Selecting logging, and old secondary vegetation conserve biodiversity and composition of bacteria and arbuscular mycorrhizal fungi in a community-based forestry in the Maya Forest

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Abstract

The impacts of selective logging on arbuscular mycorrhiza and bacteria of tropical forests are little known globally. In this study, we analysed and compared the composition and diversity of bacteria and arbuscular mycorrhizal fungi (AMF) in a forest with sustainable management (stands with 6-years-old after selective logging) compared with a conserved forest and secondary vegetation recovered from agriculture (20-years-old) in Nuevo Becal, Campeche, Mexico. The analyses were based on environmental DNA sequences using Illumina miseq platform and morphological diversity of AMF glomerospores. We found 30 species of virtual AMF taxa (10 potential new virtual taxa) based on DNA sequences, 22 AMF species based on morphology, and 3,963 amplicon sequence variants (ASVs) for bacteria. For AMF, the most abundant order (in the whole study) were the Glomerales (with higher significant abundance in secondary vegetation), followed by Gigasporales and Diversisporales, while for bacterial phylum, Proteobacteria and Actinobacteria were highly represented, followed by Acidobacteria, Planctomycetes, Nitrospirae, Bacteroidetes, and Gemmationonadetes. Actinobacteria showed significantly higher relative abundance in conserved forests, Chloroflexi in managed forests, and Verrucomicrobia in secondary vegetation. Bacterial and glomerospores community composition did not showed significant differences among the three sites analysed. However, AMF VT community composition were significant different between the conserved forest and secondary vegetation. Forest management showed higher bacteria and glomerospores diversity (Shannon index) compared to the conserved forest and secondary vegetation. Our study showed that stands 6 years after selective logging and old secondary vegetation conserved an important bacteria and AMF species compared with conserved forests.

Introduction

Tropical forests are considered hotspots of diversity, species endemism, cultural diversity, they provide major ecological and socioeconomic services, such as biodiversity conservation, food production, mitigation of climate change, ecotourism, and medicinal plants (Myers et al. 2000; Davis et al. 2020). Tropical forests support one of the highest concentrations of biodiversity, and many species have yet to be discovered (Dirzo and Raven 2003; Costello et al. 2013). Land-use changes to agriculture and pastures and timber extractions are among the main causes of biodiversity loss, deforestation, and degradation (Kissinger et al. 2012). Land-use changes and selective logging modify landscape connectivity between ecosystems, alter the community structure of soil microorganisms, and could drastically change ecosystem multifunctionality (Wagg et al. 2004; Zemanova et al. 2017; Sun et al. 2020; Lan et al. 2021).

Arbuscular mycorrhizal fungi (AMF) and bacteria are among the soil microorganisms that play a fundamental role in the function of tropical forest ecosystems (van der Heijden et al. 2008) and are a good indicator of soil disturbance (Moora et al. 2014). AMF and bacteria contribute synergically to plant nutrition (Nacoon et al. 2020), regulate CO_2 emissions, (Zimmermann et al. 2009; Zhang et al. 2020), promote plant health, stimulate plant growth (Artursson et al. 2006), enhance host plant defences against soil pathogens (Pérez-de-Luque et al. 2017), and are the primary drivers of litter decomposition and nutrient and carbon cycling in soils (Horner-Devine et al. 2004; López-Mondéjar et al. 2020). However,

despite fulfilling multiple functions in tropical forests, the diversity and community structure of the soil microbiota in these environments and types of vegetation are poorly understood (Tripathi et al. 2012; Marinho et al. 2018; Stürmer et al. 2018).

Selective logging is the major timber producer in the tropics and is becoming important to conservation efforts due to the rapid loss of primary tropical forests (Asner et al. 2005; Edwards et al. 2013; Putz et al. 2019). In the Yucatan Peninsula, tropical evergreen and semi-evergreen forests are important vegetation types that are refuges for several species, including ungulates and felines that need large undisturbed areas of tropical forest habitat (Reyna-Hurtado and Tanner 2005). In this region, an important number of ejidos (communities) base their economy on forest harvest and occupy about seven million hectares of tropical forest, with an important extension of the Mesoamerican corridor that includes protected areas, such as the Calakmul Biosphere Reserve, one of the last remaining pristine tropical forests in Mesoamerica (Ellis et al. 2019). Community-based forestry includes selective logging as part of a forest management plan called a polycyclic silvicultural system, which includes 25-year cutting cycles, with at least a 75-year rotation (Ellis et al. 2014). This forest management system is recognised as an effective strategy for conserving biodiversity and is characterised by low harvest intensity, reporting ≥ 77% of intact forest in logging blocks (Ellis and Porter-Bolland 2008; Putz et al. 2019). Selecting logging in the region includes mainly tropical tall-to medium-stature forests (≥ 25 m) that maintain similar vegetative species composition across the region. Low-sub-perennial-flooded forests (8–15 m) differed in vegetation species from the medium and tall forests, and mainly it has a strong influenced by agricultural activity. An important extension of lowlands has been recovering from agriculture practices, since primary activities are forest management, leaving secondary vegetation in different years of recovery. Environment changes due to different intensities of selective logging and time since the last harvest, and, vegetation type resulting in heterogeneous effects in removing or replacing tree species and modifying canopy gaps and soil conditions that could alter microbiota structure, composition, and function (Tomao et al. 2020; Lan et al. 2021).

Bacteria and fungi have been shown to be differentially affected by these environmental changes. In evergreen and deciduous forests, Surendra et al. (2021) found that repeated selective logging could reduce plant diversity and aboveground carbon stocks, even at low intensity. Kerfahi (2014) found that fungi β-diversity did not show differences between unlogged, once-logged, and twice-logged forests; however, they found a lower abundance of environmental fungal ITS sequences in a logged forest than in an unlogged forest. Similar results have been found in a tropical forest in Brazil with lower abundance and richness of glomerospores in selective logging compared with a natural forest used as a control, as well as a differential effect between diameter and selective logging (Pereira et al. 2018). This reduction in abundance and richness might have a direct implication for tree recruitment and nutrient cycling (Kerfahi 2014).

Glomerospore-based studies are complementary to environmental sequences to provide an overall picture of biodiversity and are an important tool to understand the shift in the AMF community in perturbated soils (Sosa-Hernández et al. 2018; Vieira et al. 2018). The richness of glomerospores is generally higher in

tropical forests, with 228 species, representing 75% of the richness known worldwide (Marinho et al. 2018; Stürmer et al. 2018; Stürmer and Kemmelmeier 2021). Tropical forest tree species, including high-value commercial wood species, are mainly associated with AMF, and they have shown a positive effect on the establishment of seedling and plant growth (Tótola and Borges 2000; Pérez-Moreno and Negreros-Castillo 2011; Rajan et al. 2020; Falcón et al. 2021). However, AMF communities have shown clear differences in local communities, which are influenced by environmental variables, edaphic properties, and natural disturbances (Rodríguez-Echeverría et al. 2017). Unfortunately, few studies have been carried out in semi-evergreen tropical forests, especially those that comprise the Mesoamerican biological corridor (Polo-Marcial et al. 2021). The aims of this work were to analyse and compare the composition and diversity of bacteria and AMF in a tropical semi-evergreen forest with selective logging, conserved forest (medium and tall forest), and > 20-year-old secondary vegetation (seasonally inundated forest) in Nuevo Becal, Campeche, Mexico, based on environmental DNA sequences (16S rRNA and 18S rRNA gene for bacteria and AMF, respectively) and AMF morphological analysis.

We hypothesised that sustainable forest management in stands 6 years after selective logging does not have a significant effect on the soil microbiota (AMF and bacteria) in terms of their composition, abundance, and diversity in relation to a highly conserved forest. However, we expected that secondary forests would differ in alpha diversity and composition from managed and conserved forests, since comprised different vegetation and contrasting environments.

Materials And Methods

Study area

The communal lands of Nuevo Becal, Campeche, Mexico are located at 18°48’00” and 89°15’45” N 9°08’00” and 89°20’05” W and cover an extension of 52,800 ha (Fig. 1). The area is a continuum of the Calakmul Biosphere Reserve, the largest tropical reserve in the country, and an important biological corridor connecting in the south to the Maya Forest in northern Nicaragua and Belize. The area is a relatively flat relief, with an average elevation of 250 to 375 masl in the Zoh-Laguna plateau (Martínez and Galindo-Leal 2002). This region consists mainly of calcium carbonate platforms, and prevailing soils derived from the limestone parent material are shallow, young, and have poorly defined horizons (López-García et al. 1990). The predominant vegetation is represented by semi-evergreen forests that, according to tree height and phenology, are characterised by tropical tall-to medium-stature forests (≥ 25 m) with significant leaf loss between 25 and 50%, medium-stature forests with trees between 18 and 25 m high and seasonally inundated low-stature forests with trees between 8 and 15 m in height (Martínez and Galindo-Leal 2002; Henricus et al. 2007). The climate of the study area is characterised by average annual precipitation that ranges from 1100 to 1200 mm, with 600 mm of precipitation in the driest month, and an average annual temperature of 26°C, with wind from September to December (Martínez and Galindo-Leal, 2002). Common tree species include: *Swietenia macrophylla*, *Metopium brownei*, *Pseudobombax ellipticum*, *Bursera simaruba*, *Dendropanax arboreus*, *Manilkara sapota*, *Lonchocarpus castilloi*, *Bucida buceras*, *Brosimun allicastrum*,and *Lysiloma bahamensis*. Land

use in the communal lands of Nuevo Becal includes forest management (selective logging), natural conserved forest, chewing-gum production, secondary vegetation ≥20 years, and agriculture. At present, 25,000 ha are under permanent forest management, and in 2016, this area was certified following the criteria and indicators for sustainable forest management according to the standards of the Forest Stewardship Council (FSC).

Description of the study sites

Forest management is characterised by selective logging based on diameter, with a minimum cutting diameter between 35 and 55 cm diameters at breast height (DBH) and cutting cycles of 25 years, low harvest intensity with 20–30% wood extraction in logging blocks of 500 h per year. The soil samples were collected in areas with tree stands six years after selective logging. The vegetation type is classified into medium sub-evergreen forest, and primary harvested species include: *Swietenia macrophylla*, *Manilkara sapota*,and *Metopium brownie*.Natural forests are characterised by the minimum management of gum harvests or conserved forests. Secondary vegetation is abandoned land lacking agriculture-dominant species for 20 yearsand a low-sub-perennial-flooded forest vegetation type.

Soil collection and physicochemical analysis

The sites were chosen according to the geographic delimitation of forest use, natural conserved forest, and secondary vegetation. Soil collection was carried out in November 2020 during the rainy season. We collected 25 soil samples in each environment, and randomly selected seven independent soil samples according to the best DNA quality and quantity to sequencing (n =21), and 14 samples per glomerospores isolation in each study area (n =42). To avoid edge effects, the samples were collected at least 300 m from roads. We collected soil samples with a trowel at a depth of 20 cm. Freshly fallen leaves were carefully removed after sample collection, and approximately one kilogram of soil was collected in polyethylene bags. Soil samples were homogenised, and with the aid of spatula, a 50 ml falcon tube was filled with soil for DNA extraction. Trowels and spatulas were thoroughly rinsed with H_2O and cleaned with 70% alcohol among samples. The samples were kept refrigerated at −4°C and transported frozen to the laboratory, where they were stored in an −80°C ultrafreezer until processing.

The physicochemical characteristics of soil were determined using standardised methods. For organic matter and organic carbon, the methods reported by Walkley (1974) and Jackson (1976) were followed. Total nitrogen was evaluated following the methodology reported by Parsons et al. (1984), while calcium carbonate was determined following the protocol of Molnia (1974). The redox potential and pH were measured directly at the surface level of the sample, with the specific electrode for each parameter and an OAKTON mod. 300 series potentiometer.

DNA extraction and sequencing

DNA was extracted using the DNeasy PowerSoil Kit (QIAGEN, Hilden, Germany) according to the manufacturer's instructions. The quantity and quality of the DNA were determined using 1.5% agarose gel

and a Nanodrop 1000 (Thermo Scientific, USA). DNA was sent to the sequencing service of ZymoBIOMICS ™ to process and analyse the composition of bacteria (*n* = 21 samples) and fungi (*n* = 21 samples). The fungal 18S rRNA region was amplified using the fungus-specific primer pair AMV4.5NF (5' AAGCTCGTAGTTGAATTTCG 3') and AMDGR (5' CCCAACTATCCCTATTAATCAT 3') (Suzuki et al. 2021). For bacteria, the V3–V4 hypervariable region of the bacterial 16S rRNA gene was amplified. Briefly, the V3–V4 region of the 16S rRNA gene for bacteria and 18S rRNA for fungi was amplified using the Quick-16S ™ NGS Library kit (Zymo Research, Irvine, CA, USA) using the specific primers for each group. The library was quantified using real-time PCR in a mixture based on equal molarity to avoid the formation of chimeras. The final library mix was purified with the Select-a-Size DNA Clean and Concentrator ™ kit (Zymo Research, Irvine, CA) and then quantitated with TapeStation® and Qubit®. The final library was sequenced on Illumina® MiSeq ™ with Reagent Kit v3 (600 cycles). Representative sequences for each virtual taxa (VT) for fungi and amplicon sequence variant (ASVs) for bacteria are available on the NCBI website under Bioprojects PRJNA806153 and PRJNA808063, respectively.

Phylogenetic analysis

To determine the genera or families of Glomeromycota taxa, phylogenetic analysis was performed. A representative sequence for each VT in the study and sequences from the MaarjAM database (Öpik et al. 2010), and NCBI (www.ncbi.nlm.nih.gov) were used for multiple alignment with MAFFT version 7.149bv (Katoh et al. 2002). The phylogenetic tree was assembled using the neighbouring method with the MEGA 7 programme (Tamura et al. 2011) and the Kimura-2 model (Kimura, 1980). The bootstrap method (Felsenstein 1985) was used with 1000 replicates to support the branches. *Henningsomyces candidus* (AF334916) sequences were obtained from the GenBank database (www.ncbi.nlm.nih.gov) and used as an outgroup. VT with ≤ 95% sequence similarity that did not form a cluster corresponding to a known genus were considered potential new species (Jiang et al. 2018).

Glomerospore isolation and morphological identification

The glomerospores were extracted from 50 g of dry soil by the sieving and wet decanting method with a sucrose gradient (Błaszkowski 2012). Glomerospores were grouped by morphology and mounted with polyvinyl alcohol-lacto-glycerol (PVLG) and PVLG + Melzer (v / v). Morphospecies were identified using the specialised literature (Schenck and Pérez 1990; Błaszkowski 2012). We classified them following Wijayawardene et al. (2020), and we accepted the generic term *Rhizoglomus,* proposed by Sieverding et al. (2014) instead of *Rizophagus,* proposed by Schüßler and Walker (2010). We also adopted the terms glomerospores and glomerocarps (Goto and Maia, 2006; Jobim et al. 2019). The slide-mounted reference samples were photographed with PVLG and Melzer with a Nikon 7200 camera coupled with a light microscope adapter (Leica, Wetzlar, Germany) with a micrometre to estimate spore size.

Bioinformatic and statistical analyses

To estimate the diversity of fungi and bacteria, as well as the sampling effort, species accumulation curves and coverage curves were created for each environment using the iNEXT Online programme.

Alpha diversity (-diversity: Chao1, Shannon, and Simpson index) and beta diversity (β-diversity) were calculated to assess the diversity of AMF and bacteria. To identify differences in alpha diversity and soil chemical properties, we used the ANOVA test with the R platform using version 4.2.0, implemented with the RStudio graphical interface (RStudio Team, 2015). One-way ANOSIM permutation tests were used to analyse differences in the communities of AMF and bacteria in conserved, managed, and secondary forests. Subsequently, we visualised the compositional data using non-metric multidimensional scaling ordination (NMDS). Multivariate analysis was based on Bray–Curtis distances of AMF and bacteria composition and abundance using 9999 permutations and the Bonferroni correction of probabilities. Similarity percentages analysis (SIMPER) based on AMF and bacterial abundance was used to identify the contribution of each species to differences between sites using PAST version 4.03 software (Hammer et al. 2001). The diversity and overlap of AMF virtual taxa, glomerospores, and bacteria in the conserved forest, managed forest, and secondary vegetation were visualised in a bipartite network with R package BIPARTITE using the number of reads or glomerospores per site as a proxy for interaction frequency (Dormann et al. 2008). To evaluate the potential associations between microorganisms and the physicochemical variables of the soil, a redundancy analysis (RDA) was carried out using R software version 3.5.2. Significance in all statistical analyses was established at $\alpha < 0.05$.

Results

Soil chemical properties

The chemical properties in the conserved forest, secondary vegetation, and managed forest showed only statistical differences in potential redox (ANOVA $F = 5.27$; $p = 0.018$), with a higher measurement in secondary vegetation, followed by the managed forest and conserved forest (Table 1). The chemical variables, such as pH, organic matter, organic carbon, total nitrogen, and carbonates, did not differ between sites (Table 1). The pH was slightly alkaline (7.3–7.4) with a moderate content of organic matter (12–17%) and organic carbon (6.9–9.7%) and a high content of carbonates (22–27%).

Read processing and taxonomic assignment

After filtering raw data for high-quality Illumina sequences, we obtained 255,518 sequences of bacterial 16S rRNA genes (*n* = 17 samples successfully sequenced: 7 from conserved, 6 from managed, and 4 from secondary vegetation), 34,483 sequences for AMF 18S rRNA genes (*n* = 20 samples successfully sequenced: 7 from conserved, 6 from managed, and 7 from secondary vegetation), and 415 glomerospores (*n* = 42 samples: 14 from each site). The bacteria samples ranged from 8958 to 24,623 sequences (size ~400 bp), with an average of 15,310 per sample. The AMF varied from 218 to 8861 sequences (size: ~250 bp), with an average of 1723 sequences per sample. Bacteria sequences were assigned to 3963 ASVs, and phylogenetic analyses of AMF VT revealed 20 ribotypes with ≥ 97% identity in the gene databases, 10 ribotypes < 95% identity that represent new virtual taxa (Fig. 2), and 22 AMF species were found based on glomerospore morphology (Table 2; Fig. 3). The rarefaction curves based

on the ASVs and AMF VT show that all samples reached the saturation plateau, indicating that the sequencing depth was sufficient to reflect microorganism diversity (Fig. S1).

Microbial community composition

On average, the most abundant bacteria phyla across contrasting environments were Proteobacteria (45.7%) and Actinobacteria (25.3%), followed by Acidobacteria (10%), Verrucomicrobia (4.5%), Planctomycetes (3.3%), Nitrospirae (2.9%), Chloroflexi (2.9%), Bacteroidetes (2.2%), and Gemmatimonadetes (1.4%; Fig. 4A).

Forest management did not show a difference ($p > 0.05$) in the most abundant bacterial phyla (Proteobacteria) between conserved and secondary vegetation. The same result was also found for Acidobacteria, Planctomycetes, Nitrospirae, Bacteroidetes, and Gemmationonadetes (Table 3). However, in the second most abundant phylum, Actinobacteria, the conserved forest showed significantly ($p < 0.05$) higher relative abundance compared with managed forest and secondary vegetation. The phylum Verrucomicrobia was statistically ($p < 0.05$) higher in secondary vegetation compared with conserved and managed forests, and Chloroflexi was significantly higher in the managed forest (Table 3).

The dominant AMF VT were orders Glomerales (94.1%), Gigasporales (3.4%), and Diversisporales (2.3%) (Fig. 4B). The relative abundance of the order Glomerales was statistically higher ($p = 0.038$) in secondary vegetation compared with conserved and managed forests. However, the Diversisporales and Gigasporales did not differ statistically ($p > 0.05$) among conserved, managed forests and secondary vegetation (Table 3). According to spore morphology, Glomelares, Gigasporales, and Diversispores were no statistical differences in relative abundance among the sites analysed (Table 3).

The dominant AMF VT species throughout the study were Glomeromycota VT new 1, Glomeromycota VT new 2, Glomeromycota VT new 3, VTX130 (related to *Glomus*), and Glomeromycota VT new 4 (Fig. 4B). The dominant species of AMF was represented by *Dominikia* sp. 1, *Glomus* sp. 1, *Funneliformis* sp. 1, *Sclerocystis* sp. 1, *Glomus* sp. 2,and *Funneliformis halonatum* (Table 2).

Microbial community comparison

No significant differences were found in bacterial (ANOSIM: $R = 0.157$; $p = 0.061$; Fig. 4A) and glomerospore community composition (ANOSIM: $R = 0.004$; $p = 0.372$; Fig. 5C) among the three sites analysed. However, we found significant differences in AMF VT community composition between the conserved forest and secondary vegetation (ANOSIM: $R = 0.20$; $p = 0.035$; Fig. 5B). According to SIMPER analysis, the species that contributed the most to the differences between the conserved forest and secondary vegetation were VT new 1, VTX130, and VT new 4, with a dissimilarity percentage of 35%. The resulting Venn diagrams revealed a high number of bacterial ASVs in the forest management system (35.1%), followed by conserved (25.4%) and secondary vegetation (15.9%), with a core microbiome of 7.8% (Fig. 5D). AMF virtual taxa and glomerospores presented a higher number of shared species among the three systems (18%) and a lower number of unique species per site (Fig. 5E and F). The bipartite

network also showed high interaction with bacteria phyla and glomerospores in forest management, and high richness and abundance of AMF virtual taxa in secondary vegetation (Fig 6).

The relationship between microorganisms and the physicochemical variables of the soil was determined through redundancy analysis (RDA); however, the models were not statistically significant (physicochemical–Bacteria: F = 0.6106, p = 0.903; physicochemical–AMF VT: F = 01.0283; p = 0.4409; physicochemical–glomerospores: F = 0.8212, p = 0.616).

Microbial diversity

Bacterial ASV sequences, according - (Chao1 and Simpson; Fig. 7a and b) and β-diversity (Fig. 7d) did not differ across the three analysed environments (p > 0.05). However, bacteria in the managed forest had a significantly (F = 2.83, p = 0.045) higher Shannon index diversity compared to the conserved forest and secondary vegetation (Fig. 7c). Glomeromycota VT did not show significant differences (p > 0.05) in the three environments (Fig. 7e–h). Glomerospores showed higher Simpson and Shannon indexes (F = 5.24; p = 0.0096 and F = 5.73; p = 0.006, respectively) in the managed forest compared to the conserved forest and secondary vegetation (Fig. 7j and k) and showed significantly lowest β-diversity in secondary vegetation (F = 7.66, p = 0.0016: Fig. 7i).

Discussion

Mechanical activities associated with selective logging, the intensity of harvest, and the opening of holes in the canopy could cause a loss of biodiversity in the soil microbiota and change ecosystem multifunctionality (Sun et al. 2020; Lan et al. 2021). Due to its low impact on natural forests, Yucatán Peninsula, Mexico has good forest management, and this is considered a good strategy to conserve biodiversity (Ellis and Porter-Bolland 2008).

Our study supported the hypothesis that stands 6 years after selective logging were not affected by a reduction of bacterial and AMF diversity (richness, Shannon, and Simpson's indexes) compared to the conserved forest and 20-year-old secondary vegetation recovered from agriculture. In contrast, we found a higher diversity of bacteria and glomerospores in the managed forest compared with the conserved forest and secondary vegetation. This result may be because in the selective logging areas there is more intensity of light, microclimates, and different levels of soil moisture, and as part of the management, there is an accumulation of organic matter that can favour the fungal community of microorganisms (Tomao et al. 2020). The high richness of soil microbiota in a forest with anthropogenic intervention is congruent with the low harvest intensity that left 77% intact forest in logging blocks in the Yucatan Peninsula (Putz et al. 2019). This also suggests that some species of AMF are resilient and can exploit conditions of anthropic disturbance (García de León et al. 2018). However, this still requires long-term analysis of biodiversity because vegetation structure in harvest areas changes according to market demand for soft and hardwoods, which might change the richness and abundance of soil microbiota. The analysis should be extended to those sites with twice-logged forests, where a lower abundance of environmental fungal ITS sequences has been recorded (Kerfahi 2014).

As we expected, there were differences in the community structure of the AMF VT in the contrasting sites with the conserved forest and secondary vegetation, but no differences in the community structure of AMF VT between managed and conserved forests. Secondary vegetation is characterised by short-stature forest, is seasonally flooded, and has a different function compared with tall and medium-stature forests (conserved and managed forests), and we found that it harbours distinct mycorrhizal fungal communities, similar to Davison et al. (2020). In this type of vegetation, we recorded a high abundance of potential new VT and high richness compared with the conserved forest, which could be important for Glomeromycota and bacterial conservation.

In the overall study, AMF VT represented 18.63% (30 VT) of the glomerospore richness recorded for Mexico, and 8.7% worldwide, and based on glomerospore morphology represented 13.6% (22 species) and 6.4% worldwide (Chimal-Sánchez et al. 2021; Polo-Marcial et al. 2021; www.amf-phylogeny.com). The state of Campeche, Mexico, has been poorly sampled for AMF diversity analysis, with only two species recorded: *Sclerocystis sinuosa* and *Rhizoglomus intraradices* (Zulueta et al. 2010). In this context, the species *Glomus clavisporum*, *Glomus spinuliferum*, *Funneliformis halonatum*, *Sclerocystis coremioides*, and *Racocetra fulgida* constitute a new state record for the state of Campeche, Mexico.

Throughout the study, the dominant AMF species were the order Glomerales and Diversisporales, with more than 90% of the species, which is in accordance with previous field studies (Öpik et al. 2013; Davison et al. 2015). This result was expected because both Glomerales and Diversisporales are dominant in most ecosystems in Mexico (Polo-Marcial et al. 2021). Interestingly, the genus *Acaulospora* was poorly represented in the semi-evergreen forest despite having been a co-dominant genus with *Glomus* in agroecosystems and natural vegetation in Mexico (Polo-Marcial et al. 2021). However, seasonal variation studies and implementation of AMF trap cultures are still needed to complete the inventory of AMF, so the richness observed here could be wider. AM fungi are dynamic and may experience seasonal variation, and AMF trap cultures can increase the number of detected species compared to field soil samples (Bever et al. 2001; Leal et al. 2009; Drumbrell et al. 2011; Lara-Pérez et al. 2020), mainly in those species of ephemeral or rare sporulation (Błaszkowski et al. 2015; Corazon-Guivin et al. 2019).

Bacteria ASVs were best represented by Proteobacteria and Actinobacteria, which contributed more than 70% of bacterial richness. Less abundant (< 1%) phyla in the study were Acidobacteria, Verrucomicrobia, Planctomycetes, Nitrospirae, Chloroflexi, Bacteroidetes, and Gemmatimonadetes. This result is in concordance with Pacchioni et al. (2014), who also found that Proteobacteria and Actinobacteria are abundant in the Atlantic Forest and Caatinga biomes in north-eastern Brazil.

Acidobacteria and Proteobacteria are the most abundant and widely distributed bacterial groups in different soil environments (Janssen 2006). In contrast to the present study, Acidobacteria only represented 10% of the sequences obtained. The most abundant phylum, Proteobacteria, together with Acidobacteria, Planctomycetes, Nitrospirae, Bacteroidetes, and Gemmationonadetes, were stable between the three analysed sites. This could be explained because there were no significantly contrasting soil

chemical properties in the three different environments, including pH and nitrogen, that could affect Acidobacteria and Nitrospirae, respectively (Zhalnina et al. 2015). Proteobacteria, Actinobacteria, and Acidobacteria had an important influence on network structure, and some groups of the two latter phyla are keystone taxa in tropical rainforest soils and rubber plantations (Lan et al. 2021). The most abundant phyla found in tropical evergreen forests may contribute synergically to nutrient cycling and complement plant nutrition and growth (Horner-Devine et al. 2004; Naccon et al. 2020). Consequently, conservation of microbiota is fundamental to maintaining forest ecosystem multifunctionality (Lan et al. 2021).

Actinobacteria were the only phyla significantly more abundant in conserved forests than in managed forests. Actinobacteria reduction could influence ecosystem health and plant growth. Some genera of Actinobacteria play crucial roles in nutrient cycling and as beneficial symbionts, and they intervene in humic formation that can affect soil nutrition. Some species exhibit antibiotic plant growth regulatory activity, so a reduction of these groups can also alter plant health (Strap et al. 2011; Hamedi and Mohammadipanah 2015). Considering the important contribution to soil microbiota on the ecosystem's ecological role, it is necessary to analyse the main functions of the different genera that comprise Actinobacteria to gain a better understanding of the benefits in managed forest soils.

Verrucomicrobia were most abundant in secondary vegetation, and Chloroflexi were most abundant in the managed forest. Most information on the ecology of Verrucomicrobia abundance with environmental parameters indicates that soil moisture significantly changes community structure in natural ecosystems (Buckley and Schmidt 2001). Secondary vegetation is flooded part of the year, and this could affect Verrucomicrobia abundance. Verrucomicrobia are an important component of terrestrial and aquatic ecosystems and are widely distributed around the world (Buckley and Schmidt 2001). Despite their abundance in different environments, there is a poor understanding of the ecological significance of this phylum. However, current studies have recorded species association inside roots and found that it promotes root growth function in rice (Bünger et al. 2020). Trivedi et al. (2016) concluded that, on a global scale, Chloroflexi have been more abundant in anthropogenic systems compared with natural systems, which is in agreement with this study.

Conclusions

This study analysed the diversity in tropical evergreen forests in conserved forests, stands 6 years after selective logging and 20-year-old secondary vegetation, using high throughput sequencing with 16S rRNA for bacteria and 18S rRNA for Glomeromycota and taxonomic morphology based on glomerospores. We did not find evidence of the reduction of diversity in selective logging, except for the β diversity of the fungal community for glomerospores, which was lower in secondary vegetation. Conversely, we found a higher diversity of bacteria and glomerospores in the managed forest compared with the conserved forest and secondary vegetation. Community structure was only different in the AMF VT in the conserved forest and secondary vegetation, but no differences were found in the AMF VT and bacteria in managed forest with conserved sites. However, at the phylum level, we found that Actinobacteria were significantly most abundant in conserved forests, Chloroflexi in managed forests, and Verrucomicrobia in secondary

vegetation. Actinobacteria and Proteobacteria were the dominant bacteria phyla, and for the AMF, the Glomerales and Diversiporales were the dominant orders in tropical conserved evergreen forest, selective logging areas, and secondary vegetation. Secondary vegetation and the managed forest together may contribute to bacteria and Glomeromycota conservation. Further investigations are needed to analyse changes in the Actinobacteria genus, the second most abundant phylum, that could have an effect on the functionality of the forest in selective logging areas.

Declarations

Author contribution statement

CPH contribute to conceptualization, methodology, visualization writing- original draft preparation, formal analysis. MHP Methodology, writing- Reviewing and Editing MQM and ACM contribute to formal analysis and visualization. DEA and BZP Methodology, Writing- Reviewing and Editing. SGG Formal analysis. EGG and MMS edit the manuscript and provided additional expertise. LALP contribute to conceptualization, methodology, visualization, formal analysis, supervision, writing- original draft preparation, project administration, funding acquisition. All authors approved the final version of the manuscript.

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Consent for publication All authors consent to publication.

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Tables

Table 1. Chemical properties of the soils along conserved, management and secondary vegetation in Nuevo Becal, Campeche, Mexico

Atributes	Conserved	Management	Secondary	F
REDOX (mV)	94.1 ± 12.8^{b}	118.2 ± 5^{b}	131.8 ± 4.1^{a}	5.2*
pH	7.3±0.12	7.4±0.06	7.3±0.12	0.53^{ns}
MO %	17.5±2.8	15.1±0.9	12.4±1.2	1.8^{ns}
OC %	9.7±1.5	8.4±0.5	6.9±0.6	1.8^{ns}
Carbonates %	27.1±3.7	24.6±6.5	22.2±4.6	0.2^{ns}
Total nitrogen µmol/g	438±60	604±27	558±63	2.6^{ns}

Average values of three technical samples. Different letters on the column are significant different (ANOVA and Tukey test). MO: denotes organic matter; OC: organic carbon

Table 2. Relative abundance of arbuscular mycorrhizal fungi associated with conserved, secondary and managed forests. RA=Relative abundance.

Species	RA Conserved	RA Secondary	RA Management
Acaulospora sp. 1	0	0	0.01
Acaulospora sp. 2	0	0	0.04
Diversispora sp. 1	0	0.04	0.02
Glomus clavisporum	0	0	0.02
Glomus sp .1	0	0.03	0.07
Glomus spinuliferum	0	0	0.02
Glomus sp. 2	0.17	0.11	0.10
Glomus sp. 3	0.01	0	0.03
Glomus sp. 4	0	0.03	0.01
Glomus sp. 5	0	0	0.04
Glomus sp. 6	0	0.24	0.09
Glomus sp. 7	0	0.01	0
Dominikia sp. 1	0.36	0.28	0.36
Funneliformis halonatum	0.09	0.03	0.01
Funneliformis sp. 1	0.23	0.07	0.02
Halonotospora sp. 1	0.01	0	0
Septoglomus sp. 1	0.03	0.02	0
Rhizoglomus sp. 1	0	0	0.05
Sclerocystis coremioides	0	0.07	0
Sclerocystis sp. 1	0.07	0.01	0.10
Gigaspora sp. 1	0.02	0.04	0
Racocetra fulgida	0.03	0	0.02
Total	10	13	17

Table 3. Relative abundance (%) of most abundant (>1%) soil bacteria phylum, arbuscular mycorrhizal fungi virtual taxa and glomerospores (Mean±SE) asociated with conserved forest, forest management and secondary vegetation. Different letters on the column are significant different (Kruskal–Wallis test).

Bacteria phyla	Conserved	Management	Secondary	P=value
Proteobacteria	45.3±3.1	48.3±2.6	46.1±3.4	0.762
Actinobacteria	32.3±20[a]	24.3±1.8[b]	22.3±1.5[b]	**0.022**
Acidobacteria	6.6±1.1	10.6±1.5	11.6±0.7	0.079
Verrucomicrobia	4.4±1.0[b]	2.6±0.4[b]	6.5±1.8[a]	**0.037**
Planctomycetes	2.9±0.6	3.4±0.2	3.5±0.5	0.942
Nitrospirae	1.5±0.4	2.6±0.8	3.6±0.8	0.303
Chloroflexi	1.8±0.3[b]	3.3±0.2[a]	1.9±0.3[b]	**0.019**
Bacteroidetes	1.26±0.2	1.5±0.2	1.0±0.2	0.256
Gemmatimonadetes	1.7±0.5	2.4±0.3	1.9±0.2	0.241
Glomeromycota VT orders				
Glomerales	92.4±4.3[b]	90.8±1.8[b]	96.9±0.7[a]	**0.038**
Diverisporales	2.5±1.6	4.7±2.2	2±0.6	0.448
Gigasporales	2.9±1.9	4.1±2	2±0.6	0.779
Glomerospores order				
Glomerales	92.2±4.3	86.9±6.0	92±3.6	0.816
Diversisporales	0	4.7±3.2	5.4±3.4	0.679
Gigasporales	7.7±4.3	8.3±5.7	2.4±1.8	0.828

Figures

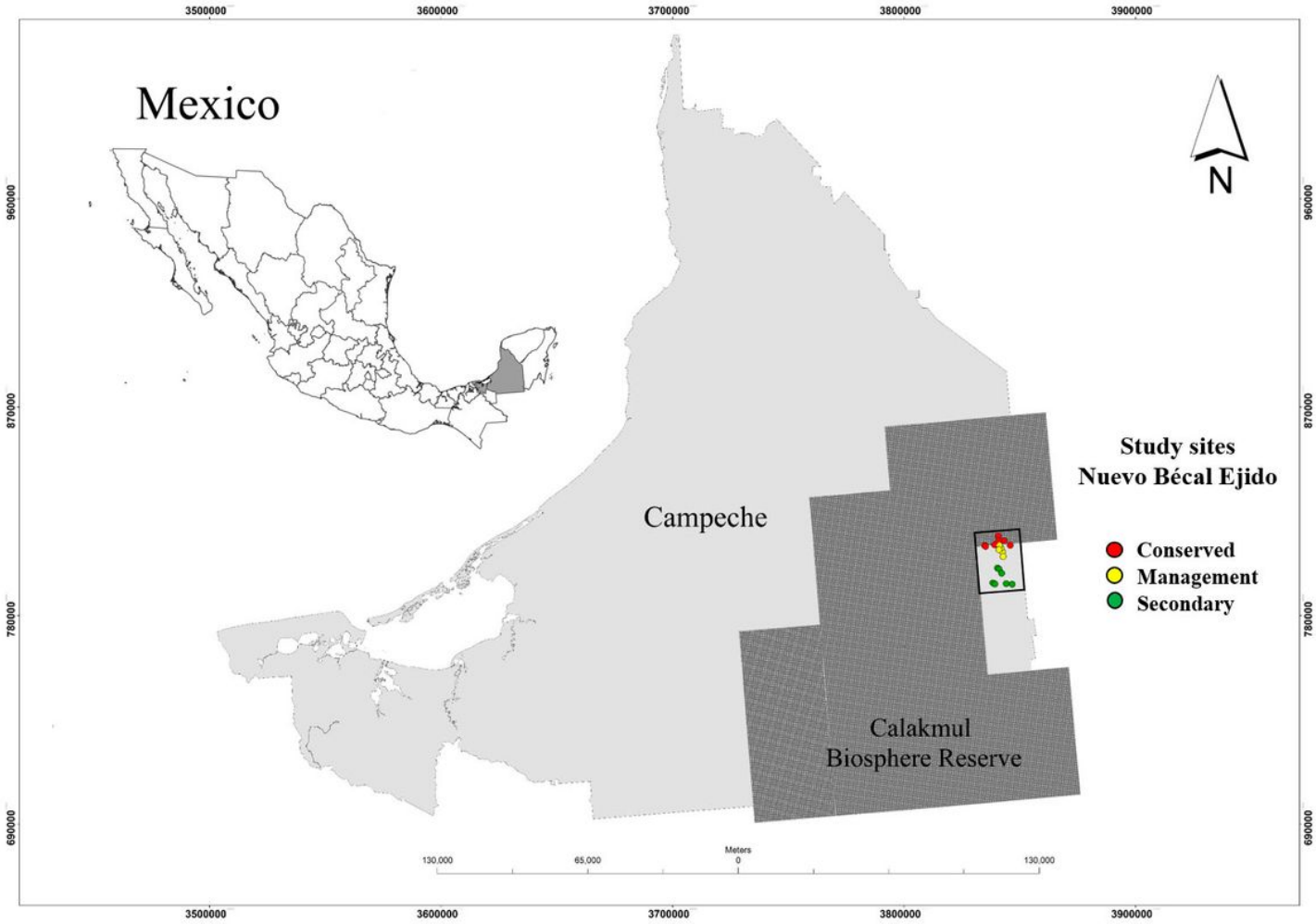

Figure 1

Location of the study area in Nuevo Becal, Campeche, Mexico.

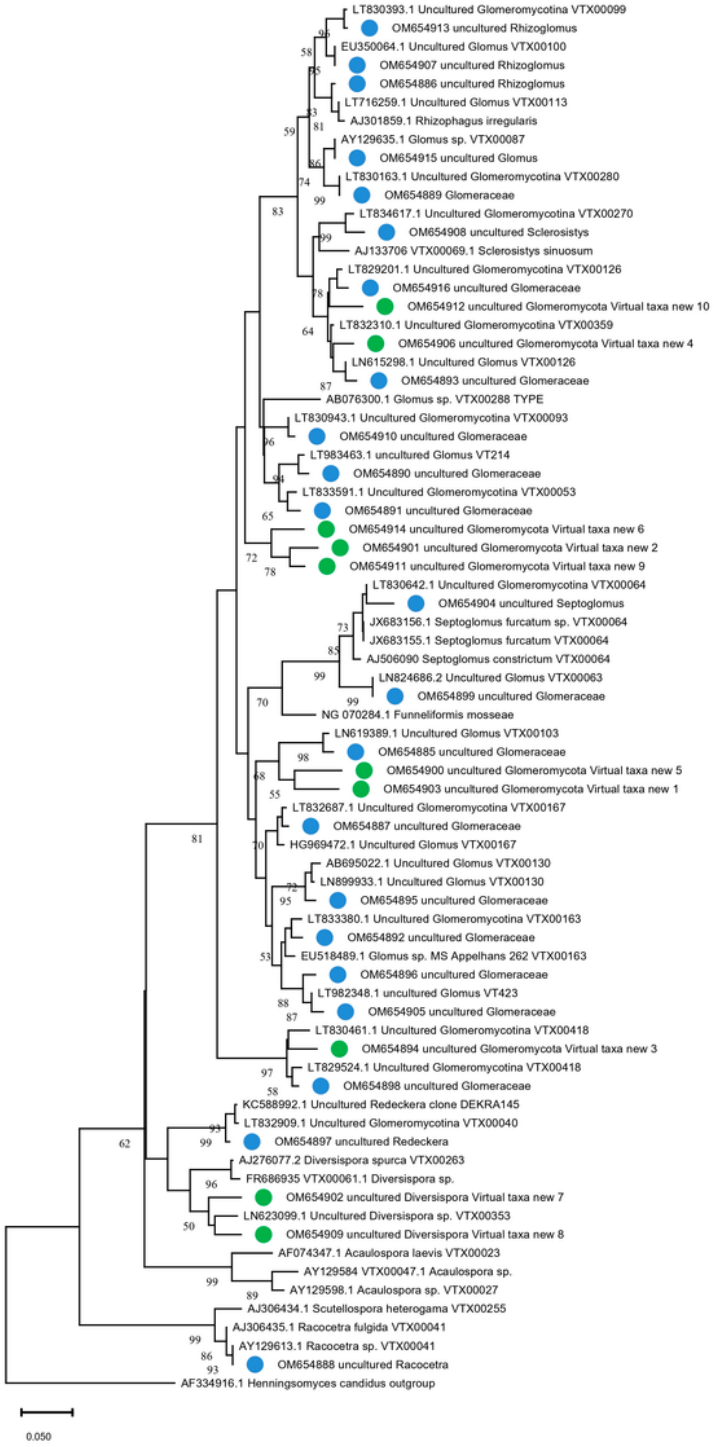

Figure 2

Phylogenetic tree of representative sequences of arbuscular mycorrhizal fungi virtual taxa associated with conserved forests, forest with management and secondary vegetation in the Nuevo Becal ejido, Campeche, Mexico. Reference sequences from the MaarjAM database (Öpik et al. 2010) and NCBI (www.ncbi.nlm.nih.gov). Bootstrap support values >50 (999 iterations) is shown. Green circles represent

species with ≥ 97% similarity to the MaarjAM base, and blue circles represent potential new species with <97% in the MaarjAM base.

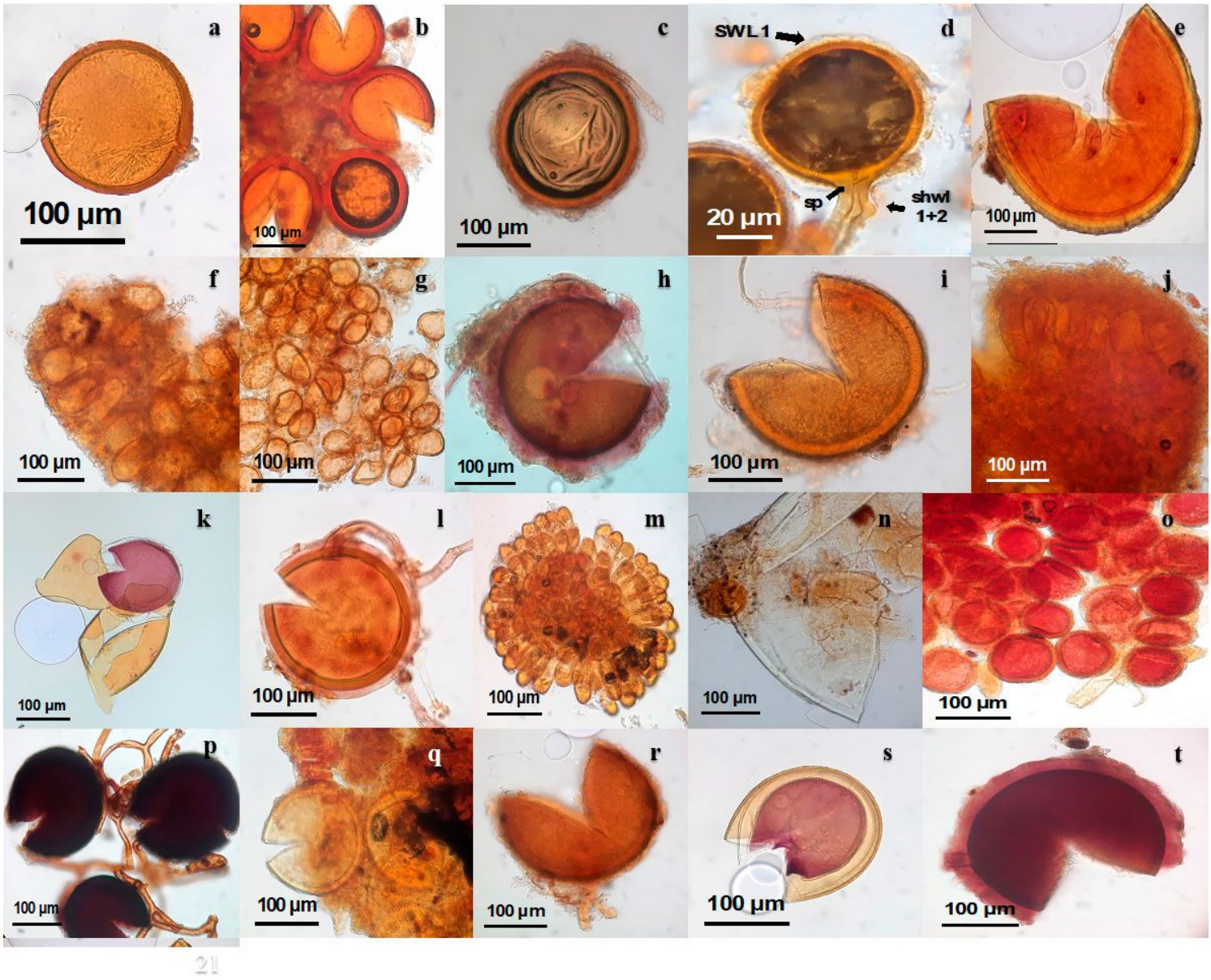

Figure 3

Representative glomerospores associated with conserved forest, forest management and secondary forest. a) *Diversispora* sp. 1, b) *Glomus* sp. 2, c) *Glomus* sp. 3, d) *Dominikia* sp. 1, e) Gigaspora sp. 1., f) *Sclerocystis* sp. 1, g) *Glomus* sp. 4, h) *Funneliformis halonatum*, i) *Glomus* sp. 5, j) *Sclerocystis* aff. *coremioides*, k) *Acaulospora* sp. 1, l) *Funneliformis* sp. 1, m) *Glomus clavisporum*, n) *Racocetra fulgida*, o) *Glomus* sp. 6, p) *Septoglomus* sp. 1, q) *Glomus* sp. 7, r) *Glomus spinuliferum*, s) *Acaulospora* sp. 2, t) *Halonatospora*-like.

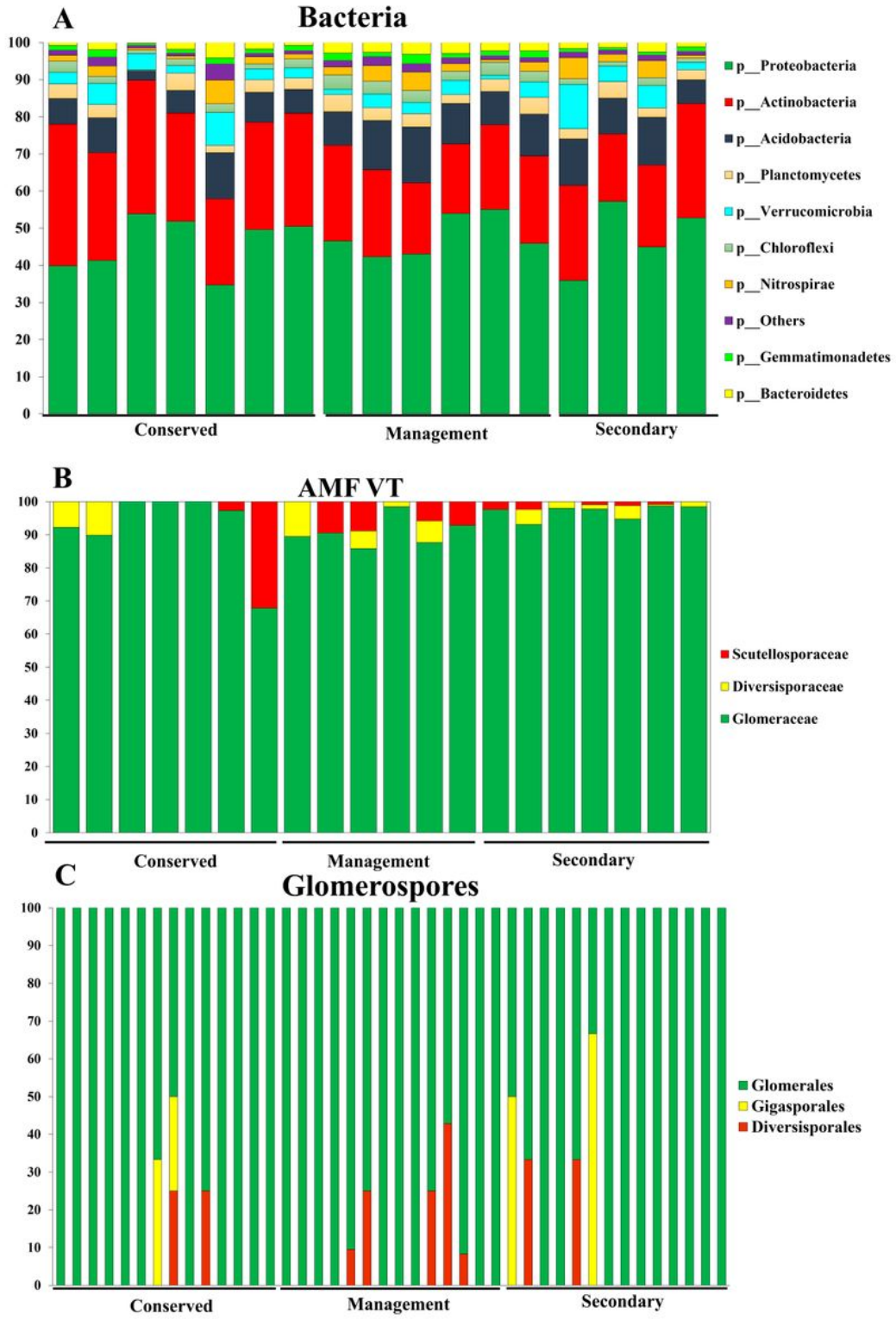

Figure 4

Composition of microbial communities in conserved forest, management and secondary vegetation. A) Relative abundance bacteria at phylum level, B) Relative abundance arbuscular mycorrhiza fungi virtual taxa at family level, C) Relative abundance of Glomerospores at order level.

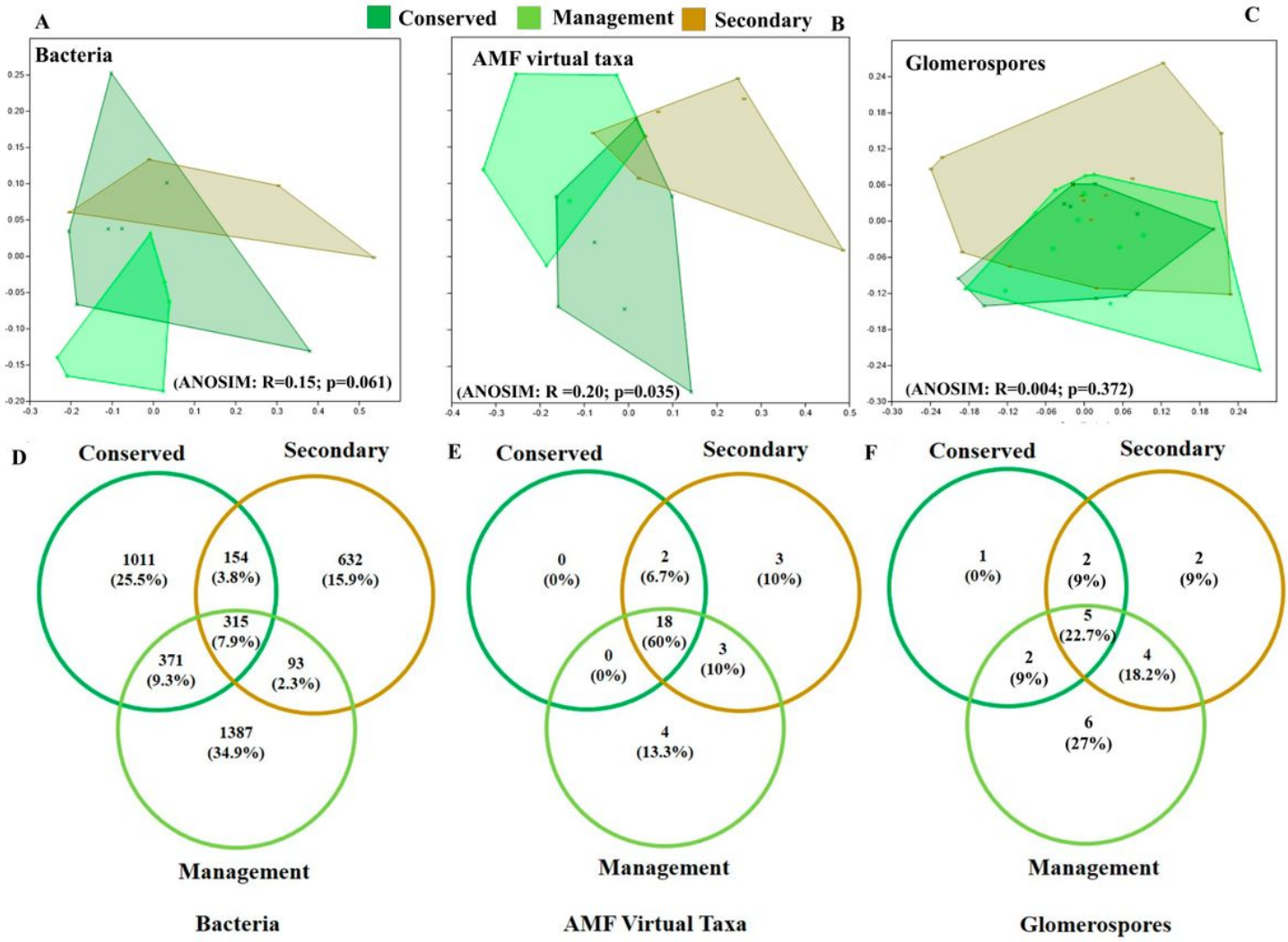

Figure 5

Non-metric multidimensional scale ordering based on Bray-Curtis distances and Venn diagram of A) bacteria B) AMF virtual taxa and C) Glomerospores associated with conserved forests (conserved), forest management (management) and secondary vegetation (secundary) in the Nuevo Becal ejido, Campeche, Mexico.

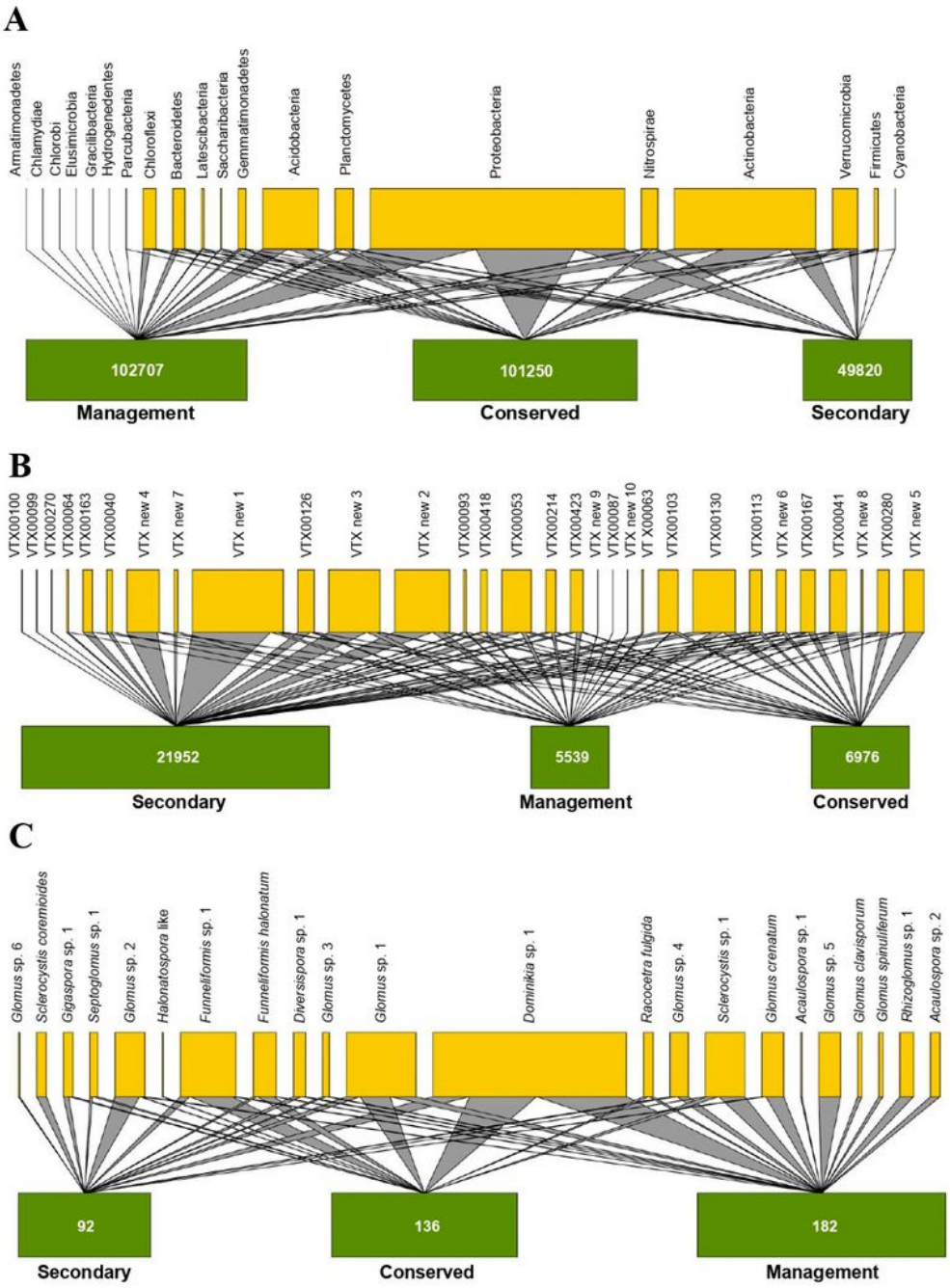

Figure 6

Bipartite network that represents the diversity and abundance of a) AMF virtual taxa. b) Glomerospores and c) bacteria phyllum associated with conserved forests, forest management and secondary vegetation in the Nuevo Becal ejido, Campeche, Mexico. Each box in the upper level represents a species of AMF or bacteria phyllum that is linked to the habitat (s) where it was found (boxes in the lower level).

The width of each AMF and bacteria taxon and habitat box is proportional to the number of reads or abundances of glomerospores for each habitat, respectively.

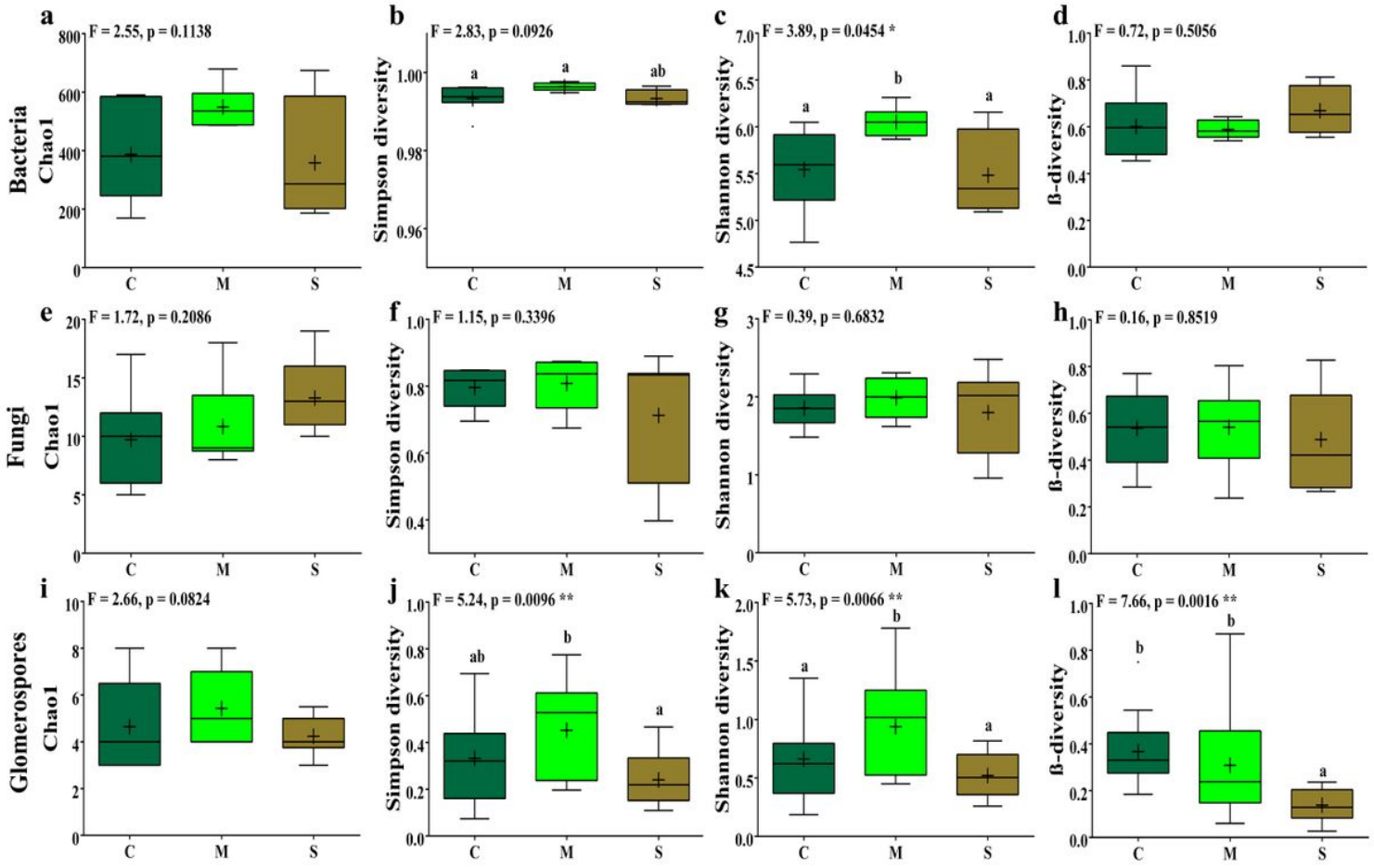

Figure 7

Microbial diversity of bacterial (a-d) and fungal (e-h: DNA sequences; i-l: glomerospores) measurements of soils under different successional stages. C) Conserved forest; M) Forest management; S) Secondary vegetation.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- FigureS1.docx