



Soil Biological Properties and Arbuscular Mycorrhizal Fungal Communities of Representative Crops Established in the Andean Region from Ecuadorian Highlands

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Abstract

Biological activities determine quality, sustainability, health, and fertility of soils. The purpose of this study was to evaluate chemical and biological characteristics of soils from Ecuadorian highlands subjected to different management practices, as well as the density and diversity of arbuscular mycorrhizal fungi (AMF). Soils from naturalized grasslands and other previously cropped plots with *Zea mays* and *Solanum tuberosum* were analyzed in laboratory for soil biochemical properties, enzyme activity, and AMF colonization to determine the effect of the soil management over its quality. The characterization of AMF propagules associated to spontaneously colonizing plants in the above soils was also performed. Soil previously cropped with *S. tuberosum* showed the highest glomalin content; at the same time, naturalized grassland and *Z. mays* cropped soils showed higher hyphal length. The acid phosphatase activity was higher in naturalized grasslands and *Z. mays* cropped soils compared with that in the *S. tuberosum* cropped soils. Moreover, the highest AMF colonization rates and spore number were found in different spontaneous plant species growing in the naturalized grasslands. This study represents the first characterization of AMF propagules of different cropped and naturalized grassland soils, and also is one of the first reports about changes on biochemical and microbial activities occurring in Andean soils from the highlands of Ecuador, undergoing determinant soil management activities.

Keywords Arbuscular mycorrhizal fungi · Enzyme activities · Grassland · Maize · Potato

1 Introduction

Soil tillage deprives soil microorganisms from their primary carbon (C) energy source and exposes soil to negative climatic

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impacts (Lal and Stewart 2010; Farooq and Siddique 2015; Kumar et al. 2015). Intensive soil management systems as used in the highlands of Ecuador, including continuous tillage aimed to increase crop yields and food production, have contributed to the soil erosion in the region (Espinosa 2014). As an alternative, conservation tillage is considered a good soil management option for crop production. Some conservation tillage alternatives have been widely used in Europe, Asia, North America, and in parts of South America (Derpsch et al. 2010). Sometimes the crop residues are left on the topsoil, increasing the organic C on the surface and stimulating the microbial activities, helpful for nutrient cycles which enhance soil fertility and crop yields (Lal 2011; Samal et al. 2017). Particularly, the microbial activities are key factors scarcely studied in Andean soils, where soil conservation efforts need to be reinforced in order to attain sustainability.

One of the most important microbes found in soils are the arbuscular mycorrhizal fungi (AMF), which form symbiotic associations with the majority of plant roots in natural and

agricultural ecosystems (Cornejo et al. 2017; Anwar et al. 2018). AMF are well known as helpful microorganisms which increase plant growth, water stress tolerance, and plant health (Santander et al. 2017, 2019). Soil management practices affect not only soil properties and microbial responses but also AMF activities and their plant colonization ability (Cornejo et al. 2009; Barea and Pozo 2013; Manoharan et al. 2017). Therefore, their density, activity, and diversity in soils are main factors in sustainable agriculture. Moreover, soil enzyme activities, particularly those associated to nutrient cycles, are important soil quality indicators that can measure the effects of tillage and are considered warning sensors of soil quality degradation (Gianfreda 2015; Gajda et al. 2018; Lin et al. 2018). Since the microbial and enzyme activity in soils vary according to soil management such as tillage and cropping, this presents an interesting question about their effect over chemical and biological characteristics of highland soils from Ecuador. Additionally, the knowledge about AMF-plant relations in these particular types of soils can be of great interest for crop production in the region.

There is scarce information regarding biological characterization of highland soils from Ecuador. Therefore, in order to contribute with these lacking information, we aimed to evaluate AMF and biochemical characteristics of some representative agroecosystems in the highlands of Ecuador subjected to different soil managements during the last decades, and to describe the AMF presence and diversity in these soils. Here, we hypothesized that the physicochemical and biological soil properties show a better performance in soils from naturalized grasslands compared with soils under intensive land management. For this, we selected a naturalized grassland plot as representative of conservation tillage management, and soils previously cropped with potato and maize, subjected to intensive tillage. This information will serve as a baseline for further studies in the region, based on the implementation of contrasting tillage systems and fertilization, using AMF characteristics and the soil's biochemical and microbial characteristics as early indicators of shifts in soil quality. This will allow a more sustainable management of soils currently subjected to strong degradation and erosion.

2 Materials and Methods

2.1 Site Description

We studied three plots previously maintained: (i) a naturalized grassland that has remained unaltered for 7 years, (ii) a plot cropped with maize (*Zea mays*), and (iii) a plot cropped with potato (*Solanum tuberosum*) at Universidad Central del Ecuador Experimental Station, Tumbaco locality, Quito, Ecuador (0° 13' 49" S, 78° 21' 18" W; 2505 m a.s.l.). The plots with maize and potatoes have been used for at least

10 years in crop rotations with intensive conventional soil tillage. The mean annual precipitation in this site is 870 mm, relative humidity is 72%, and annual average temperatures are 10.3 °C min and 23.1 °C max. The dimensions of the plots were 35 × 35 m for the naturalized grassland and 40 × 25 m for the maize and potato plots, respectively. The naturalized grassland plot is located at the south-western side of the maize plot. The distance between both plots is 200 m. The maize plot corresponds to the central-northern plot, while the potato plot is located at the south-eastern side of the maize plot, adjacent to it.

2.2 Soil and Plant Sampling

The soils presented typical characteristics from the northern highlands of Ecuador: dark, volcanic ash-derived soils with allophane material. The soil at this site has been preliminarily characterized as a Mollisol. Nine soil samples were taken in September 2017 from each plot, randomly collected at 0–20 cm depth and homogenized in sealable plastic bags to obtain a total of three composed samples per plot. Soil samples were randomly collected considering a separation of 10–15 m and avoiding the plot's border. Soil samples were stored in sealable plastic bags and kept in coolers with ice for their transportation. An aliquot of each above described soil samples was kept frozen (–20 °C) until the implementation of enzyme activities analysis. Additionally, for descriptive purposes, individuals of herbaceous plants with their intact root system, which were found into the plots, were stored in sealable plastic bags and used for botanical classification (shoots) and AMF colonization (roots).

2.3 Soil Chemical Determinations

Soil parameters such as pH (2:5 w/v in water), electrical conductivity (EC, 1:5 w/v in water), available P, total N, and soil organic matter (SOM) were determined according to standard lab protocols (Zamudio et al. 2006; Espinosa et al. 2014). Available P was extracted and measured according to the Olsen and Sommers (1982) method.

2.4 Soil Biochemical Determinations

The acid phosphatase (A-Pase) activity was measured according to Tabatabai (1994). This method is based on the colorimetric determination of the liberated p-nitrophenol, when soil is incubated with a buffer (pH 6.5) of p-nitrophenyl phosphate disodium salt at 37 °C for 1 h, showing an intense yellowish coloration, measured in spectrophotometer at 420 nm. For the fluorescein diacetate activity (FDA) determination, 15 mL of potassium phosphate buffer was added to 2 g of soil in centrifugation tubes, plus 0.2 mL FDA stock solution (1000 µg mL⁻¹ FDA:acetone), and incubated for 30 min at

30 °C with shaking. Reaction was stopped by adding 5 mL acetone, followed by 5-min centrifugation at 2000g. The amount of FDA hydrolyzed was measured at 490 nm according to the Schnürer and Rosswall (1982) method, using a fluorescein solution as standard.

Total glomalin-related soil protein (TGRSP) was extracted according to Wright and Upadhyaya (1998), with minor modifications. For this, 8 mL of citrate buffer (50 mM, pH 8.0) was added to 1 g of soil and then autoclaved for 1 h at 121 °C. This step was repeated several times on the same sample until the red-brownish color disappeared from the supernatant. The TGRSP content was determined spectrophotometrically by means of the Bradford protein assay (Bio-Rad Protein Assay; Bio-Rad Labs) at 595 nm, using bovine serum albumin as standard.

2.5 Arbuscular Mycorrhizal Fungal Structures in Soil and Roots

AMF spores were isolated from soil by means of wet-sieving and decanting (Sieverding 1991) followed by sucrose gradient centrifugation. After centrifugation, supernatants with the spores were washed for 1 min and transferred to Petri dishes for sorting; then, the total number of spores per 100 g of soil was quantified ($\times 40$ –80). The total isolated spores were placed on microscope slides for visualization and identification (see Supplementary Material 1). Additionally, the AMF communities present in these soils were characterized by means of the species richness (S' , represented as the total different spores' morphotypes), evenness Shannon-Wiener diversity index (H'), and Simpson's dominance index (D'), according to Marín et al. (2016). Detailing, for H' , we used the following equation:

$$H' = - \sum_{i=1}^S (D_i \times \log_2 D_i)$$

where S' is the spores' morphotype richness and D_i is the relative density of each spores' morphotype (proportion of each spores' morphotype number with respect to the total spore number in a sample); meanwhile, for D' , we used the following equation:

$$D' = \sum_{i=1}^S D_i^2$$

The hyphal density in soil was measured by using the method described by Rubio et al. (2003) and using Newman's intersection formula (Newman 1966). In plant roots, the AMF root colonization was determined according to each taxonomically identified and randomly collected plant individual (3 to 5 samples per plant species in each plot). Roots were cleared and stained according to the Phillips and Hayman (1970) and Koske and Gemma (1989) methods, but

using Parker Quink blue ink (Rodríguez et al. 2015) for staining. The presence of AMF structures within the roots was observed at $\times 40$ –100 in a gridded Petri dish, according to Giovannetti and Mosse (1980).

2.6 Statistics

All composed samples ($n = 3$) were considered and analyzed as independent experimental individuals being checked for the normality (Shapiro-Wilk test) and homoscedasticity (Levene test). For each variable, an ANOVA was performed followed by Tukey's multiple range test. Correlation among variables was evaluated using the R Pearson coefficient. The statistical significance was established at $p < 0.05$. Also, principal component analysis and cluster analysis using both the experimental variables and experimental individuals were performed. Statistical analyses were carried out using the IBM SPSS © software v. 19.0. Additionally, a heat map was elaborated for AMF species abundance and their correlation with soil variables as a visual summary, using the software R v. 3.2.2 (R Development Core Team 2015).

3 Results and Discussion

In this study, we expected that the different soils showed contrasting characteristics due to their previous management, being analyzed for chemical and biochemical characteristics, as well as other fungal traits such as AMF spore density, hyphal length, and TGRSP content (Table 1). Our results showed strong differences for pH, EC, available P, total N, SOM, A-Pase, and TGRSP among the three plots. The potato soil presented lower pH values, presumably due to strong previous fertilizations, which also would explain high available P contents. Higher SOM, total N content, and A-Pase values were found in the naturalized grassland and potato soils compared with maize soils (Table 1). These results agree with previous reports by Alvear et al. (2007), who found in an Ultisol from Southern Chile that the N content originated in the SOM mineralization and enzyme activity was narrowly correlated, mainly explained by an increased soil microbial and fungal biomass. Macronutrients such as P and N are continuously being liberated from labile SOM, which also improve the conditions for enzymatic processes, influencing the biodynamics of nutrient cycling (Borie et al. 2019).

Strong differences for SOM were found in the three different soils, being evident that the maize cropping is reducing the total amount of SOM. This aspect deserves to be analyzed in depth, since maize is one of the most cropped species in the Ecuadorian highlands. The highest values of SOM in naturalized grasslands strongly agree with the report of Percival et al. (2000), who worked with 167 volcanic soils from New Zealand and concluded that in such soils the type of SOM

Table 1 Physicochemical and biological properties of Andean Ecuadorian soils from a naturalized grassland and after maize and potato crops

Variable*	Grassland	Maize	Potato	F-value
pH	6.54 ± 0.01 b	6.57 ± 0.01 a	6.11 ± 0.1 c	1490***
Available P	37.13 ± 0.42 c	68.5 ± 0.60 b	152.27 ± 0.50 a	13530***
SOM	3.84 ± 0.5 a	2.96 ± 0.5 b	3.77 ± 0.3 a	123***
Total N	0.19 ± 0.01 a	0.15 ± 0.01 b	0.19 ± 0.01 a	915***
C/N ratio	10.50 ± 0.05 a	10.66 ± 0.14 a	10.48 ± 0.08 a	1.13 ns
EC	0.46 ± 0.01 a	0.29 ± 0.01 c	0.36 ± 0.01 b	180***
A-Pase	685 ± 44 a	682 ± 88 a	720 ± 52 a	16.2**
FDA	164 ± 24 a	172 ± 52 a	112 ± 27 a	2.30 ns
TGRSP	2.4 ± 0.01 b	2.4 ± 0.08 b	2.8 ± 0.08 a	46.9***
AM fungal spores	4397 ± 346 a	2227 ± 453 b	1327 ± 128 c	65.8***
Hyphae length	1.13 ± 0.5 a	0.88 ± 0.5 a	0.88 ± 0.2 a	0.33 ns
S'	8.0 ± 0.0 a	8.0 ± 0.0 a	6.0 ± 0.0 b	231***
H'	1.92 ± 0.02 b	2.03 ± 0.02 a	1.70 ± 0.05 c	86.7***
D'	0.12 ± 0.0 b	0.14 ± 0.0 b	0.20 ± 0.0 a	43.6***

*pH in water (2:5 w/v); available P as Olsen (mg kg⁻¹). SOM, soil organic matter (%); total N, total nitrogen (%); EC, electrical conductivity (mmhos cm⁻¹); A-Pase, acid phosphatase activity (µg PNP g⁻¹ h⁻¹); FDA, fluorescein diacetate activity (µg fluorescein g⁻¹ h⁻¹); TGRSP, total glomalin-related soil protein (mg g⁻¹); AM fungal spores in 100 g of dry soil; hyphae length (m g⁻¹); S', AM fungi species richness; H', evenness Shannon-Wiener's index; D, dominance Simpson's index. The values represent the treatment mean ± standard error (n = 3). Different letters among treatment for the same variable represent statistical differences according to Tukey's multiple range test (p < 0.05). ns, non-significant; *p < 0.05; **p < 0.01; ***p < 0.001

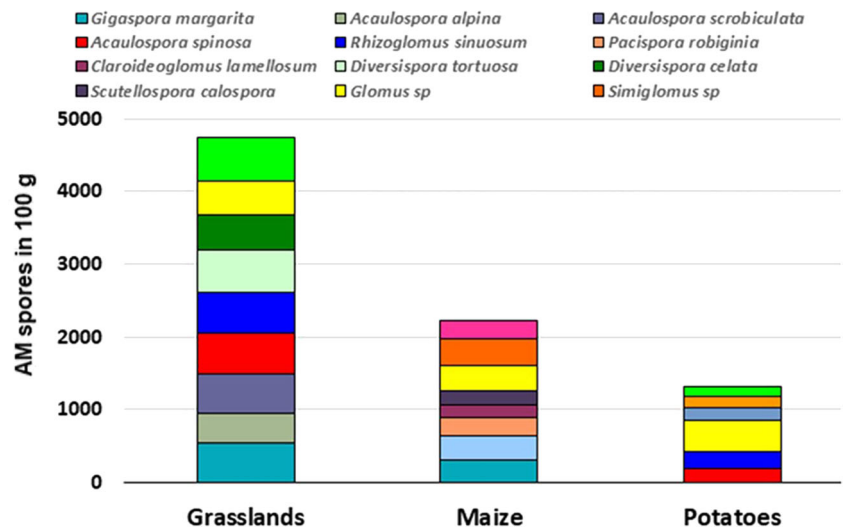
chemical stabilization is a key process for C accumulation. In this sense, the C/N ratio was also assessed as an important trait of SOM stability. Our study reported that the C/N ratio for the three plots was about 10.5 (Table 1), which can be considered an ideal range and suggests a high degree of SOM polymerization (Medina et al. 2015). Such values could support biochemical processes led by soil microorganisms in an ideal way, by allowing the mineralization of the crop residues or even some recalcitrant SOM constituents (Shahbaz et al. 2017).

Several studies show that the TGRSP is a good indicator of stable C in soil, due to its recalcitrance and the increase of the soil aggregate stability (Borie et al. 2008; Curaqueo et al. 2011; Aguilera et al. 2019). Here, we evidenced higher TGRSP content in soils from the potato plot compared with maize and the naturalized grassland plots (Table 1). Despite the underlying mechanisms by which TGRSP contributes to the C sequestration being still largely unknown, it is recognized that TGRSP can act as a regulator of the SOC accumulation, also helping in the P transportation to the plants, maybe as a transient storage. Previous studies by Rillig (2004) and Lovelock et al. (2004b) mentioned that the soil type, management, quality, and fertility influence on the TGRSP concentrations. Additionally, studies by Mohan et al. (2014) and Soudzilovskaia et al. (2015) indicate that the TGRSP and SOC relation was also affected by differences in the crops and AMF community composition.

Considering the importance of AMF in agroecosystems, here we included the description of the communities' diversity, being this one of the first studies focused on the AMF communities in agricultural soils in the highlands of Ecuador. Additionally, for descriptive purposes, we analyzed all the different plant species spontaneously growing in the three plots to corroborate their AMF status. Interestingly, our screening evidenced that the AMF colonization occurs practically in all the plants analyzed, even in plant species belonging to widely recognized non-AM host botanical families (Supplementary Material 2). Detailing, four AMF-colonized plant species were present exclusively in the naturalized grassland plots where higher AMF spores and hyphal length were found, while three plant species were present exclusively in the potato plots, and one plant species was found exclusively in the maize plot. Noticeably, we found AMF colonization in roots of plant species that belong to botanical families well-recognized as non-AM-host, such as *Chenopodium paniculata* and *Amaranthus blitum* (Amaranthaceae family), which reinforce the need of deep analysis of AMF-host associations considering species-specific relation (Teixeira-Rios et al. 2018; Zeng et al. 2018), in particular agroecosystems as the tropical highlands from Ecuador.

The morphological analysis of AMF spores evidenced the presence of a total of 16 AMF species, with seven families and 12 genera into the Glomeromycota phylum (Oehl et al. 2011) (Fig. 1). Thirteen species were identified as previously

Fig. 1 Arbuscular mycorrhizal fungal species according the number of spores per 100 g of soil for three contrasting crop managements (naturalized grassland, maize crop, and potato crop) in an Andean Ecuadorian soil. The grassland was maintained unaltered for 7 years; meanwhile, the other soils have been used in crop rotations with intensive soil management for 10 years, being maize or potato the last species cropped in the respective plot



described species, whereas the other three might correspond to undescribed ones. Previous studies by van der Heyde et al. (2017) indicate that some effects among crops can be evidenced at different time scales, and therefore, there are time-related responses, especially in plots used for grazing. Thus, the effects of soil management on AMF community composition and fungal structures density could be affected by multiple fungal-specific responses along the time. Particularly, here we found clear differences in both size (density of AMF spores) and presence of AMF species (Table 1; Fig. 1), being the naturalized grassland the land management system where the AMF community seems to be more stable according to the different diversity indices obtained (Fig. 2). Here, the presence of some AMF species limited to some soils only can suggest a fungus-host selection, which previously

has been described in plant species and even at the genotype level (Aguilera et al. 2014, 2017). Moreover, our results suggest that both available P and SOM have a strong effect on the AMF community composition (Fig. 3), being also the main experimental variables that allow the complete separation of fungal communities. Detailing, several variables were grouped in a high association degree according to a linear correlation analysis (Table 2) and also considering the PCA (Fig. 2a), especially focusing on the SOM and available P (Fig. 3). Also, the two first principal components after factorial analysis accounted for more than 90% of experimental variance (Fig. 2), where clearly it was possible to associate some soil traits with the presence of particular AMF species, and finally evidencing their influence over the diversity of AMF communities for each soil management (Fig. 2b).

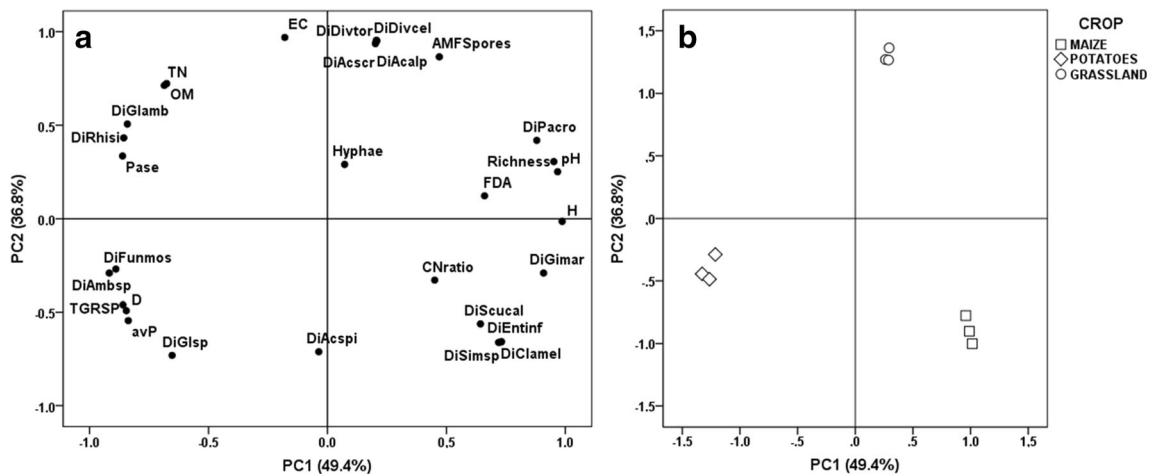
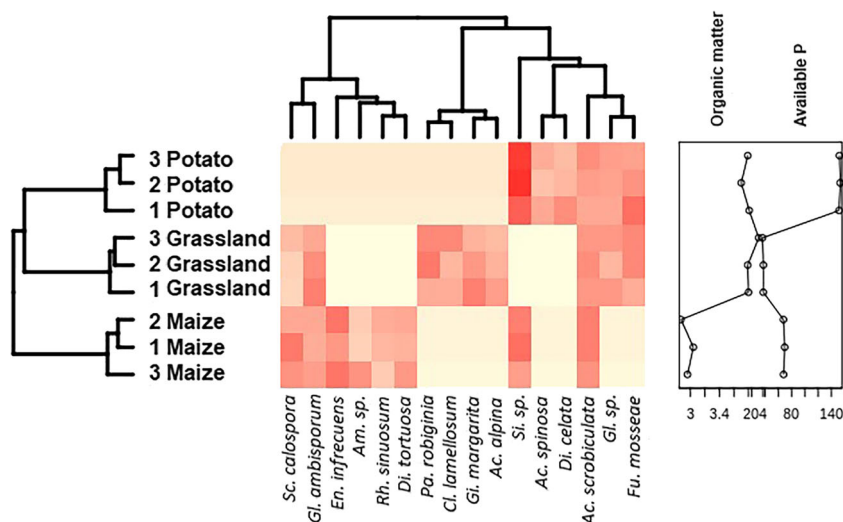


Fig. 2 Principal component (PC) analysis for **a** the studied experimental variables in the rhizosphere of three contrasting soil managements (naturalized grassland, maize crop, and potato crop) and **b** the grouping of the experimental individuals according to the soil management in an Andean Ecuadorian soil. Percentage values in parentheses indicate the experimental variance explained by each PC. avP, available P; OM, soil organic

matter; TN, total nitrogen; EC, electrical conductivity; Pase, acid phosphatase activity; FDA, fluorescein diacetate activity; TGRSP, total glomalitin-related soil protein; H, evenness Shannon-Wiener's index; D, Simpson's dominance index. For the arbuscular mycorrhizal (AM) fungal species, we used the relative density (Di) for the PCA analysis. For the detail of all the AM fungal species, please see the legends in Fig. 1

Fig. 3 Heat map and clustering classification according the Bray-Curtis dissimilarity, showing the 16 arbuscular mycorrhizal (AM) fungi species described in the rhizosphere of three contrasting soil managements (naturalized grassland, maize crop, and potato crop) in an Andean Ecuadorian soil and their relationship with the most significant experimental variables (available P and soil organic matter (SOM)) according to canonical correspondence analysis post-backward analysis



Regarding the multivariate analyses, an inverse significant correlation was observed between pH and TGRSP content ($r = -0.95$, $p < 0.01$). Also, the TGRSP content showed a correlation with the available P content ($r = 0.97$, $p < 0.01$). Although it is recognized that fertile soils with higher P, Ca, or K levels present less glomalin, while those with high C/N ratios such as low-fertility soils present more glomalin, Lovelock et al. (2004a) explain that a “recently” produced glomalin can be found in fertile soils from tropical forests. Therefore, our observation could be explained by climate traits that deserve to be analyzed in future research in Ecuadorian highland soils to understand the mechanisms of SOM transformation or turnover of AMF structures that determine high glomalin (as TGRSP) levels associated to fertile soils. Also, we highlight a strong positive correlation between SOM and A-Pase activity ($r = 0.80$, $p < 0.01$), necessary to hydrolyze P from SOM (Borie et al. 2019). This is noticeable, because here the high A-Pase activities were registered in soils with the high amounts of available P. Finally, the direct and strong correlation between the N content with the SOM ($r =$

0.81 , $p < 0.01$) suggests that SOM is mainly condensed, presumably as humins, humic acids, and glomalin (Hayes and Swift 2018). The above correlations can be good indicators of the effects of management practices over the soil biological activities, where microbial-mediated processes are affected by shifts in both physical and chemical traits, and also by changes in AMF community diversity and structure (Aguilera et al. 2017).

4 Conclusions

Soil chemical and biochemical characteristics here found showed strong shifts maybe due to the precedent management practices, such as tillage, fertilization, and crop rotations, which are mainly reflected in the arbuscular mycorrhizal fungi (AMF) diversity and community structure. In this sense, assuming that naturalized grasslands are associated to a most conservative soil management, the levels of richness and diversity of AMF communities are concordant. Therefore, we

Table 2 Correlation matrix among the experimental variables obtained for three different soil plots in an Andean Ecuadorian soil

	Available P	A-Pase	SOM	Total N	C/N ratio	EC	TGRSP	Hyphal length
pH	-0.95**	0.76*	-0.47	-0.48	0.34	0.07	-0.95**	0.16
Available P		0.54	0.18	0.19	-0.20	-0.38	0.97**	-0.22
A-Pase			0.80**	0.81**	-0.57	0.49	0.53	-0.28
SOM				0.99**	-0.52	0.82**	0.25	0.22
Total N					-0.60	0.81**	0.26	0.21
C/N ratio						-0.34	-0.18	0.09
EC							-0.30	0.23
TGRSP								-0.03

pH in water (2:5 w/v); available P as Olsen (mg kg^{-1}); A-Pase, acid phosphatase activity ($\mu\text{g PNP g}^{-1} \text{h}^{-1}$); SOM, soil organic matter (%); total N, total nitrogen (%); EC, electrical conductivity (mmhos cm^{-1}); TGRSP, total glomalin-related soil protein (mg g^{-1}); hyphal length (m g^{-1}). * $p < 0.05$, ** $p < 0.01$

suggest that the shifts in AMF community composition could be considered as a tool to characterize contrasting soil management systems oriented to support soil conservation and sustainability actions in the Ecuadorian highland region, currently characterized by strong soil degradation and erosion. This study represents a baseline for further research and analyses and constitutes a record of changes in soil (bio)chemical properties undergoing different soil managements.

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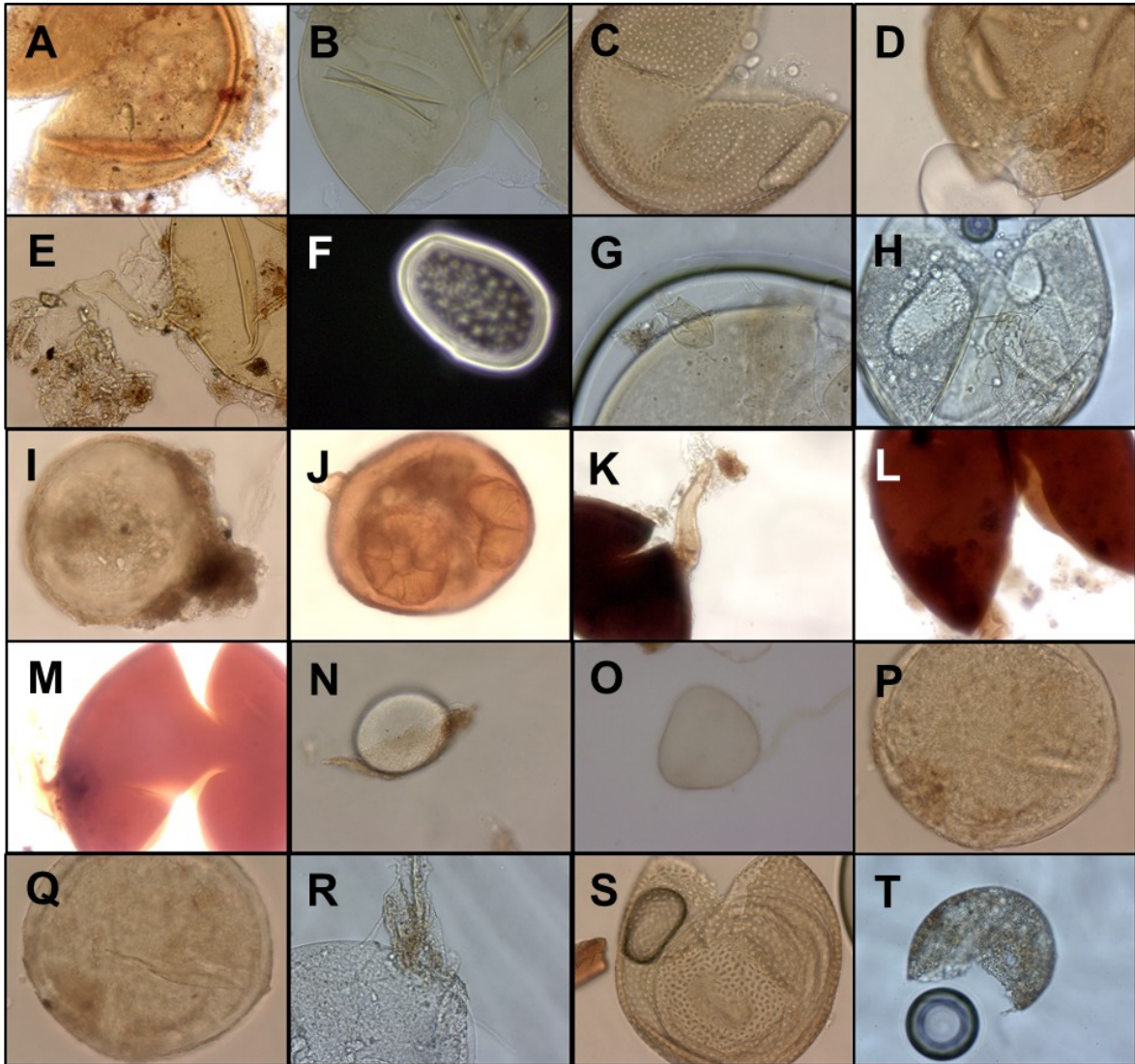
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Supplementary Material 1. General view of the most abundant spores of arbuscular mycorrhizal fungi found in the three analyzed plots.

Supplementary Material 2. AM root colonization (%) of the different plant species present in the analysed plots subjected to three different managements in an Andean Ecuadorian soil.

Plant species	Soil management		
	Grasslands	Maize	Potato
<i>Pennisetum clandestinum</i>	54	59	55
<i>Verbena litoralis</i>	26		
<i>Cynidon dactylon</i>	43	60	
<i>Solanum nigrum</i>	83		
<i>Conyza floribunda</i>	56		
<i>Avena sativa</i>	70		
<i>Bidens leucanta</i>	56	45	
<i>Trofolium repens</i>	56	44	
<i>Galinsoga parviflora</i>	45	12	62
<i>Galinsoga ciliata</i>		21	18
<i>Taraxacum officinalis</i>		70	
<i>Chenopodium paniculata</i>		18	23
<i>Amaranthus blitum</i>		31	26
<i>Senecio vulgaris</i>		30	28
<i>Malvastrum peruvianum</i>			17
<i>Verbena sp.</i>			45
<i>Physalis peruviana</i>			35