$, 15 g agar, and 10 g CMC in 1 L distilled water (Avellaneda-Torres et al., 2014a). A pH value of 7 was used for bacteria, and a pH of 5.0 was used for fungi, which required the addition of 34 mg L^{-1} chloramphenicol. All counts were performed in triplicate, and microorganisms were later isolated, purified, and preserved.

Taxonomic identification of the isolated microorganisms

The different morphotypes of the isolated bacteria and fungi were characterized by macroscopically and microscopically using molecular markers. For bacteria, the 16S rDNA sequence was detected: colonies were suspended in 200 µL TE 2X with 10 mL L^{-1} Tween, boiled for 10 min, and then centrifuged for 2 min at 14,000 rpm. Subsequently, 5 mL of the supernatant was used to conduct PCR analysis with the primers 27F and 1492R according to the procedures by Lane (1991) and Avellaneda-Torres et al. (2015). For fungi, DNA was extracted, and the internal transcribed spacer (ITS) region of the rDNA was amplified using 5 µL of the supernatant and water to a final volume of 50 µL, which also contained a buffer solution with PCR 1X, 2.0 mM $MgCl_2$, 0.25 mM deoxynucleotides (dNTPs; Promega, Madison, WI), 0.2 µM ITS1, and ITS4 initiators and 2.5 U μL^{-1} high-efficiency Taq DNA polymerase (Invitrogen) (Płaza et al., 2004). The DNA sequencing was performed in a 3730XL DNA Analyzer (Applied Biosystems, Macrogen, Korea) as specified by the manufacturer. The sequences were analyzed using the Basic Local Alignment Search Tool (BLAST) (Altschul et al., 1990; Benson et al., 2000) and Genius PRO 5.1.5 software.

Statistical and diversity analyses

The null hypotheses were evaluated with a four-factor linear model and analyses of variances. In the linear model, land use was defined as a fixed factor with three levels (i.e., potato cultivation, livestock farming, and conserved *Páramo*) which generates first- and second-order interactions. Similarly, the farms were considering a fixed factor with three levels (i.e., Buenos Aires, El Edén, and La Secreta), which generated two types of interactions. As well, sampling time was considered a fixed factor because of its two levels, generating two first- and second-order interactions. Observation quadrats correspond to the natural replicates for each combination of factors; they were included in the model as a random factor with three levels nested in the second-order interaction Farm (F) × Use (U) × Season (S). This source of variation and its degrees of freedom were used as a denominator to adequately estimate the corresponding *F*-ratio for each factor and their interactions. In this model, residuals represent the variability between the three laboratory measurements of the same soil sample. This unnatural variation was included in the model to precisely remove from unexplained natural variation (i.e., variability between replicates quadrants) the variation added by the measurement error.

The diversity of microorganisms in the soil samples was described through two components: species richness and microbial structure (i.e., composition and abundance of each species). For the first descriptor, the total number of species registered in each sample was used as species richness of the sample, and the variation of this variable among all the samples was partitioned with the 4-factor model described previously. Also, variation in the microbial structure was determined with the analyses of similarities. For this, the data was organized in a species × sample matrix, and the entries were the abundance values of each microorganism in each sample. The abundance values were fourth-root transformed, and the similarity in microorganism composition and abundance between each pair of samples was then analyzed using the Bray-Curtis similarity index (Clarke, 1993). The fourth-root transformation reduces the weight of the most dominant species and increases the relative importance of rare species when calculating the similarity index. Once the similarity matrix was generated, the total variation was decomposed using the previously proposed linear model and permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). In both analyses, the probabilistic significance of each source of variation was estimated using 9999 permutations of residuals under the reduced null model.

Furthermore, multivariate dispersion tests were performed (PERMDISP) (Anderson et al., 2006) to test the null hypothesis of equal variability in microbial structure among the three land-use types, and this analysis was carried out for each farm in each sampling regime. The similarities in microbial structure among the soil types for each farm and sampling regime were plotted using nonmetric multidimensional scaling (nMDS) (Clarke, 1993). Finally, canonical discriminant analysis of principal coordinates (CAP) (Anderson and Willis, 2003) was performed by similarity matrices, which were used to plot differences between regimes at each farm. Then, the individual species that might be responsible for differences among the regimes were investigated by calculating product-moment correlations of the original variables with canonical ordination axes. All of the statistical analyses were performed using the PRIMER v6 program with the PERMANOVA add-on (Clarke and Warwick, 2001; Anderson et al., 2008).

RESULTS

Microbial richness

Microbial isolation and determination of count were determined using selective. In total, 1,060 soil microorganisms were associated with nitrogen-fixing (bacteria), phosphate-solubilizing (bacteria and fungi), and cellulolytic functional groups (bacteria and fungi) (Avellaneda-Torres and Torres-Rojas, 2015). They belonged to 190 microbial morphotypes isolated in different selective media, including 98 cellulolytic (59 fungi and 39 bacteria), 57 phosphate solubilizers (22 fungi and 35 bacteria), and 35 nitrogen fixers (bacteria). An average of 20 microorganism phylotypes were detected per soil sample (± 3.9); however, differences in average richness were not detected of *Páramo* soils due to the cultivation of potatoes and livestock (Tables 1 and 2) in any of the farms or any of the sampling regimes (‘U’ factor and its first- and second-order interactions at $p>0.05$).

Microbial structure

Three key results were obtained from the PERMANOVA. The first and most important result was the significance of the second-order interaction U × F × S ($p<0.05$; Table 1), which implies that the effect of land use on the microorganism functional groups is not independent of the farm and fluctuates with time. Thus, to adequately estimate the differences in microbial structure among the different land uses, data of each farm was evaluated independently. In all cases, the differences were statistically significant ($p<0.05$).

Table 1. PERMANOVA of richness and microbial structure for the data series related to effects of potato cultivation and livestock on microorganism functional groups of Neotropical high Andean *Páramo* soils of Nevados National Natural Park, Colombia

Factor	d.f.	Richness			Microbial structure		
		SS	*F*	*p* (perm)	SS	Pseudo-*F*	*p* (perm)
Use (U)	2	133.05	3.01	0.073	10106	4.59	0.0001
Farm (F)	2	51.49	1.17	0.340	73940	33.59	0.0001
Season (S)	1	0.01	0.00	0.980	61622	55.99	0.0001
U × F	4	105.32	1.19	0.383	10120	2.29	0.0001
U × S	2	17.20	0.39	0.676	6560	2.97	0.0001
F × S	2	431.57	9.77	0.001	50443	22.92	0.0001
U × F × S	4	155.84	1.76	0.156	11519	2.62	0.0001
Quadrat (U × F × S)	36	795.33	3.02	0.001	39623	2.92	0.0001
Residuals	108	789.33			40705		
Total	161	2479.10			3.0464E5		

d.f.: degrees of freedom; SS: sum of squares.

Table 2. Mean microbial richness (S) by soil sample according to land use, farming, and sampling of Neotropical high Andean *Páramo* soils of Nevados National Natural Park, Colombia

S	Buenos Aires		Total Buenos Aires	El Edén		Total El Edén	La Secreta		Total La Secreta	General total
	Rainy	Dry		Rainy	Dry		Rainy	Dry		
Crop	19.9a	20.4a	20.2a	21.7a	19.7a	20.7a	20.2a	24.1a	22.2a	21.0a
Livestock	19.9a	24.2a	22.1a	25.9a	19.9a	22.9a	21.0a	20.3a	20.7a	21.9a
Páramo	17.9a	18.3a	18.1a	23.8a	18.0a	20.9a	17.4a	22.6a	20.0a	19.7a
General total	19.2a	21.0a	20.1a	23.8a	19.2a	21.5a	19.6a	22.3a	20.9a	20.8a

The second key result was the significant effect of land use (potato cultivation, livestock farming, and conserved *Páramo*), which appears to have a smaller effect than the season (i.e., rainy or dry), and the size of this effect can be observed in figure 1a. This observation was confirmed in the evaluation of the magnitudes of the variation of the components estimated in the PERMANOVA (Table 1). Thus, to measure the differences among the types of land uses, the analyses were conducted separately for each of the farms in the respective sampling regimes.

Third, significant variation was observed in the composition and abundance of culturable microorganisms (nitrogen fixers, phosphate solubilizers, and cellulolytic) among the different quadrats subject to the same combination of treatments (U × F × Season (S); $p<0.05$; Table 1). This indicates a high variation in the diversity of the microbial structure of the soils at the smallest spatial scale measured in this study.

Buenos Aires farm

The PERMANOVA for the Buenos Aires farm (Supplementary File) showed that the differences in the culturable microorganism functional groups among the different land uses were not independent of the sampling season (S × U; $p<0.05$), so pairwise comparisons were performed between seasons with differences in the land uses for each sampling time. The PERMANOVA also indicated that the variation associated with quadrats was significant [Q (S × U); $p<0.05$]. During the rainy season, significant differences were detected between the soils under potato cultivation and *Páramo* as well as between livestock and *Páramo* ($p<0.05$) (Table 3), but no significant differences were noted between the composition and abundance of the microorganisms in soils under potato cultivation

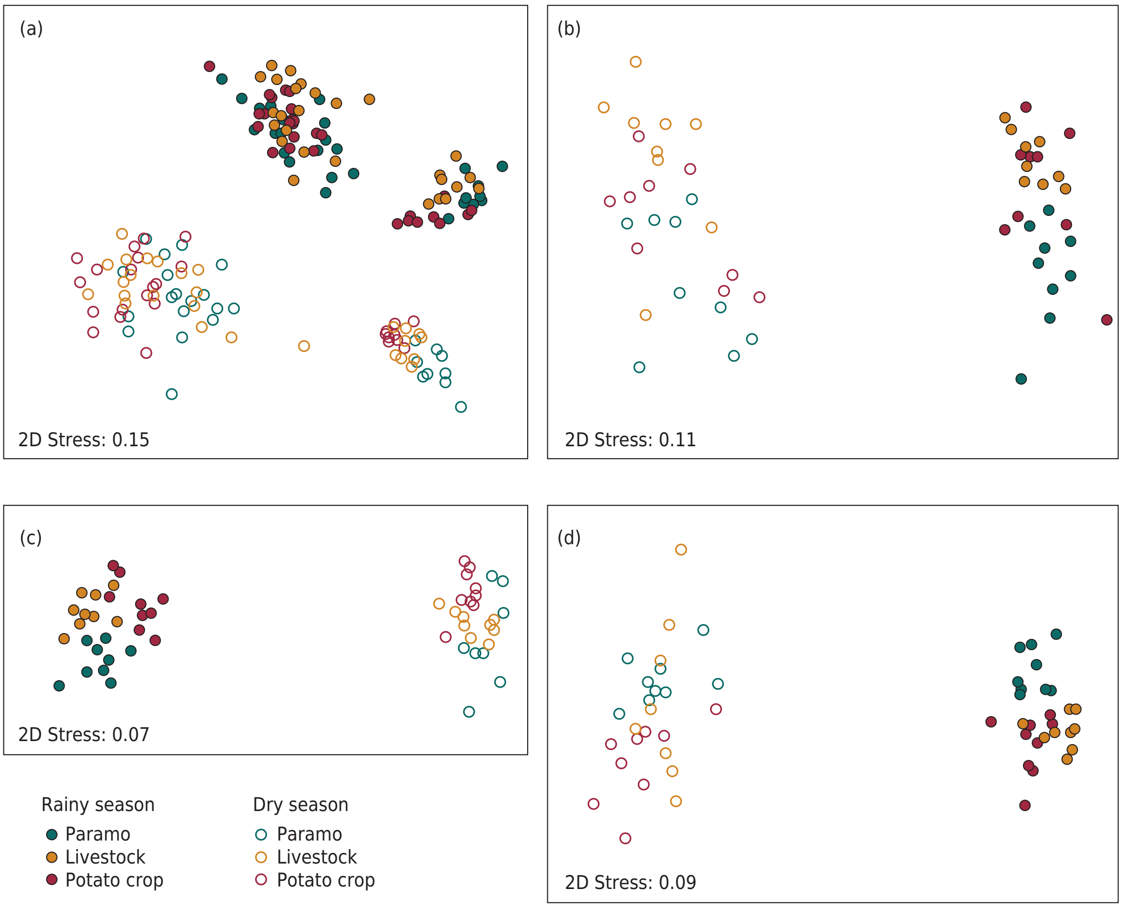

Figure 1. nMDS Bray-Curtis similarity matrix of culturable functional groups (nitrogen fixers, phosphate solubilizers, and cellulolytic) of Neotropical high Andean Páramo soils of Nevados National Natural Park, Colombia. Global (a), Buenos Aires farm (b), El Edén farm (c), and La Secreta farm (d).

and livestock farming (p>0.05). The differences between the abundance and composition of microorganisms during the dry season were not significantly different among potato cultivation, livestock farming, and *Páramo* (p>0.05; Table 3). These results indicate that differences in microbial communities caused by land use were greater during the rainy season than during the dry season.

The temporal difference in the microbial structure of the soil, as well as the differences between the *Páramo* soil and the impacted soils sampled during the rainy and dry seasons, were pointed out, although, the dispersion within treatments was much higher than that during the first sampling period (Figure 1b). The results of this analysis also show that the intragroup dispersion was lower in the rain than in the dry season (Table 4). During the rainy season, the dispersion was significantly lower in soils under cultivation compared with *Páramo* and livestock farming (PERMDISP, paired test, and *t* values at p<0.05) (Table 4), but *Páramo* and livestock exhibited similar dispersion (PERMDISP, p>0.05). These results indicate that potato cultivation has a greater impact on microorganism functional groups relative to livestock farming. During dry season sampling, the dispersion was similar among the three types of soil (PERMDISP, paired test, and *t* values at p>0.05), which was significantly higher than that reported for the rainy season, and the variation within each group (for S and U) increased the intragroup dispersion during the dry season. Thus, a multivariate dispersion analysis was conducted for each season for the Buenos Aires farm.

The CAP-A shows a canonical separation among the three groups of microorganism structures according to the type of land use: potato cultivation, livestock farming, and *Páramo* (Figures 2a and 2b). A greater distance was observed between the samples under potato cultivation and *Páramo* compared with those between livestock and *Páramo*, and this pattern suggests a transition process from *Páramo* to livestock to potato, which reflects the fallow after potato cultivation and before livestock farming. Such fallow coincides

Table 3. *t*-test pairwise comparisons between soils under different land uses on the Buenos Aires, El Edén and La Secreta farms of Neotropical high Andean *Páramo* soils of Nevados National Natural Park, Colombia

Season	Farm/Use	Buenos Aires	El Edén	La Secreta
		p	*p*	*p*
Rainy	*Páramo*, Crop	0.0039	0.0087	0.0091
	Páramo, Livestock	0.0398	0.0206	0.0195
	Crop, Livestock	0.1526	0.0022	0.4460
Dry	*Páramo*, Crop	0.0794	0.0490	0.0066
	Páramo, Livestock	0.1169	0.0671	0.0035
	Crop, Livestock	0.4302	0.0571	0.0215

The probability values were obtained with Monte Carlo-type simulations.

Table 4. Mean multivariate dispersions by season and land use on the Buenos Aires, El Edén, and La Secreta farms of Neotropical high Andean *Páramo* soils of Nevados National Natural Park, Colombia.

Season	Farm/Use	Buenos Aires		El Edén		La Secreta	
		Average	Standard deviation	Average	Standard deviation	Average	Standard deviation
Rainy	*Páramo*	22.766	0.99177	19.704	1.19380	20.667	1.1922
	Crop	17.055	0.83005	17.330	0.89335	21.588	1.5107
	Livestock	23.581	2.39100	17.708	1.39080	21.449	1.0074
Dry	*Páramo*	24.641	1.24730	22.064	2.49160	20.986	1.1454
	Crop	26.288	1.80220	14.415	1.32780	24.383	2.0795
	Livestock	27.086	0.96415	14.050	0.85364	30.463	2.3724

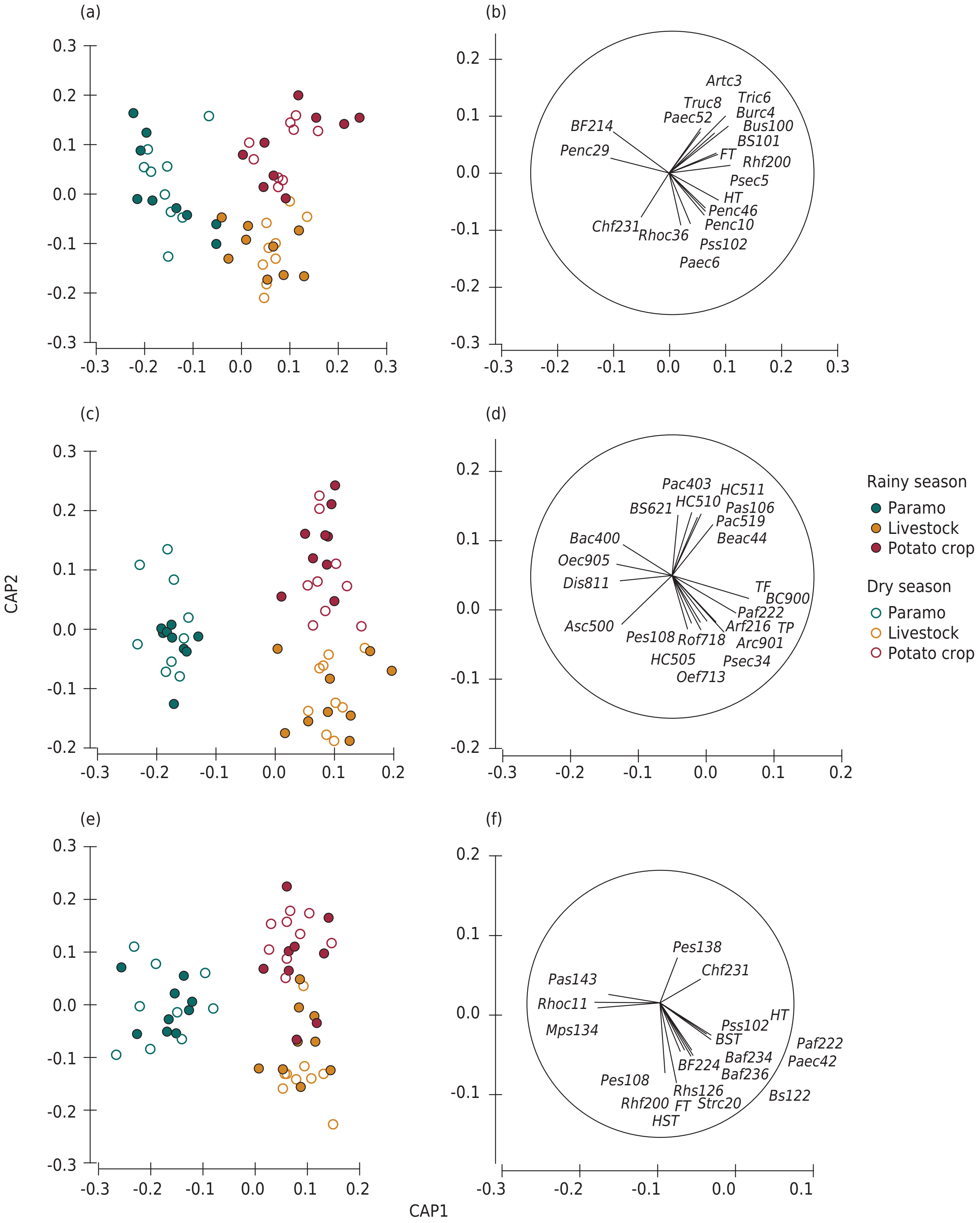

Figure 2. The CAP functional groups of microorganisms of Neotropical high Andean *Páramo* soils of Nevados National Natural Park, Colombia. Buenos Aires farm behavioural functional groups (a). Buenos Aires farm species with higher correlations on CAP in figure 2a (b). El Edén farm behavioural functional groups (c). El Edén farm species with higher correlations on CAP in figure 2c (d). La Secreta farm behavioural functional groups (e). El Edén farm species with higher correlations on CAP in figure 2e (f).

with reductions in the application of fertilizer and chemically synthesized pesticides and the mechanical manipulation of the soil that is typical of potato cultivation. The greater distances between samples could be interpreted as a possible re-establishment of the microbial community during this fallow period.

The CAP-B identified the species that had the strongest correlation with the canonical axes representing the samples associated with potato cultivation, livestock, and *Páramo*, and they can be interpreted as the species with the greatest influence on the characteristics of the functional groups present in each land-use scenario (Figures 2a and 2b). The abbreviations used in the different CAPs are listed in table 5. The species or microbial groups with the strongest correlations (>0.6) were as follows: soils under *Páramo* - *Penicillium glabrum*, *Chitinophaga arvensicola*, and nitrogen-fixing bacteria 214; soils under potato crops - *Paenibacillus sp.* C3, *Truncatella angustata*, *Arthrobacter* sp., *Trichoderma* sp. C1, *Burkholderia glathei*, solubilizing bacteria 101, *Rhodococcus* sp., *Pseudomonas* sp. C1, and total fixers; and soils under livestock pastures - *Pseudomonas fluorescens*, *Penicillium canescens*, *Penicillium* sp. C2, *Paenibacillus* sp., *Rhodococcus* sp., and total fungi.

El Edén Farm

The PERMANOVA for El Edén agroecosystem showed that the differences in culturable microorganism functional groups between the soils under different land uses were not

Table 5. Abbreviations of species or indicator groups projected in the CAP

Abbreviation	Description	FG	Abbreviation	Description	FG
Penc29	*Penicillium glabrum*	C	Pss102	*Pseudomonas fluorescens*	PS
Rhoc36	*Rhodococcus* sp	C	Pes138	*Penicillium* sp. S5	PS
Paec6	*Paenibacillus* sp.	C	Pas106	*Paenibacillus* sp.	PS
Penc10	*Penicillium* sp. C2	C	Pes108	*Penicillium* sp. S2	PS
Penc46	*Penicillium canescens*	C	BS621	BS621	PS
Psec5	*Pseudomonas* sp. C1	C	Bus100	*Burkholderia glathei*	PS
BC900	BC900	C	Pas143	*Paenibacillus* sp. S2	PS
Burc4	*Burkholderia glathei*	C	BS101	Solubilising bacteria 101	PS
Paec42	*Paenibacillus* sp. C3	C	Mps134	*Mortierella* sp. S2	PS
Strc20	*Streptomyces aureus*	C	HST	Total solubilising fungi	PS
Pac403	*Paenibacillus* sp. C4	C	Rhs126	*Rhodococcus* sp.	PS
Tric6	*Trichoderma* sp. C1	C	Dis811	*Diplogelasinospora* sp. S2	PS
Truc8	*Truncatella angustata*	C	Bs122	*Bacillus* sp. S3	PS
Artc3	*Arthrobacter* sp.	C	BST	Total solubilising bacteria	PS
Rhoc11	*Rhodococcus* sp. C1	C	Chf231	*Chitinophaga arvensicola*	NF
Bac400	*Bacillus* sp. C2	C	Paf222	*Paenibacillus* sp.	NF
Oec905	*Oerskovia* sp.	C	Rhf200	*Rhodococcus* sp.	NF
Asc500	*Aspergillus fumigatus*	C	BF224	BF224	NF
HC505	HC505	C	Baf236	*Bacillus* sp. F4	NF
Psec34	*Pseudomonas putida*	C	BF214	BF214	NF
Arc901	*Arthrobacter nicotinovorans*	C	Baf234	*Bacillus* sp. F2	NF
HC511	HC511	C	Oef713	*Oerskovia* sp.	NF
Beac44	*Beauveria* sp.	C	Rof718	*Roseomonas gilardii*	NF
Pac519	*Paecilomyces* sp. C1	C	Arf216	*Arthrobacter* sp.	NF
HC510	HC510	C	FT	Total fixers	NF
HT	Total fungi	NA	PT	Total prokaryotes	NA

FG: functional group; C: cellulolytic; PS: phosphate solubilizer; NF: nitrogen fixer; NA: not applicable.

independent of the sampling season (E × U; $p<0.05$), so pairwise comparisons were performed between the land uses for each sampling times. The PERMANOVA also indicated that the variation associated with the quadrats was significant [Q (S × U); $p<0.05$]. In the first sampling regime (rainy), significant differences were detected among the soils under potato cultivation, livestock farming, and *Páramo* ($p<0.05$) with greater impacts on the composition and abundance of microorganism functional groups associated with potato cultivation and livestock farming. However, in the second sampling regime (dry), the observed differences in the abundance and composition of microorganisms among potato cultivation, livestock farming, and *Páramo* were not significant ($p>0.05$), which correspond to the results for the Buenos Aires farm. This result shows that in Buenos Aires and El Edén, the differences in the microbial communities caused by land use are greater in the rainy season than in t he dry season.

Consistent with the results of the Buenos Aires farm, the nMDS results for the El Edén farm reflect the differences in a microbial community structure caused by season, which is perceived to be greater than those caused by land use (Figure 1c). However, land use caused greater differentiation among the samples during the first sampling regime (rainy season) than that observed during the dry season, which is consistent with the previously discussed PERMANOVA results. For El Edén, the observed dispersion differences were not as high as those observed at the Buenos Aires farm, which may be because of the greater soil slope homogeneity at the El Edén farm relative to the Buenos Aires farm. The dispersion analysis for the rainy season (Table 4) shows that the soils under potato cultivation, livestock farming, and *Páramo* have the same dispersion (PERMDISP, paired test and t values at $p>0.05$). During the second sampling regime (dry season), the dispersion was significantly greater in the *Páramo* soils than those under potato cultivation and livestock farming (PERMDISP, paired test and t values at $p<0.05$).

The CAP-A for the Edén farm (Figures 2c and 2d) shows a significant canonical separation among the three microorganism diversity local groups (potato cultivation, livestock farming, and *Páramo*), which correspond to the results for the Buenos Aires farm and demonstrates differences in the microbial community among these three land uses. A greater distance was observed between the samples under potato cultivation and *Páramo* than between the samples under livestock and *Páramo*, alluding to the transition that occurs in the El Bosque Village during fallow from *Páramo* to livestock to potato; the less intense agriculture related to livestock production may promote the recovery of the microbial community structure.

In CAP-B (Figures 2c and 2d), the species or microbial local groups that had the strongest correlation (>0.6) with the canonical axes were as follows: soils under *Páramo* - *Bacillus* sp. C2, *Oerskovia* sp., *Diplogelasinospora* sp. S2, and *Aspergillus fumigatus*; soils under potato crops - cellulolytic bacteria 900, *Paenibacillus* sp., total fungi, total prokaryotes, *Arthrobacter* sp., *Arthrobacter nicotinovorans*, *Roseomonas gilardii*, *Pseudomonas putida*, cellulolytic fungi 505, *Oerskovia* sp., and *Penicillium* sp. S2; and soils under livestock pasture - solubilizing bacteria, *Paenibacillus* sp. C4, cellulolytic fungi 510, cellulolytic fungi 511, *Paenibacillus* sp., *Paecilomyces* sp. C1, and *Beauveria* sp.

La Secreta farm

Consistent with the Buenos Aires and El Edén farms, the PERMANOVA for the La Secreta agroecosystem showed indicated that the differences in the microbial community among land uses (potato cultivation, livestock, and conservation *Páramo*) were not independent of the sampling season (E × U; $p<0.05$).

As in the analyses of the other farms, pairwise comparisons were performed between the land uses for each sampling time. The PERMANOVA results indicated that the variation of the quadrats was significant [Q (S × U), $p<0.05$], and when analyzing the paired comparisons between the land use in the rainy season, the differences between crops and *Páramo* and between livestock and *Páramo* were statistically significant (p<0.05) (Table 3). However, no significant differences were observed between the composition and abundance of the microorganisms in the soils under potato cultivation and the soils under livestock pasture (p>0.05), which is consistent with the results for the Buenos Aires farm.

During the dry season, the differences in microorganism abundance and composition among potato cultivation, livestock, and *Páramo* were statistically significant (p<0.05) in the three paired comparisons. This result indicates that significant effects of land use on the microbial communities were observed during both the rainy and dry seasons on La Secreta farm, which is inconsistent with the results for the other farms, where statistically significant differences in the paired comparisons were only observed for the rainy season. This result could indicate a greater capacity to mitigate changes caused by land use in farms at higher elevations during the dry season, as La Secreta was influenced by climate and is located at a lower altitude; the closer proximity of the two high-altitude farms to the snowy peaks surrounding the study area, which affects the moisture regime of these farms, could also improve their resilience against the impacts generated by agriculture. For example, the Buenos Aires agroecosystem, at 3,600 to 4,000 m a.s.l., has a pluvial cold climate with daily average temperatures of 6 to 9 °C and average annual precipitation between 2,000 and 4,000 mm (IGAC, 2004; Avellaneda-Torres et al., 2018). In contrast, the La Secreta agroecosystem, at 3,000 to 3,600 m a.s.l., has a cold and humid climate, average daily temperatures between 9 and 12 °C and average annual precipitation between 1,000 and 2,000 mm (Avellaneda-Torres et al., 2018).

At the nMDS for La Secreta farm, there were larger differences in the microbial community between sampling seasons because of the impact of land use (Figure 1d), which correspond to the results from the Buenos Aires and El Edén farms. The PERMDISP analysis included paired comparisons for the rainy and dry seasons and indicated that the dispersion in the samples for potato cultivation, livestock farming, and *Páramo* did not exhibit statistically significant differences (PERMDISP, paired test and *t* values at p>0.05).

The CAP-A for the La Secreta farm showed a canonical separation among the three land uses for microorganism diversity (potato cultivation, livestock, and *Páramo*) (Figures 2e and 2f), which is consistent with the results from the Buenos Aires and El Edén farms. However, a smaller effect was observed between the livestock and potato samples than between these two groups and the *Páramo* samples.

In CAP-B, the species or microbial local groups that had the strongest correlation with the canonical groups were: soils under *Páramo* - *Paenibacillus* sp. S2, *Rhodococcus* sp. C1 and *Mortierella* sp. S2; soils under potato - total fungi, *P. fluorescens*, *Paenibacillus* sp., total solubilizing bacteria, total solubilizing fungi, total fixers, *Bacillus* sp. F2, *Paenibacillus* sp. C3, *Bacillus* sp. S3, *Rhodococcus* sp., *Bacillus* sp. F4, and *Penicillium* sp. S2; and soils under livestock - *Penicillium* sp. S5 and *C. arvensicola* (Figures 2e and 2f).

A global analysis of the species and microorganism groups that acted as indicators of change on the three farms, Ascomycota fungi were dominant over Zygomycota (Figure 3). At the level of bacteria, four phyla represented indicator phylotypes: Actinobacteria, Firmicutes, Proteobacteria, and unidentified. However, cellulolytic was dominant over the other groups, and bacteria were dominant over fungi as indicators. Global counts of functional groups acted as indicators in the three farms.

DISCUSSION

The joint analysis of abundance and diversity data for microorganism functional groups in El Bosque Village of Nevados NNP showed statistically significant differences in all treatments (land use, farm, and sampling season). However, these differences were

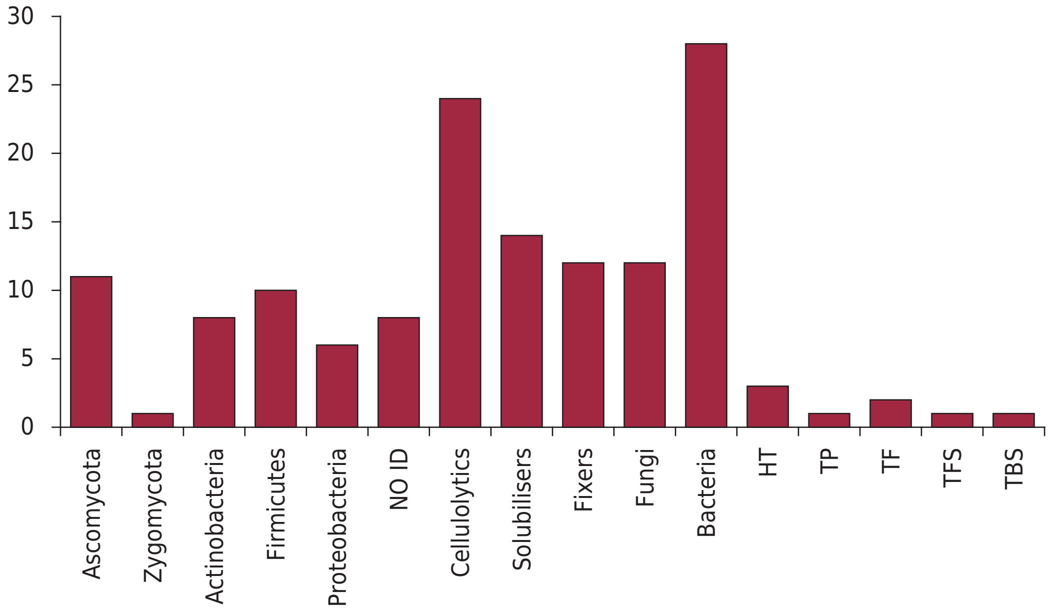

Figure 3. Frequency distribution of phylotype indicators for the three farms of Neotropical high Andean Páramo soils of Nevados National Natural Park, Colombia, with the frequency indicated on the Y axis. HT: total Fungi; TP: total prokaryotes; TNF: total nitrogen fixers; TSF: total solubilizer fungi; TSB: total solubilizer bacteria.

dependent on the elevation and climate of the specific farm, indicating that although practices associated with potato cultivation and livestock farming do modify the microbial community of nitrogen fixers, phosphate solubilizers, and cellulolytic, this impact is also strongly influenced by other factors. Thus, the initial hypothesis of this study was validated and was dependent on factors such as the elevation of the farms and the sampling period.

Several studies have investigated the possible impact of crops and their associated cultivation on microbial communities. For example, continuous cultivation of the same product in the same soil has been proposed to negatively affect soil productivity and quality, known as “soil diseases” (Kreye et al., 2009; Nayyar et al., 2009; Gentry et al., 2013; Zhou et al., 2014). However, in the *Páramo*, particularly in Nevados NNP, the impact of potato cultivation in rotation with livestock on the soil microbial communities has been unknown. This lack of information is problematic because the potato crop in Nevados NNP is developed in a framework of peasant family agricultural processes with cultivation occurring for a maximum of two consecutive years followed by resting periods with livestock farming for 7 to 10 or more years. Livestock farming in Nevados NNP is characterized by a low cattle head to farm area ratio (0.24-0.36 head of cattle ha^{-1}). Therefore, agriculture inside Nevados NNP can be very similar to that which occurs in other *Páramos* that are found within natural national parks such as *Chingaza*, *El Cocuy*, *Nevado del Huila*, *Paramillo*, *Pisba*, *Sierra Nevada de Santa Marta*, *Sumapaz*, *Tamá*, *Tatamá* (Morales et al., 2007). But in contrast, it varies from at lower altitudes in other regions of Colombia, where potato cultivation and livestock farming are primarily commercial enterprises characterized by more intense production (Avellaneda-Torres et al., 2014b).

Several investigators have shown that vegetation and season influence the diversity of soil bacteria and fungi (Kowalchuk et al., 2002; He et al., 2008; Zhang et al., 2013). For example, experiments have shown that the abundances of bacteria and fungi in tilled soils of mountainous regions of subtropical China are significantly reduced (17.2 and 28.4 %, respectively) by one hour of simulated rain (Huang et al., 2013). Even, during corn production in rotation with soy over 18 years in Canada, seasonal fluctuations influenced the microbiological properties of the soil to a higher degree than tilling practices and phosphorous fertilization, indicating that sampling season had a most significant influence on the microbial and physico-chemical properties evaluated (Shi et al., 2013).

Microorganisms in the soil respond to climate, the water content of the soil, porosity and organic matter concentration, and all these factors are interrelated partly dependent on soil management (Spedding et al., 2004; Hamel et al., 2006; Shi et al., 2013). Therefore, the response of microorganisms to potato cultivation and livestock is a result of the complex interactions among climate, altitude, soil taxonomic properties, and agriculture. This finding agrees with the results of other studies that reported changes in the structure of microbial communities due to the conditions at the time of sampling, which produced greater variability than cultivation practices such as fertilization, crop rotation, drainage, tillage or waste retention (Spedding et al., 2004; Shi et al., 2013).

In this study, the PERMANOVA results for the three evaluated farms indicated that statistically significant differences in the abundance and composition of the soil microbial communities occurred between *Páramo* and potato cultivation and between *Páramo* and livestock farming during the rainy season, but such differences were not observed between potato cultivation and livestock farming. However, in the Buenos Aires and El Edén farms (agroecosystems located at higher altitudes), these differences were not statistically significant during the dry season, which indicates that the impacts of agricultural practices, such as topsoil removal, agrochemical applications, and cattle, are stronger during the rainy season than during the dry season. Besides, this result demonstrates that agroecosystems at higher elevations have a greater capacity to mitigate these impacts during the dry season, which may be related to the greater moisture and reduced temperature at higher elevations.

The question then arises of whether additional to anthropogenic factors such as the cultivation of potatoes and livestock, apparently “natural” aspects such as the elevation of farms and climate are significantly affecting the microbial diversity of *Páramo* soils. The current notion is that phenomena such as climate change are directly affecting the thawing of snow peaks and that the “natural” conditions of a certain elevation or climate such as the *Páramos* are being strongly influenced by human activities that generate climate change. In this sense, the changes in the microbial diversity of the soils of *Páramos*, by to the results of this study, are due to human actions, i.e., activities related to agriculture for the cultivation of potatoes and livestock. However, these changes must also be due to climate and elevation, which are a combination of both natural aspects and human modifications that affect the neotropics and therefore the soils of these high-Andean *Páramos*.

The nMDS of the data set and each farm (Figure 1) analysis showed that the impact of climate during sampling was greater than the impact of potato cultivation and livestock farming. This result suggests that differences in precipitation, temperature, and humidity associated with climate change would have a greater influence on the microbial communities relative to that of the agricultural activities of the peasants of El Bosque village. Thus, additional studies are needed to investigate the impact of climate on functional groups and identify additional factors for analysis that may support or contradict this hypothesis. Moreover, climatic factors such as humidity, temperature fluctuations, freeze-thaw cycles, and ultraviolet radiation have been reported to have a profound impact on soil microbial communities (Lipson, 2007; Albert et al., 2008; Bell et al., 2008; Zumsteg et al., 2013).

The CAP of the three evaluated farms (Figure 2) showed a clear separation among the potato cultivation, livestock farming, and conserved *Páramo* samples. Because no studies comparing the effects of farming activities on microbial richness and structure in *Páramo* ecosystems, these results must be compared with those associated with other types of crops. Several authors have reported that microbial communities are modified as a result of agricultural activities, including significant changes due to the continuous mono cultivation of cucumber (*Cucumis sativus L.*) (Zhou et al., 2014). Similar results have been found for pea (Nayyar et al., 2009; Lupwayi et al., 2012), soy (Li et al., 2010), and cotton (Acosta-Martínez et al., 2010), and such impacts can be first induced by changes in vegetation cover, which transitions from the characteristic *Páramo* vegetation to vegetation related to potato cultivation and livestock pasture. Therefore, plant type is one of the main factors determining soil microbial communities because leaf litter and rhizodeposition (low-molecular-weight metabolites, amino acids, secreted enzymes, mucilage, and cell lysates) are the main providers of specific carbon and energy sources (Garbeva et al., 2004; Dennis et al., 2010), and plant species differ in their biochemical compositions (Zak et al., 2003; Nilsson et al., 2008), which leads to differences in the microbial communities that grow in the rhizospheric soils.

The interaction between plants and soil microorganisms is complex because plants can influence the activity and composition of soil microorganism communities through the liberation of organic compounds (Bais et al., 2006; Bever et al., 2012), whereas soil microorganisms provide plants with nitrogen, phosphorous, and other minerals through the decomposition of organic material in the soil (Singh et al., 2004). Therefore, changes in edaphic microorganisms can be a cause as well with modifications to crops (Zhou et al., 2014). This phenomenon may be observed in potato cultivation in El Bosque; after two years of continuous cultivation, production significantly decreases, which is why the local peasants allow the soil to lie fallow for seven to ten years. According to experimental conditions reported by researchers, continuous cucumber mono cultivation should not be performed for more than five harvests (Zhou et al., 2014). Thus, the restoration of the vegetation during fallow increases genetic diversity and changes the structure of the soil bacterial community (Zhang et al., 2013).

It has been suggested that high plant diversity can promote greater microbial species richness because of the higher number of niches in the rhizosphere and the greater number of specific interactions between plants and microorganisms; thus, lower plant diversity should be indicative of reduced microbial diversity (Brodie et al., 2003). However, some studies have not observed low of diversity in environments with lower vegetation diversity such as comparisons of soils under pastures, crops and Amazonian forests, where the conversion of forests to pasture and agriculture did not reduce bacterial or fungal diversity (Jesus et al., 2009; Fracetto et al., 2013). This result agrees with that reported here because the global analysis of richness showed slight increases in the richness of soil species under crops and livestock relative to *Páramo* as well as richness values that were similar among the three farms, although these differences were not statistically significant. This event indicates that the changes in soil coverage at El Bosque Village did not generate significant differences in the richness of microbial communities, which may have been due to the low-intensity intervention characteristic of the family-oriented agriculture in the region.

Also, the application of agrochemicals (fertilizers and pesticides) can change soil properties and microbial community structure. Estimates indicate that only 0.1 % of the applied pesticides reach the target pests, with the remaining 99.9 % accumulating in the soils and directly or indirectly affecting the microbial density and enzymatic activities (Singh and Singh, 2005; Das and Debnath, 2006; Pal et al., 2006; Angelini et al., 2013). The addition of pesticides to agricultural soils has been reported to negatively affect the bacterial population of nitrogen fixers (Angelini et al., 2013). Similarly, soil microbial communities are known to be highly influenced by management practices, and they may be reduced by the application of inorganic fertilizers and pesticides during cultivation (Moeskops et al., 2010). Furthermore, the abundance, composition and activity of microorganisms are known to be influenced by different factors such as soil fertilization, rotation, waste management, and soil acidity (Perucci et al., 1997; Peixoto et al., 2010; Shen et al., 2010; Jorquera et al., 2014).

Although pesticides could reduce microbial diversity, the slight increases in richness and the greater correlations among species with crops and livestock observed in this research would show that diversity may be greater in soils under potato cultivation and livestock farming because of the conditions in El Bosque Village, but these increases were not statistically significant and may be due to the agrochemicals acting as an initial source of nutrients for the microorganisms. Even, because the crop is only tilled for two years, pesticides do not significantly reduce the typical *Páramo* species, and the microbial structure recovers during fallow. Similarly, studies have reported increased bacterial counts in soils treated with fungicides (Martınez-Toledo et al., 1998; Monkiedje and Spiteller, 2002; Cycoń et al., 2006, 2010). Thus, the response of soil microorganisms is complex because they exhibit different mechanisms of action in response to agrochemical applications. For example, certain microorganisms grow in the presence of fungicides and absorb energy sources and nutrients from the hyphae of dead fungi; this phenomenon might have developed because bacteria experience less competition or fewer antagonistic inhibitions due to the lack of metabolites synthesized by fungi when they are eliminated from the soil, which increases the number of bacteria (Chen et al., 2003; Cycoń et al., 2010). Certain culturable bacteria have a relatively high capacity to rapidly respond to contamination events (Ellis et al., 2002), and they may use certain components of the agrochemicals to survive and even multiply in the soil after pesticide applications (Cycoń et al., 2010).

The results of this research are consistent with others reporting that environmental conditions may induce different behaviors in microorganisms by generating different microbial responses according to ecotype. Several studies have indicated that culturable bacteria respond to fungicides in the soil by changing the proportion of their populations, which produce a larger number of tolerant bacteria and leads to the dominance of special ecotypes (De Leij et al., 1994; Cycoń et al., 2010) with the capacity to degrade applied pesticides and adapt to stressful conditions. These processes depend on different characteristics, such as the properties and functions of the soil microorganisms and the intensity of the environmental stress (De Leij et al., 1994; Cycoń et al., 2010), which is why understanding the functional mechanisms of these processes and analyzing their impacts in Nevados NNP are difficult.

The analysis of the CAP and the associated vectors demonstrates that there are fewer microorganisms that correlate with *Páramo* soil in the three farms than those that correlate with soil under potato cultivation and livestock farming. Therefore, the bacterial communities in no-tillage soils (which, then, could be an approximation of soils under *Páramo*) exhibit greater modifications in their genetic structure because of hydrological stresses and slower recovery rates than those in tillage systems, which suggests that land-use practices can increase microbial functional resistance through the creation of bacterial communities with special metabolic capacities (Kaisermann et al., 2013). However, this behavior is only possible because of the fallow without the application of agro-resources, as the microorganisms that are in the process of adapting to the new biochemical conditions of the soil are not eliminated. Potato cultivation and livestock farming would have smaller impacts in the soils of El Bosque Village than potato crop systems under conventional management in other areas of the country, where potato is a monocrop tilled in the same soil without fallow.

However, of the total number of microorganisms identified as indicators of changes related to potato cultivation and livestock farming, 24 were cellulolytic, 14 were phosphate solubilizers, and 12 were nitrogen fixers, but a specific trend was not observed to the presence or absence of such functional groups in any of the evaluated land uses. An analysis of the distribution of microorganisms by agroecosystem showed that the number of cellulolytic was reduced in the La Secreta agroecosystem, which was at the lowest altitude. Cellulolytic microorganisms are sensitive to changes produced immediately after an intense disturbance, such as soil tillage (Abril, 2003), and these changes in nitrogen-fixing and phosphate-solubilizing organisms may be a response to the application of nitrogen: phosphorus, potassium fertilizers, which have a high nitrogen, and phosphorous composition and affect the dynamics of microorganisms associated with these geochemical cycles. However, changes in cellulolytic microorganisms may also be attributed to changes in the carbon cycle, in which elements such as the type of organic material and vegetation cover may have increased importance. This result agrees with that reported by Avellaneda-Torres et al. (2018), who suggested that the most significant physico-chemical modifications occurred in the organic material because of changes in vegetation coverage and mechanical impacts on the soil related to potato cultivation and livestock farming.

Even, redundant microorganisms were observed, such as the total fungi on the three farms, and they functioned as indicators of change among all three farms and were correlated with potato cultivation and livestock. The nitrogen-fixing microorganisms were also redundant on two of the farms, indicating a stronger correlation with potato cultivation. Thus, the growth of total fungi and nitrogen fixers may be promoted by practices associated with potato cultivation and livestock farming. Madriñán et al. (2013) found more fungal morphotypes in fallow and forest soils than in soils under two potato varieties, and the authors argued that certain groups may be inhibited due to agrochemical use. Also, they cited other authors such as Wardle et al. (1994), who also recorded a reduction in active fungi populations in tilled soils related to the application of pesticides and fertilizers and observed a high number of fungi in latent stages, including resistance propagules (Wardle et al., 1994). However, the redundancy of total fungi and nitrogen fixers as indicators of change caused by land-use suggests their potential for use in the subsequent discrimination and identification of each of the microorganisms involved.

The solubilizing bacteria *P. fluorescens* was also identified as an indicator in both farms, and it was correlated with soils under potato cultivation and livestock farming. Certain studies have suggested that *P. fluorescens* is an inducer of phosphate solubilization efficiency in conjunction with *P. striata* and *T. harzianum* in neutral soils, but the soils in this research were acidic or extremely acidic compared with those reported for *P. striata* and *T. harzianum* and the alkaline soils for *P. fluorescens* and *T. harzianum* (Shen et al., 2013). The nitrogen-fixing bacteria *C. arvensicola* was redundant on two farms and was correlated with livestock farming on one farm and *Páramo* on the other, indicating that it is a possible transitional species. The nitrogen-fixing bacteria *Rhodococcus* sp. was present on two farms and suggest a high correlation with potato cultivation; the practices associated with this crop increase the abundance of this bacteria. Most of the indicator microorganisms were cellulolytic, although none indicated redundancy similar to that of the previously cited nitrogen fixers and phosphate solubilizers.

Other results have indicated that incorporating organic amendments and practicing minimum tillage increase the relative diversity of fungal populations and bacterial species richness (Rames et al., 2013), which is why the recommendation for crops produced inside the Nevados NNP is to transition to using *Páramo* substrates as a source of nutrients to imitate the natural cycles of conserved *Páramo* soils. Organic conditioners stimulate a variety of organisms as a result of carbon and other nutrient inputs (Chaudhry et al., 2012; Rames et al., 2013), and there is evidence that the application of organic resources over a long period produces positive effects on the fungal and bacterial communities in Kenyan soils (Kamaa et al., 2012). Increased microbial diversity and organic crop performance have also been observed under conventional treatments (Girvan et al., 2004; Melero et al., 2006; Sharma et al., 2010), so the richness and diversity of microbial communities in soils treated with manure may be improved, which would positively correlate with soil productivity (Parham et al., 2003).

CONCLUSIONS

The hypothesis raised for this investigation was confirmed given that changes were observed in the microbial structure (abundance and composition) of microorganism functional groups as with potato cultivation and livestock farming on *Páramo* soils, although these changes were dependent on the farm elevation and climate. Furthermore, these changes were statistically significant during the rainy season in three of the studied agroecosystems and during the dry season on one of the farms (La Secreta). These results reveal that climate has a greater impact on microbial communities than land use. The changes in microbial communities were usually significantly different between potato cultivation and *Páramo* and sometimes significantly different between livestock farming and *Páramo*. However, the differences between potato cultivation and livestock were smaller, reflecting the impact of the agriculture associated with potato cultivation on microorganisms and indicating that livestock farming represents a transitional state between cultivation and *Páramo*. Statistically significant differences in microbial richness were not observed with the evaluated factors, although slight increases in microbial richness were observed due to agriculture. The best indicators of changes were total fungi, nitrogen-fixing microorganisms, the solubilizing bacteria *P. fluorescens* and the nitrogen-fixing bacteria *C. arvensicola* and *Rhodococcus* sp., that showed increased numbers in soils under potato cultivation and livestock farming, with *C. arvensicola* also increasing in the *Páramo* as well.

APPENDIX A. SUPPLEMENTARY DATA

Supplementary data to this article can be found online at https://doi.org/10.36783/18069657rbcs20190122

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