

Soil Fungal Diversity of the Aguarongo Andean Forest

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Fungi represent an essential component of ecosystems, functioning as decomposers and biotrophs, and they are one of the most diverse groups of Eukarya. In the tropics, many species are unknown. In this work, high-throughput DNA sequencing was used to discover the biodiversity of soil fungi in the Aguarongo forest reserve, one of the richest biodiversity hotspots in Ecuador. The rDNA metabarcoding analysis revealed the presence of seven phyla: Ascomycota, Basidiomycota, Mortierellomycota, Mucoromycota, Glomeromycota, Chytridiomycota, and Monoblepharomycota. A total of 440 identified species were recorded. They mainly belonged to Ascomycota (263) and Basidiomycota (127). In Mortierellomycota, 12 species were recorded, among which *Podila verticillata* is extremely frequent and represents the dominant species in the entire mycobiota of Aguarongo.

Keywords: Andes ; environmental DNA ; fungal biodiversity ; metabarcoding ; natural reserve ; forest ecosystems tropical mycobiota vulnerable species

1. Introduction

The Andes represent the largest mountain range on Earth and cross the western part of South America. In Ecuador, the inter-Andean valley is composed of humid areas at high altitudes, with physiognomies ranging from grasslands to forest formations, combined with andisol soils, which develop from volcanic ash and show little or moderate evolution, forming a unique ecoregion. The forest soils in the Andean highlands have high biodiversity and unique environmental characteristics. It is an endangered ecosystem, and little is known about its microbial community. Fungi represent an essential functional component of terrestrial ecosystems as decomposers and biotrophs (mutualists, pathogens, and necrotrophs), and they are one of the most diverse groups of Eukarya ^{[1][2]}.

The soil fungal communities are affected by numerous biotic and abiotic factors, including seasons, soil characteristics, age and plant host species, and different soil managements ^{[3][4]}. The study of the ecological factors that underlie the dynamics of fungal communities remains a challenge due to its high taxonomic and ecological diversity.

Molecular methods based on PCR and ribosomal DNA sequencing have been successfully used to identify fungi at different taxonomic levels in different environmental samples and have helped to elucidate the ecological conditions that affect the structure and diversity of fungal communities ^{[5][6][7]}. The internal transcribed spacer region (ITS) is now widely used as a DNA barcode marker for the identification of fungal species ^[8]. Recent studies have demonstrated the potential of advances in DNA sequencing for quantifying and characterizing the fungal diversity, especially in those areas of the planet where biodiversity is very rich and complex ^[9].

Ecuador is one of the 17 megadiverse countries in the world, according to the World Conservation Monitoring Centre (WCMC) of the United Nations Environment Program. Ecuador has approximately 4.6 million hectares that have been declared as natural areas, which contain invaluable biodiversity and are a rich source of necessary ecological services. The fungal biodiversity of the natural areas in Ecuador is little known due to its extreme richness and complexity. The analysis of genetic material directly extracted from environmental samples coupled with DNA next-generation sequencing technology is useful in discovering its mycobiota and the monitoring of its biodiversity over time and in different ecological conditions ^[10].

Rich literature can be found on the fungal biodiversity of Ecuador, mainly focused on taxonomy and distribution of a single taxon at the species or hierarchical higher level ^{[11][12][13][14][15]}. Many papers focus on pathogenic fungi for important crops or on the relation between fungi and environments ^{[16][17][18][19]}. Recently, environmental fungal DNA was analyzed for community composition studies of disturbed areas ^{[20][21]} or specific substrates such as plants ^{[22][23]}. Investigation of mycobiota of natural areas in Ecuador focused on biodiversity, distribution, and ecology of mycorrhizae ^{[24][25][26]}. Data collected from environmental DNA concerning the entire mycobiota from natural areas and reserves of Ecuador are missing or rare.

2. Soil Chemical Characteristics

Concentrations of N, P, K, Mg, Ca, S, Cu, Mn, Zn, Fe, Na, exchangeable Al, and chlorides are presented in **Table 1** for each site. The analyses revealed that some chemical parameters vary significantly among the sampling sites; altitudinal levels could be one of the conditions that influence the chemical properties of the soil, but type of soil must be considered as well.

Table 1. Soil chemical properties. Values are expressed in mg/kg for each compound, except Al expressed in meq/100 g, while N and organic matter are expressed in % s.m.s. Values with different letters in the same column are significantly different ($p < 0.05$).

Sampling Sites	pH	Organic Matter	N	P	K	Mg	Ca	S
L1	4.9 ^b	10.9 ^a	0.68 ^b	3.6 ^b	203.3 ^b	425.7 ^b	1776.3 ^b	846.4 ^b
L2	4.8 ^a	15.5 ^a	0.82 ^a	5.9 ^a	128.0 ^a	162.7 ^a	564.7 ^a	1012.6 ^a
L3	4.6 ^a	12.3 ^a	0.71 ^a	5.3 ^a	126.7 ^a	177.7 ^a	885.3 ^a	790.4 ^a
Sampling Sites	Cu	Mn	Zn	Fe	Na	Cl	Al	
L1	10.5 ^b	118.7 ^b	16.0 ^a	834.3 ^a	28.7 ^a	11.8 ^a	6.4 ^a	
L2	8.7 ^a	72.7 ^a	15.7 ^a	926.0 ^a	31.3 ^a	15.1 ^a	6.9 ^a	
L3	12.7 ^a	107.7 ^a	16.0 ^a	1197.3 ^b	24.3 ^a	371.8 ^b	7.1 ^a	

The values of pH, N, P, K, Mg, Ca, S, Mn, and Cu are similar in L2 and L3 but are significantly different from L1. The content of Zn, Na, and exchangeable Al did not show differences between L1, L2, and L3. Site L1 showed the greatest differences, with lower values of N and P compared to the other locations, while in the case of Mg and Ca, it presents higher values.

3. Soil Fungal Assemblage Composition

The sequencing on the Illumina MiSeq Platform of the DNA of the 20 pooled soil samples produced a total of 3,699,594 reads, with an average of 184,979.7 reads per sample. After the cutting and filtering process, the reads were reduced to 2,794,683, with an average of 139,734 reads per sample. It was observed that L1 showed the highest abundance with an average of 833 OTUs, followed by L2 with an average of 780 OTUs and L3 with an average of 711 OTUs (**Figure 1**).

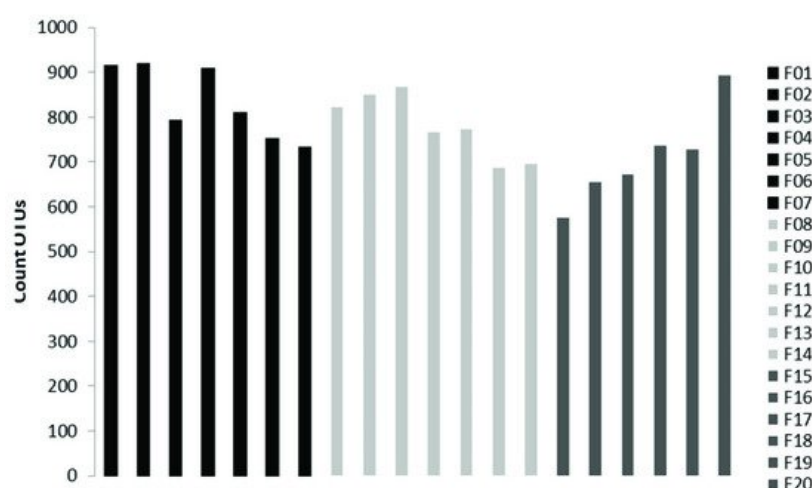


Figure 1. Number of OTUs present in each sample, with F1, F2, F3, F4, F5, F6, F7 belonging to altitudinal level L1, F8, F9, F10, F11, F12, F13, F14 belonging to L2, and F15, F16, F17, F18, F19, F20 belonging to L3.

Metagenomic data were taxonomically organized in this work following the high-level classification of the Fungi reported by Tedersoo et al. [27]. The analysis revealed the presence of seven identified phyla in the soil samples: *Ascomycota* and *Basidiomycota* (subkingdom of *Dikarya*), *Mortierellomycota*, *Mucoromycota* and *Glomeromycota* (subkingdom *Mucoromyceta*), and *Chytridiomycota* and *Monoblepharomycota* (subkingdom *Chytridiomyceta*). The most abundant phylum was *Ascomycota*, with a relative abundance of 32–36%, followed by *Mortierellomycota* (25–28%), *Basidiomycota* (9–

11%), and *Mucoromycota* (3–7%). The less abundant phyla were, as expected, *Glomeromycota*, (0.1%) *Chytridiomycota* (0.02%), and *Monoblepharomycota* (0.0005%). The identified phyla were equally distributed in each sampling site, except *Glomeromycota*, which was more abundant in Site L3, the highest in altitude. The share of fungal OTUs assigned to “Unidentified” was quite abundant in each site, reaching 17–35% of the total. In total, 408 taxa identified at the species level were found. All recorded species with their relative abundances in each sampling site are listed in [Supplementary Table S2](#) (available online at <https://www.mdpi.com/article/10.3390/biology10121289/s1>).

3.1. Subkingdom Dikarya

Ascomycota

Within the phylum *Ascomycota*, the analysis revealed the recording of 11 classes (**Figure 2**). The most abundant classes were *Sordariomycetes* (8–17% of the total fungi), mainly represented by the orders *Hypocreales* and *Chaetosphaeriales*; *Leotiomyces* (3–9% of the total fungi), mainly represented by the order *Helotiales*; *Eurotiomycetes* (2–8% of the total fungi), mainly represented by *Eurotiales* and *Chaetothyriales*; and *Dothideomycetes* (2–5% of the total fungi) mainly represented by *Pleosporales* (**Figure 3**).

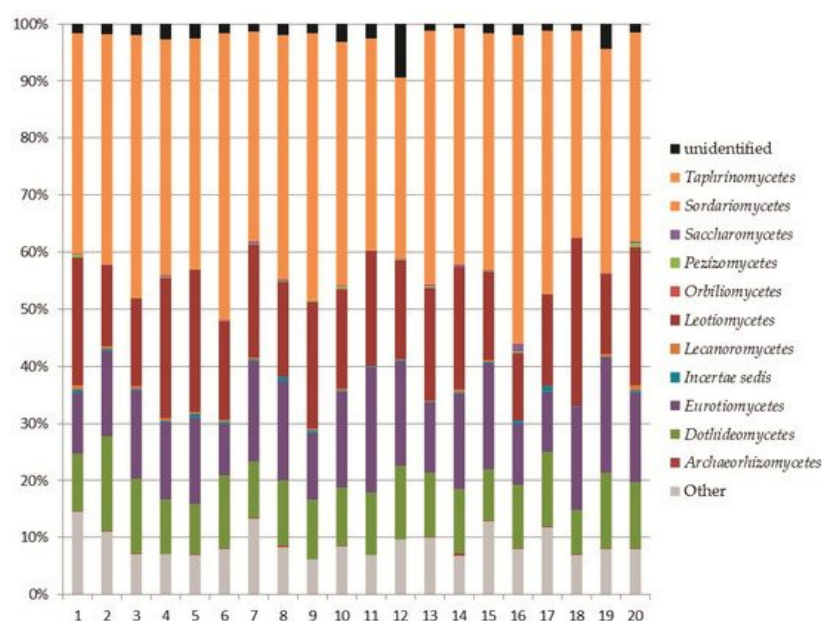


Figure 2. Relative abundance of *Ascomycota* classes in the soil samples.

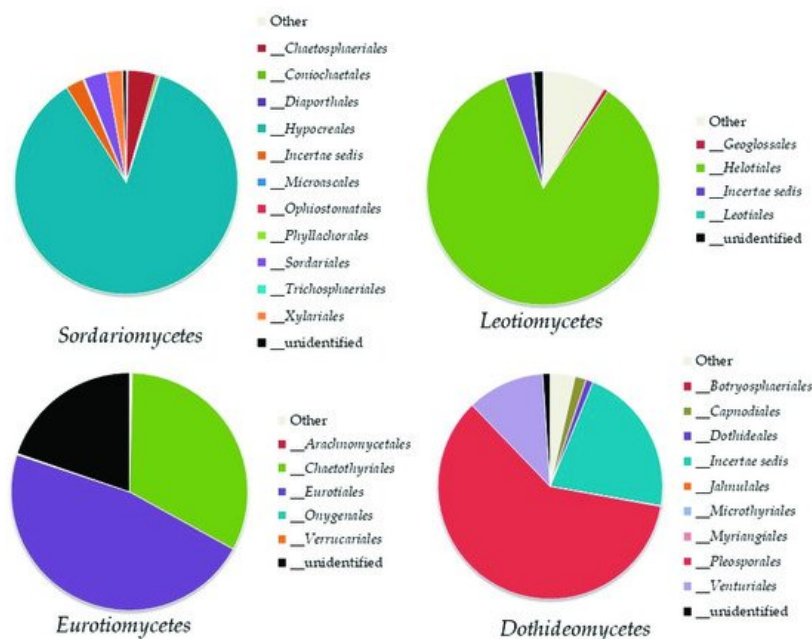


Figure 3. Order abundance in the most highly represented classes of *Ascomycota*: *Sordariomycetes*, *Leotiomyces*, *Eurotiomycetes*, and *Dothideomycetes*.

In *Ascomycota*, 263 identified genera were recorded; 58 genera reached at least 0.1% of the total fungi and were present in at least one of the samples with this value. Among them, the most abundant genera were: *Fusarium* (6–

12%), *Penicillium* (0.5–6%), *Oidiodendron* (0.1–2%), *Bipolaris* (1–2%), and *Ilyonectria* (0.4–1%). The other genera were recorded at less than 0.01%.

The ascomycetous taxa identified at the species level were 235 (Supplementary Table S2). Most of them belonged to *Penicillium* (nine species); *Trichoderma* (six), *Oidiodendron* (five), *Cladonia*, *Cyphellophora*, *Exophiala*, *Peltigera*, and *Phialophora* (all with four species each), and *Acremonium*, *Aspergillus*, *Chalara*, *Chlonostachys*, *Hirsutella*, and *Metarhizium* (three species each).

Top Ten Most Abundant Species of Ascomycota

Among the identified taxa, *Fusarium oxysporum* s. lat. was, undoubtedly, the most abundant species, reaching 7–10% of the total fungal assemblage. *Pleotrichocladium opacum* was well represented (3%), together with *Penicillium spinulosum* and *Curvularia lunata* (2%). Other abundant identified species were *Trichoderma asperellum* and *Ilyonectria panacis* (1%), *Tetracladium apiense* and *Chaetosphaeria vermicularioides* (up to 0.5%), *Leptobacillium leptobactrum* (up to 0.4%), and *Penicillium donkii* (up to 0.3%).

Basidiomycota

Basidiomycota was represented by eight classes (Figure 4); the most abundant ones were *Tremellomycetes*, represented by the order *Trichosporonales*, and *Agaricomycetes* (both, up to 11% of the total fungi), mainly represented by the orders *Agaricales* and *Thelephorales* (Figure 5).

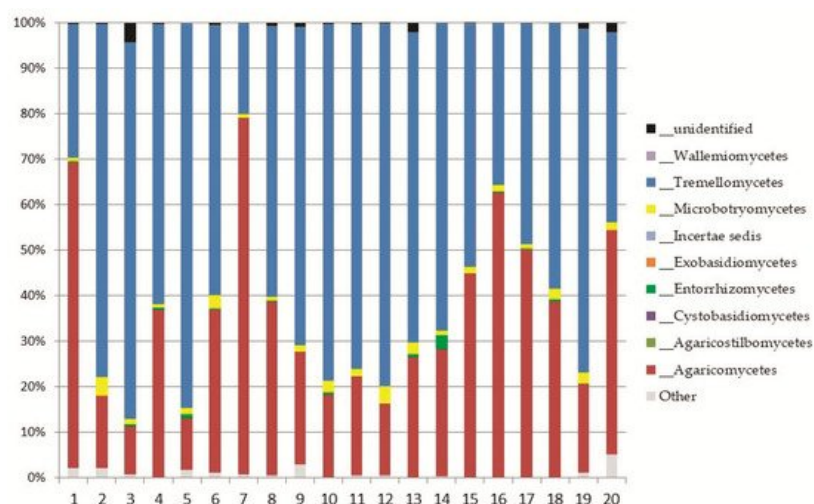


Figure 4. Relative abundance of classes of *Basidiomycota* in the soil samples.

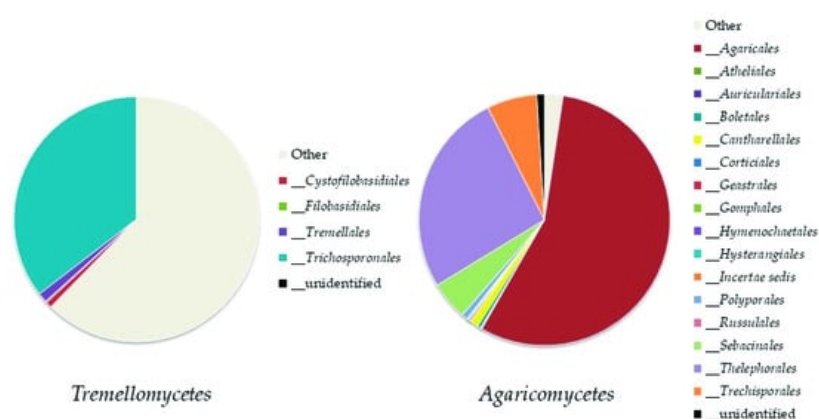


Figure 5. Abundance of orders in the most represented classes of *Basidiomycota*: *Tremellomycetes* and *Agaricomycetes*.

The recorded genera of *Basidiomycota* were 118. Only 29 of these genera reached at least 0.1% of abundance of the total fungi. Among them, the most abundant ones were: *Cuphophyllus*, *Saitozyma*, and *Trichosporon* (up to 7% of the total fungi), *Tomentella* (up to 6%), and *Hygrocybe* (up to 2%).

The basidiomycetous taxa identified at the species level were 127 (Supplementary Table S2). Most of the identified species belonged to *Entoloma* (11 species), and *Lepiota* (5 species).

Top Ten Abundant Species of Basidiomycota

The following species were the most abundant: *Saitozyma podzolica* (3–4%), *Apiotrichum wieringae* (1–2.5%), and *Tomentella testaceogilva* (1%). *Apiotrichum dulcitum*, *Clitocybe nebularis*, *Fomes fomentarius*, *Porpolomopsis calyptriformis*, *Sarcodon atroviridis*, and *Serendipita vermifera* were represented by less than 0.2%.

3.2. The Subkingdom *Mucoromycota*

Mortierellomycota

Mortierellomycota was the second highest represented phylum. In the class *Mortierellomycetes*, the analysis revealed the presence of 5 genera and 12 species ([Supplementary Table S2](#)). The most dominant species were *Podia verticillata* (50%), *Podia horticola* (21%), *Mortierella alpina*, and *Linnemannia gamsii* (12% each) (**Figure 6**).

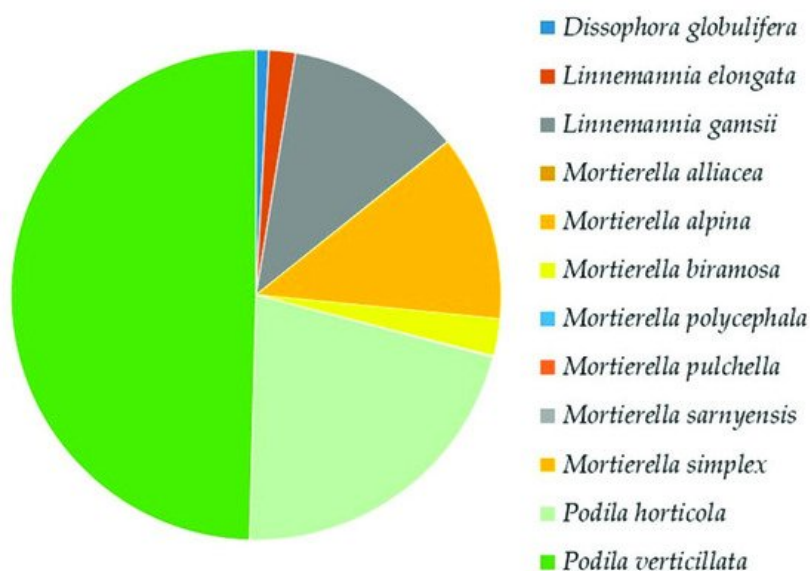


Figure 6. Relative abundance of species in *Mortierellomycetes* (*Mortierellomycota*), following the most recent taxonomic classification at the species level [28].

Mucoromycota

The three classes of *Mucoromycota* were all represented in the soil samples with a total of 19 species ([Supplementary Table S2](#)). *Mucoromycetes* (14 species) were dominated by *Mucor moelleri* (58%), *Mucor hiemalis*, *Sepmannia pineti* (both 11%), and *Mucor abundans* (10%) (**Figure 7**). *Umbelopsidiomycetes* (four species) was completely dominated by *Umbelopsis vinacea* (97%, **Figure 7**). *Endogonomycetes* was present with only one identified species, *Jimgerdemannia lactiflua*.

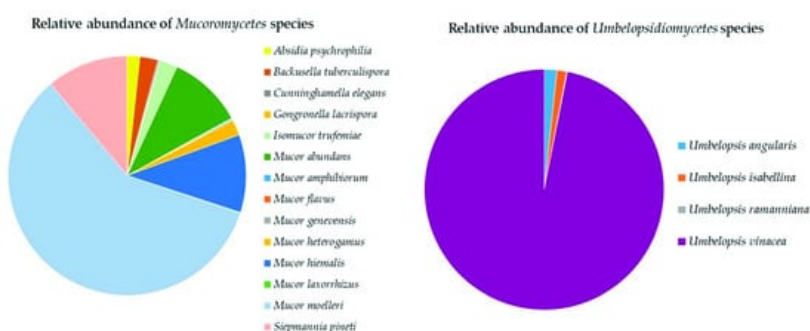


Figure 7. Relative abundance of species of *Mucoromycota* in the classes *Mucoromycetes* and *Umbelopsidiomycetes*.

Glomeromycota

The taxa belonging to this phylum were poorly identified at the species level. The detected species were seven ([Supplementary Table S2](#)), belonging to six genera: *Claroideoglossum claroideum* (2%) followed by *Acaulospora alpina*, *A. lacunosa*, *Racocetra castanea*, *R. fulgida*, *Archaeospora trappei*, and *Dentiscutata heterogama*.

The Top *Mucoromycota*

Of the total fungi, *Podia verticillata* was strongly represented (12–14%), followed by *P. horticola* (5–6%), *Mortierella alpina* (2–6%), *Linnemannia gamsii* (3%), *Umbelopsis vinacea* (2.5–3%), *Mortierella biramosa* (0.5–1%), and *Mucor*

moelleri (0.1–1%).

3.3. The Subkingdom *Chytridiomycota*

In *Chytridiomycota*, the identified species were very rare (four, listed in [Supplementary Table S2](#)). The most abundant was *Rhizophlyctis rosea* (13%), belonging to *Chytridiomycota*, followed by *Spizellomyces plurigibbosus* (6%), *Olpidium brassicae* (1%), and *Gallinipes pseudodichotomus* (1%). In *Monoblepharomycota*, the only identified species was *Monoblepharella mexicana* (3%).

4. Soil Mycobiota Diversity in the Sampling Sites

The alpha diversity found in the fungal communities of the three locations (L1, L2, L3) was similar regarding the Shannon and Simpson Indices, while the Chao 1 Index, which focuses especially on the abundance of rare species, found a significant difference between locations L1 and L3 (324 ± 26 and 275 ± 29 , respectively, $p < 0.05$ ANOVA, followed by Tukey's pairwise test, **Figure 8**).

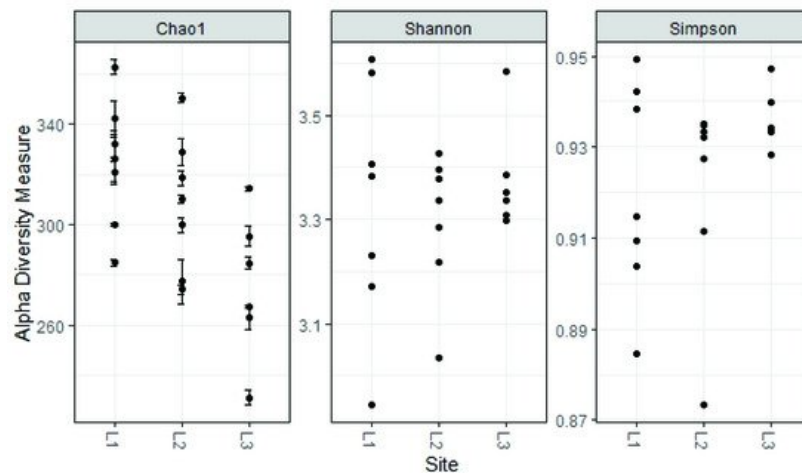


Figure 8. Estimated alpha diversity for different sampling sites.

The analysis of beta diversity present in the samples did not show any significant difference in the structure of soil fungal communities in the three sampling locations (PERMANOVA, $p > 0.05$; **Figure 9**).

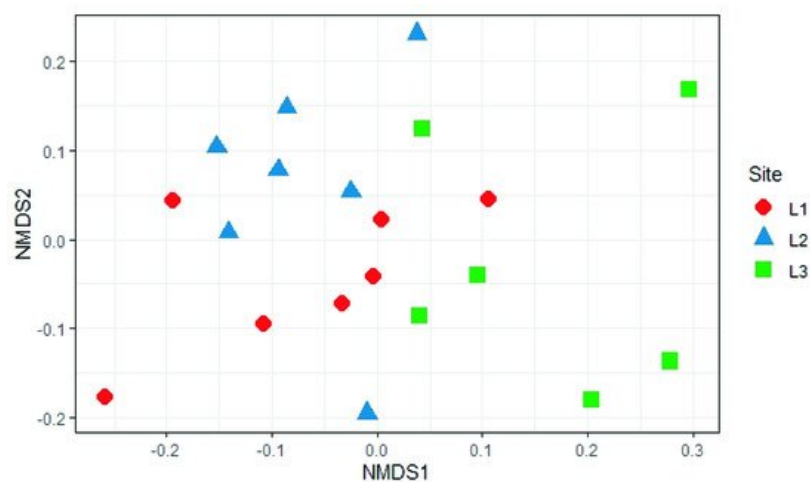


Figure 9. Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis distances of soil fungal communities in the different sample locations (L1, L2, and L3) in the Aguarongo forest.

Venn's analysis showed that 43% of all OTUs was shared between the three sampling sites. At Locations L1 and L2, the number of unique OTUs was similar (129 and 133, respectively), while L3 had a lower number of unique OTUs (97, corresponding to 10%) (**Figure 10**).

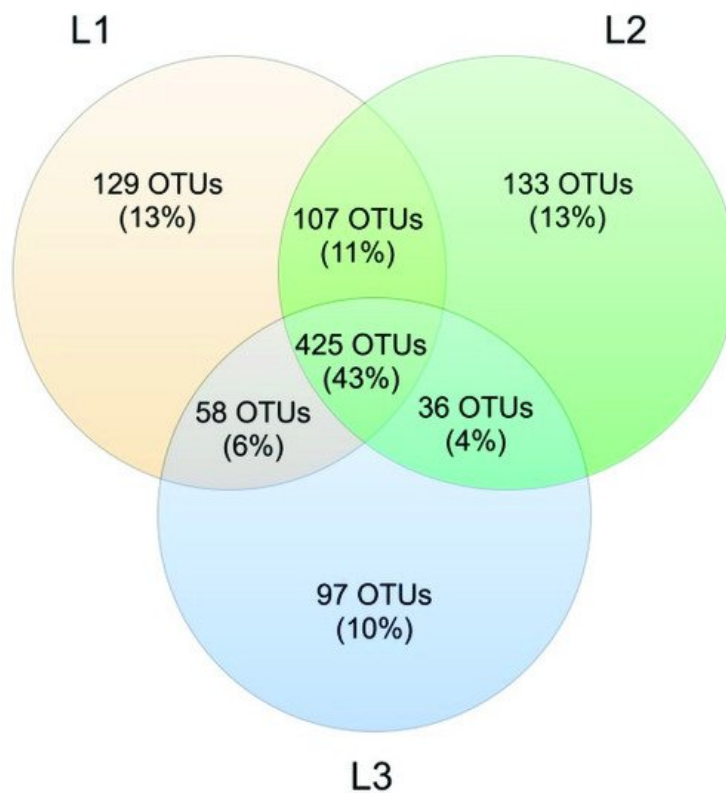


Figure 10. Venn diagram showing OTUs shared among the 3 sampling sites (L1, L2, and L3).

5. Discussion

The Aguarongo forest reserve is one of the most important biodiversity hotspots in Ecuador, and in recent years, it has been the subject of numerous research studies on flora, fauna, use of soils, and water balance [29][30].

As for all the tropics, Ecuador has huge biodiversity that has yet to be revealed, especially in natural reserves such as the Aguarongo forest. This is true above all for Fungi, a Kingdom often neglected despite its key role in the functionality of terrestrial ecosystems.

Regarding the use of next-generation sequencing in research of soil fungal communities, there are few studies in the tropics; however, a collection of metagenomic data is being implemented [31][32][33][34]. Most Ecuadorian studies on soil fungi describe the diversity of arbuscular mycorrhizal fungi (AMF) associated with crops in the Andean part of Loja and Quito [35][36]. There are also studies of the communities of AMF associated with plants growing in contaminated soils such as crude-oil-contaminated sites in the Amazon region of Ecuador [20]. Using modern molecular methods, it was possible to obtain a detailed account of soil fungal biodiversity of the Aguarongo forest and give the first list of soil fungi of this important reserve of biodiversity in Ecuador.

In this work, 408 fungal OTUs were identified at the species level. Together with *Ascomycota*, the most abundant phylum in our study was *Mortierellomycota*. Its high abundance was expected, as this result has been recorded in other studies on the mycobiota of soil in high altitude environments [32][34] or from extreme environments such as the Alps [37] or Antarctica [38][39][40]. Surprisingly, in the Aguarongo forest, the abundance of *Mortierellomycota* is similar to that of *Ascomycota*. All the OTUs referring to *Mucoromycota* in this study were updated following the recent paper of Vandepol et al. [28], in which the phylogeny of *Mortierellaceae* was resolved through a synthesis of multigene phylogenetics and phylogenomics. The present work significantly improved the global geography and environmental records of *Mortierellaceae* and contributed to the knowledge on the ecology of these species, especially in an under-sampled region such as Ecuador. These data contribute to understanding the ecological function of *Mortierellaceae*, which remains mostly unknown. Species of *Mortierellaceae* are often isolated from soils, decaying leaves, and insects [41], due to their saprotrophic nature [42].

Regarding alpha diversity, it was similar among all sampling sites; the values reported here are similar to those found for other regions of the world with altitudes above 2000 m.a.s.l. [32].

In the whole soil mycobiota of Aguarongo, the most frequent species is a *Mortierellaceae* species, *Podila verticillate*, representing 12–14% of the total of identified OTUs. This species (reported with its basionym *Mortierella verticillata*) was

first recorded in South America from mountainous environments (1950 m.a.s.l.) in Brazil ^[43]. Our findings expand the distribution of *P. verticillata* both in latitude and altitude. This is true for all of the species of *Mortierellaceae*, which were abundantly found in Aguarongo forest soil up to 3221 m.a.s.l.

Within the identified species of *Ascomycetes* in Aguarongo, important facultative plant pathogenic fungi were abundantly recorded, for example from the *Fusarium oxysporum* complex, a well-known group of taxa due to their many pathogenic forms and high frequency of isolation in soil ^[44], and *Curvularia lunata*, an important pathogen of maize ^[45]. In addition to the plant pathogens many saprotrophic fungi were recorded, such as *Pleotrichocladium opacum* and *Penicillium spinulosum*, a dominant taxon in the Aguarongo forest.

Beneficial fungi were not lacking, such as *Trichoderma asperellum*, an important biocontrol agent, applied in agriculture for controlling plant fungal pathogens and plant-growth promoters ^{[46][47]}, as well as *Arthrobotrys musiformis* *Pochonia bulbillosa*, and *P. suchlasporia*, well-known nematophagous fungi ^{[48][49]}. Particularly important in the Aguarongo forest is the presence of the genus *Metarhizium*, a genus that shows wide biodiversity in this area, with species having high potential as biocontrol agents against insects, specifically *M. anisopliae*, *M. flavoviride*, and *M. lepidiotae*, ^[50]. Although their presence is occasional, many other species with importance because of their ecological role as entomopathogens or nematopathogens, and potential application for sustainable agriculture ^[51] are found in the Aguarongo forest. This includes *Beauveria brongniartii*, *B. bassiana*, *Dactylella mammillata*, *Hirsutella minnesotensis*, *H. rhossiliensis*, *H. vermicola*, *Paecilomyces farinosus*, and *P. marquandii*.

Basidiomycetes were dominated by *Saitozyma podzolica*, a common yeast and strong decomposer of dead plant biomass isolated from soils worldwide ^[52]. *Apiotrichum wieringae* was also widely present in the soil of Aguarongo, a nonpathogenic member of the *Tricosporonaceae* family, able to degrade uric acid and aromatic compounds ^[53]. *Tomentella testaceogilva*, abundant in Aguarongo, is reported as a terricolous or lignicolous fungus associated with *Alnus*, but also with moss ^[54]. Although rarely recorded in the Aguarongo forest, a famous member of *Basidiomycetes* must be highlighted, namely *Fomes fomentarius*, an important plant pathogenic fungus rich in pharmacological compounds ^[55].

Fungi in soils of Aguarongo include members of the phylum *Glomeromycota*, which remain mainly unidentified. Some identified species are important arbuscular mycorrhizal fungi; the most abundant one was *Claroideoglossum claroideum*, considered a good plant promoter and heavy metal decontaminant ^[56]. In the Aguarongo forest, *Chytridiomycota* were dominated by *Rhizophlyctis rosea*, a highly effective plant biomass degrader and zoosporic fungus, commonly observed near the soil surface. This species has light-sensitive proteins that allow this fungus to remain in the euphotic zone ^[57]. Within *Monoblepharomycota*, only one species was recorded: *Monoblepharella mexicana*. The southernmost record of this species was reported by Steciow and Arambarri ^[58], while the present finding can be considered the record of this species at the highest elevation.

The analysis reported in this work is based on a large number of soil samples (100), thus giving a good representation of the fungal biodiversity of Aguarongo forest soil. The collection of samples along an altitudinal gradient did not reveal significant differences among the structure of the soil fungal communities in the three sampling locations (L1, L2, L3). Only Location L3 has a lower abundance of rare taxa with respect to L1, consistent with the Venn diagram.

The analysis of the records, reported in [Supplementary Table S2](#), shows the Aguarongo forest soils as a natural area rich in fungal biodiversity, with the main phyla represented by a large number of taxa, known to be beneficial fungi. In addition, the Aguarongo forest is shown to be a rich source of species having strong application potential in agriculture and in the chemical and food industry. This area hides a huge number of unknown species that could be assessed, and its protection is of the utmost importance.

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