



Resilience of soil aggregation and exocellular enzymatic functions associated with arbuscular mycorrhizal fungal communities along a successional gradient in a tropical dry forest

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Received: 22 August 2019 / Accepted: 20 November 2019 / Published online: 13 December 2019
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Abstract

Arbuscular mycorrhizal (AM) fungi are well-known contributors to soil aggregation and nutrient cycling functions, but we still know little about their capacity to resist or recover from persistent disturbance. Rangeland management may deteriorate these functions by affecting the activity of soil biota, including AM fungi, among other consequences. If affected, some soil properties show recovery when management stops and natural regeneration is allowed. We conducted an experiment to evaluate if the functions related to soil aggregation and promotion of exocellular enzymatic activities associated with AM fungal communities had been affected by rangeland management and, if they had, whether they recovered with successional time when management stopped. AM fungal communities from ten sites with different successional ages in a tropical dry forest region were inoculated to the same host growing in pots divided by mesh into a plant compartment and an AM mycelium compartment. We examined soil stable aggregates fractions and enzymatic activities produced or promoted by AM fungi. Soil aggregation changed significantly only after the study had run for 3 years, was higher in the hyphosphere than in the root compartment, and showed a low but positive relation with the successional age of the communities. The activity of phosphatase, but not casein-protease and beta-glucosidase, increased with successional age. Therefore, soil aggregation and enzyme activities associated with AM fungal communities seemed resilient because casein-protease and beta-glucosidase were unchanged, and aggregation and phosphatase were reduced by rangeland management but recovered with successional time.

Keywords Mycorrhiza · Rangeland · Resistance · Recovery · Succession · Tropics

Introduction

Soil aggregation is a key, complex process in ecosystems (O'Neill et al. 1991) that integrates soil physical, chemical, and biological properties and is the basis of other processes such as water retention and nutrient cycling (Rillig 2004; Dominati et al. 2010). Soil aggregates maintain porosity, reduce erosion, store carbon, and are good indicators of soil

quality (Dighton 2003). Highly dynamic microbial concentrations in soil aggregates participate in nutrient cycling by decomposing complex organic polymers (Kandeler 2015) through the activity of exoenzymes produced mainly by fungi and bacteria (Dick 2011; Plante et al. 2015).

Arbuscular mycorrhizal fungi (AMF) contribute significantly to soil aggregation and nutrient cycling (Lehmann et al. 2017). Arbuscular mycorrhizal (AM) fungal mycelium physically entangles soil particles and debris and secretes exudates rich in organic carbon, exoenzymes, and binding proteins (Rillig and Mummey 2006). Additionally, mycelium interacts with roots and soil microorganisms and together they promote soil aggregation and nutrient cycling by establishing a network that stabilizes soil (Jastrow et al. 1998; Rillig et al. 2002, 2005). Although plants possess a high capacity to aggregate soil, AMF and other soil biota significantly increase this capacity and can extend it to soil areas far beyond roots (Hallet et al. 2009). Agriculture and rangeland management may, however, disrupt the aggregation process and

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00572-019-00928-9>) contains supplementary material, which is available to authorized users.

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exoenzymatic activities associated with soil aggregates (Waldrop et al. 2000; Arriagada et al. 2012; Camenzind and Rillig 2013) either directly by disturbing the soil or indirectly by changing the plant communities and environmental conditions. As opposed to a large body of evidence for the effects of agricultural management on the contribution of AMF to soil aggregation and enzymatic activity related to cycling functions, the effects of rangeland management practices are largely unexplored. This knowledge gap is particularly relevant to regions where extensive cattle-ranching is a common practice, as extensive rangelands have been associated with soil and vegetation degradation (Pulido et al. 2016). Extensive, induced pastures in the tropics are especially prone to rapid degradation as a consequence of burning, compaction, erosion, overgrazing, and the imbalance caused by low return of carbon and nutrients to the soil (Costa et al. 2015).

Establishment of pastures for extensive cattle ranching is one of the main drivers of the continuous land use and land cover change in the tropics (Miles et al. 2006). These induced pastures are often abandoned after some years because of a decrease in pasture quality, low profitability of extensive rangelands, and high costs of pasture maintenance under harsh environmental conditions (Trilleras et al. 2015). Smallholders use fallow periods in an attempt to restore productivity, but prolonged, undisturbed natural regeneration is rarely allowed (Burgos and Maass 2004). Some soil properties are known to recover rapidly when management stops, such as organic matter and available nitrogen, but others like soil compaction and available P may not, or recovery may take several decades (Brevik and Fenton 2012; Duchicela et al. 2013; Ayala-Orozco et al. 2017), suggesting that the biotic or abiotic factors or conditions required to restore the functions supporting those properties were temporarily or permanently lost. Nevertheless, the resilience of soil microorganisms and of ecosystem functions and processes involving soil microorganisms to land use change and land management has been poorly investigated (Waring et al. 2016; Teste and Dickie 2017). AM fungal communities and functions being no exception.

Recent studies conducted in the dry tropics of the Pacific coast of Mexico have suggested that several soil and vegetation properties, including AMF abundance (Ayala-Orozco et al. 2017) and diversity (Carrillo-Saucedo et al. 2018), seem resilient to management as extensive pastures. AM fungal community phylogenetic structure, species richness, and diversity indexes showed minor changes along a successional gradient from active pastures to old-growth forests, suggesting resistance to pasture management (Carrillo-Saucedo et al. 2018). These findings of AM fungal communities showing few species replacements and an invariant proportion of species in the families of Glomerales and Diversisporales suggested that the functions performed by those AM fungal communities also might be resistant to pasture management and might remain unaltered along the successional gradient.

Thus, this study aimed at testing if two functions influenced by AM fungal communities (soil aggregation and promotion of enzymatic activity) had resisted or had been reduced by management as extensive pastures. If they had been reduced, did they recover along successional time or remain reduced? We hypothesized that pasture management might have decreased aggregation and exocellular enzyme promotion capabilities associated with AM fungal communities because of the selection of AM fungal species caused by vegetation changes, grazing, and burning in comparison with unmanaged sites. We expected, however, that the resilience already documented in AM fungal community phylogenetic composition would support either the resistance of AM fungal community functional capabilities or their recovery along successional time. We used a community level, rather than a species level approach, given that it is expected that AM fungal communities in each successional site have reached a composition that reflects their interaction with local biotic and abiotic factors integrated along time, and thus reflects the effects of those compositional changes on the ecosystem processes or functions performed by these organisms (Koide et al. 2013).

Materials and methods

We conducted a pot experiment that allowed us to use the same soil, host, and environmental conditions, to evaluate the functions performed by different AM fungal communities and to physically separate the plant and the AMF capabilities. It was a factorial design with two factors, AM fungal community and compartment. AM fungal communities were obtained from two active pastures with more than 15 y under this land use, six sites with secondary vegetation of different successional ages ranging from 6 to 34 years, and two old-growth forests (OGFs) located in a tropical dry forest region on the Pacific coast in Jalisco, Mexico (Table 1). The sites and the morphospecies composition of the AM fungal communities were described in detail in Carrillo-Saucedo et al. (2018). We used 25 kg pots, 60 cm diameter and 30 cm height, divided into a plant compartment and a mycelium compartment by gluing two layers of 35 μm plastic mesh across the middle of the pot. We used the same soil, a local haplic cambisol (WRB classification), sandy, with pH 6.8, 2.8% soil organic matter, 0.13% total N, 691 $\mu\text{g/g}$ total P, and 8.2 $\mu\text{g/g}$ available P (Mehlich 3), collected from a pasture site in the region where the other communities were collected. Mineral soil was collected from the top 20 cm with a shovel at random points, mixed thoroughly, and sieved through a 4-mm mesh to remove stones and coarse roots. Then, the soil was disinfected of mycorrhizal propagules by two periods of heating to 100 °C for 8 h, followed by 12 h of aeration by mixing it regularly with a shovel. Once completely cooled to ambient

Table 1 Characteristics of the sites from which AM fungal communities were collected

Current land cover	Latitude N and longitude W	Land use history after tropical deciduous forest	Vegetation richness (spp)	
			Woody (0.1 ha)	Herb (1 m ²)
Active pasture	19° 35' 43.00" 105° 02' 31.28"	Slash and burn Agriculture (2 y) Pasture (15 y) Successional (0 y)	10	20
Active pasture	19° 33' 58.28" 105° 04' 30.61"	Slash and burn Pasture (34 y) Successional (0 y)	15	32
Early successional	19° 34' 51.20" 105° 03' 38.20"	Slash and burn Pasture (30 y) Successional (6 y)	24	30
Early successional	19° 36' 02.50" 105° 03' 37.30"	Slash and burn Alternating 1 y agriculture after 5–6 y pasture, for 22 y Successional (8 y)	15	22
Intermediate successional	19° 35' 32.80" 105° 00' 32.70"	Slash and burn Agriculture (1 y) Pasture (17 y) Successional (19 y)	25	32
Intermediate successional	19° 35' 55.20" 105° 02' 53.50"	Slash and burn Alternating 1 y agriculture after 5–6 y pasture, for 19 y Successional (21 y)	30	25
Late successional	19° 38' 47.73" 105° 10' 31.13"	Bulldozer slash Pasture (6 y) Successional (34 y)	36	ND
Late successional	19° 37' 29.30" 105° 09' 18.70"	Bulldozer slash Pasture (6 y) Successional (34 y)	32	ND
Old-growth forest	19° 30' 3.70" 105° 02' 35.30"	Mature forest protected since the 1970s	23	22
Old-growth forest	19° 29' 56.20" 105° 02' 29.80"	Mature forest protected since the 1970s	27	27

Vegetation species richness obtained from Romero-Duque et al. (2007), Ocampo (2012), Mora et al. (2014), Trilleras et al. (2015). ND, not determined

temperature, the pots were filled with a mixture of 18 kg of the disinfected soil and 7 kg of soil containing the AM fungal community to be tested. Soil used to inoculate the AM fungal communities was collected from 0 to 20 cm depth, from 15 points in each site, 5 points at the high, middle, and low parts of the slope, approximately 10 m apart from each other, because all sites are located on hillsides (Carrillo-Saucedo et al. 2018). The soil was mixed thoroughly to form a composite sample for each site and was sieved through a 4-mm mesh before mixing with the disinfected soil. There also was a control treatment with no AM fungal community that received only disinfected soil.

We prepared five replicates of each AM fungal community and transferred pots to benches in an open plant nursery at Chamela Biology Field Station, within the Biosphere Reserve Chamela-Cuixmala in Jalisco, which has very similar rainfall and temperature conditions to the field sites from which the AM fungal communities were collected. We produced seedlings of *Caesalpinia eriostachys*, a perennial, woody, non-N-fixing, legume species with wide distribution in the region. Seeds were germinated in sterile sand and later transplanted as hosts to the plant compartment of each pot. Two seedlings were planted at the beginning of the rainy season and maintained in each pot until they were well established and then thinned to one. Pots were watered regularly during the first 4 months to ensure the survival of the

plants and the establishment of AMF in the pots. Weak or dying plants were replaced by new ones until stable establishment was complete. Afterwards, the pots were no longer watered; they were covered with a layer of coarse gravel to prevent growth of moss and algae and were maintained with the local temperature, photoperiod, and rainfall for the rest of the experiment (Fig. 1). Thus, pots dried out and host plants shed their leaves during the dry seasons and plants resumed growth in each rainy season for 3 years until completing three rainy seasons with active growth. Hand weeding was used regularly to prevent the establishment of other plants.

Samples were taken 279, 606, and 985 days after planting with a 3-cm diameter soil borer from 0 to 15 cm depth in each compartment. They were placed in 50-ml centrifuge tubes, allowed to air-dry, and stored until processing. Sand-free, water-stable macroaggregate fractions ≥ 1 mm and 0.25–1 mm, and microaggregates and other particles < 0.25 mm, were determined according to Angers et al. (2006). After repeated immersions in water, the fractions retained on sieves were dried to constant weight, dissolved in KOH solution, sieved, dried, and weighed again to subtract non-cementing particles. In the last sampling, a second sample was taken from each compartment and split in two parts. One was used for fatty-acid extraction and was frozen immediately, and the other was used for enzymatic activity assessment, and was kept refrigerated.

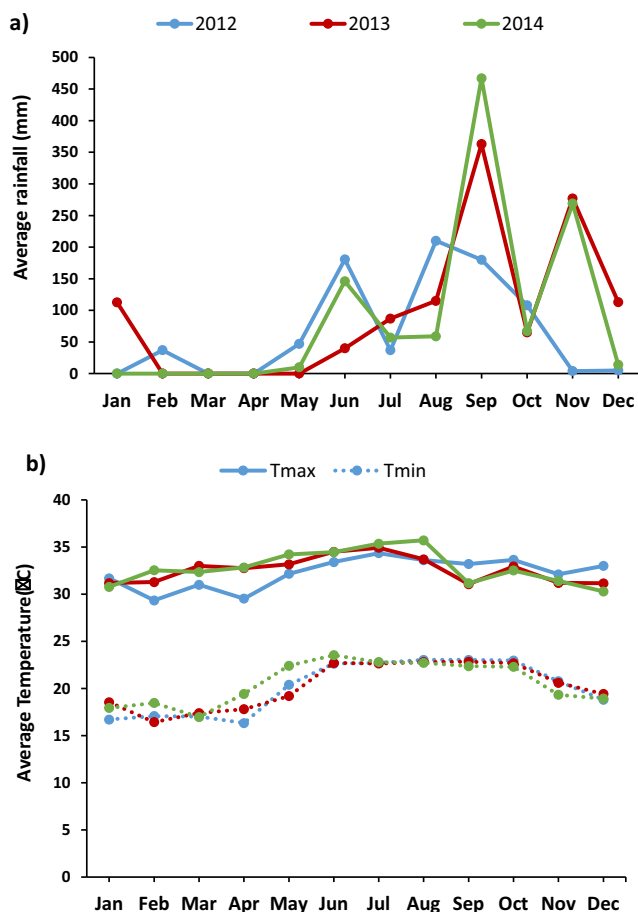


Fig. 1 a Average monthly rainfall and b maximum and minimum monthly average temperatures at Chamela Biological Station from 2012 to 2014 representing the environmental conditions during this experiment

Fatty acids were extracted and prepared for gas chromatography as suggested by Frostegård et al. (1993) from 3 g of the frozen samples finely ground in a steel-ball mill. The fatty acids in phospholipid and neutral lipid fractions were identified with MIDI software and quantified from their retention times in relation to the internal standard (fatty acid methyl ester 19:0). The abundance of functional groups of soil microorganisms was quantified with selected phospholipid fatty acid (PLFA) biomarkers: [iso, anteiso] for Gram+ bacteria, [-OH, cyclo] for Gram- bacteria, [methylated] for actinobacteria, and [18:2 ω 6,9 and 18:1 ω 9] for saprotrophic/ectomycorrhizal fungi as suggested by Högberg et al. (2007) and Ruess and Chamberlain (2010). The neutral lipid fatty acid (NLFA) fraction of the biomarker 16:1 ω 5 was used to quantify arbuscular mycorrhizal fungi (Olsson et al. 1999).

Soil hydrolase potential enzymatic activities contributing to C, N, and P cycling were used to estimate nutrient cycling functions. Although only phosphatase production has been directly attributed to AMF (Feng et al. 2002), soil exocellular enzymes produced by other

soil microorganisms or by plants (García et al. 2007; Kandeler 2015; Plante et al. 2015) also can be promoted in close association with AMF mycelium (Zhang et al. 2018), and thus were measured. β -Glucosidase (Enzyme Commission (EC) #3.2.1.21), as in Eivazi and Tabatabai (1988), was used for C cycling. One gram soil was eluted with modified universal buffer (MUB) + HCl and *p*-nitrophenyl- β -D-glucopyranoside was used as the substrate. After 1 h incubation at 37 °C, the reaction was stopped in an ice bath, color was developed with tris-hydroxymethyl-aminomethane-NaOH and CaCl₂, and para-nitro-phenol evolved was read in a spectrophotometer at 400 nm. Casein-protease (EC #3.4.21.92) according to Ladd and Butler (1972) was assessed for N cycling. Five grams of soil was eluted with Tris-HCl-Trichloroacetic acid (TCA) and casein was used as the substrate. After 2 h incubation at 50 °C, the first part of the reaction was stopped with TCA, further developed with Na₂CO₃, CuSO₄ and 30 min incubation at 37 °C, and finally, a further 5 min incubation with Folin-Ciocalteu reagent. Tyrosine evolved was read at 578 nm. Acid phosphatase (EC#3.1.3.2), as in Tabatabai and Bremner (1969), was used as a proxy for P cycling. We used 0.075 g finely ground soil eluted with MUB, and *p*-nitrophenyl-phosphate as the substrate. After 1 h incubation, the reaction was stopped in an ice bath, color was developed with NaOH and CaCl₂, and para-nitro-phenol evolved was read at 400 nm. All measurements were made with two analytical replicates and included the appropriate soil and reagent blanks for corrections.

Statistical analysis

We used mixed linear models to analyze aggregate categories, fatty-acid biomarkers, and enzymes. Aggregate categories were analyzed with AM fungal community, compartment, and sampling time as fixed factors. Given that measurements were made in the same pot at all sampling dates, compartment and time were included as random factors in the intercept of the model. The values measured in pots inoculated with old-growth forest AM fungal communities and in controls with no AM fungal community are shown separately in the figures for comparison purposes but were not included in the analyses. Fatty-acid biomarkers and enzyme activities measured only at the end of the experiment did not include time in the models.

We also used redundancy analysis (RDA) to examine correlations among response variables and the most important explanatory variables for the variables measured at the last sampling date. First, a partial RDA was carried out to examine the variation partition in the resulting aggregate fractions and enzyme activities explained by AM fungal communities, pot compartments, and fatty-acid biomarkers. Aggregate fractions and enzyme activities were Hollinger-transformed for the

analysis. A second RDA explored if aggregate fractions or enzyme activities were associated with AMF or other micro-organism groups. Finally, we conducted Spearman correlations with Bonferroni correction (not all variables had a normal distribution) between the fatty-acid biomarkers and all response variables measured at the last sampling date.

All analyses were conducted with R software (R Core Team 2017). We used MuMin, nlme, and lm4 packages for mixed models, ado4, MASS, ellipse, packfor and FactoMineR for RDA, and chart. The correlation function in Hmisc was used for Spearman correlations.

Results

Soil aggregation

Significant differences in the aggregate fractions did not become clear until the third year of assessment. Because of the minor changes measured during the first 2 years, we conducted the analysis with a simpler model including only the third-year data. After 3 years, microaggregates and other particles ≤ 0.250 mm still constituted 25–50%, the 0.25–1 mm fraction 9–35%, and the fraction ≥ 1 mm, 4–20% of the soil mass in the pots. The largest and most consistent differences were between the plant and the mycelium compartments (Table 2). The plant compartment contained more microaggregates and other particles ≤ 0.250 mm than the mycelium compartment, but contained fewer aggregates in the 0.25–1 mm and ≥ 1 mm fractions (Fig. 2(a–c)). The successional age of the AM fungal communities had a significant positive relation with the macroaggregate 0.25–1 mm fraction, and especially with the ≥ 1 mm fraction (Table 2, Fig. 2(b, c)). Despite the large variation, pots inoculated with all AM fungal communities had higher values than the control pots in the two macroaggregate fractions, but for the microaggregates and other particles \leq

0.250 mm values were similar. The old-growth forest reference had similar values to the oldest successional AM fungal communities in all fractions.

Enzyme activities

Acid phosphatase activity was slightly but consistently higher in the plant than in the mycelium compartment and increased with the successional age of the inoculated AM fungal community (Table 2, Fig. 3(a)). β -glucosidase was higher in the plant than in the mycelium compartment but did not change significantly with the successional age of the inoculated AM fungal community (Table 2, Fig. 3(b)). Neither AM fungal community successional age nor compartment had an effect on casein-protease (Table 2, Fig. 3(c)). The uninoculated control pots had lower phosphatase and β -glucosidase values than all pots inoculated with AMF communities but similar values in casein-protease activity (Fig. 3(a–c)). Phosphatase and β -glucosidase values of the OGF reference were similar to the oldest successional AM fungal communities and casein-protease values were similar to all AM fungal communities and controls.

AMF and microbial biomass

AMF community successional age and compartment had no effect on soil total microbial biomass, measured as the sum of all selected fatty-acid biomarkers (Table 2). AMF biomass in soil differed only between compartments and was higher in the plant than in the mycelium compartment (Fig. 4(a)). This was confirmed using the ratio of the NLFA fraction (indicator of fungal reserves only) and the PLFA fraction (including fungal and bacterial biomass) of the 16:1 ω 5 biomarker (Fig. 4(b)). The uninoculated control had very low values of both indicators of AMF abundance.

Table 2 Summary of the mixed linear models that were significant ($p \leq 0.05$) for the response variables measured at the third sampling date. *n.s.*, not significant; *A*, successional age; *C*, compartment; *Trans*, transformation; *NA*, not applicable

Response variables	Trans	Significant models				
		A	C	A ²	A*C	A ² *C
Fraction ≤ 0.25 mm (g g^{-1} soil)	NA	n.s.	0.00001	n.s.	n.s.	n.s.
Fraction 0.25–1.0 mm (g g^{-1} soil)	NA	0.002	n.s.	n.s.	0.008	n.s.
Fraction ≥ 1.0 mm (g g^{-1} soil)	Log	0.010	0.00001	0.010	n.s.	n.s.
Acid phosphatase ($\mu\text{moles p-nitrophenol g}^{-1}$ soil h^{-1})	Log	0.006	0.0041	0.013	n.s.	n.s.
Casein-protease ($\mu\text{moles tyrosine g}^{-1}$ soil h^{-1})	Log	n.s.	n.s.	n.s.	n.s.	n.s.
β - Glucosidase ($\mu\text{moles p-nitrophenol g}^{-1}$ soil h^{-1})	Log	n.s.	0.0063	n.s.	n.s.	n.s.
Total microbial biomass (nanomoles g^{-1} soil)	NA	n.s.	n.s.	n.s.	n.s.	n.s.
AMF biomass (NLFA 16:1 ω 5 nanomoles g^{-1} soil)	Sqrt	n.s.	0.007	n.s.	n.s.	n.s.
Ratio NLFA/PLFA (biomarker 16:1 ω 5)	NA	n.s.	0.004	n.s.	n.s.	n.s.

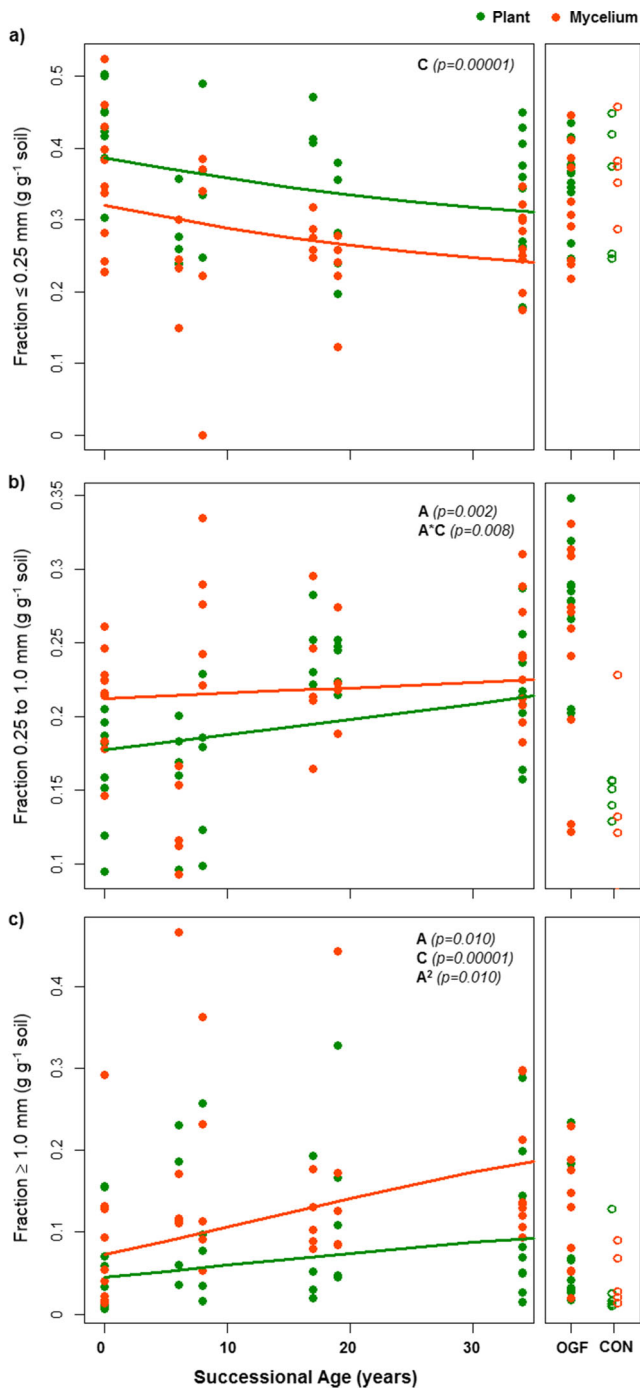


Fig. 2 Sand-free water-stable aggregates **a** ≤ 0.25 mm microaggregates and other particles, **b** 0.25–1.0 mm macroaggregates and **c** > 1.0 mm macroaggregates. The righthand box shows the reference values for the old-growth forest (OGF) AM fungal communities and the control (CON) with no AM fungal community. Significant successional age (A) and compartment (C) effects are indicated

Relations between effect aggregation and enzyme promotion traits and microbial biomarkers

Partial redundancy analysis for aggregate fractions explained 37% of the variation ($P = 0.002$), from which 17% was

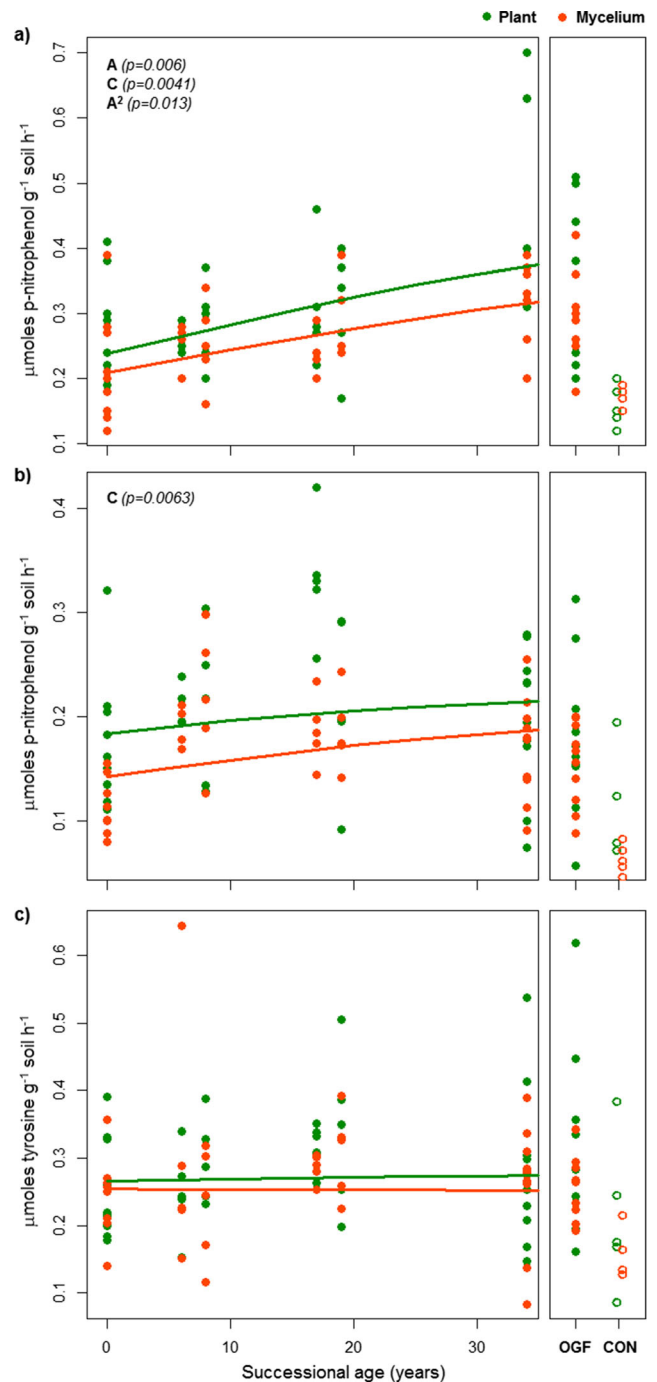


Fig. 3 Enzymatic potential activity of **a** acid phosphatase, **b** beta-glucosidase, and **c** casein-protease, measured in the soil of the plant and the mycelium compartments at the end of the experiment. The righthand box shows the reference values for the old-growth forest (OGF) AM fungal communities and the control (CON) with no AM fungal community. Significant successional age (A) and compartment (C) effects are indicated

explained by the abundance of microbial biomarkers, 13% by the successional age of the AM fungal communities and compartment, and 7% was shared. For enzyme activities, only 19% of the variation was explained ($P = 0.022$), and in this

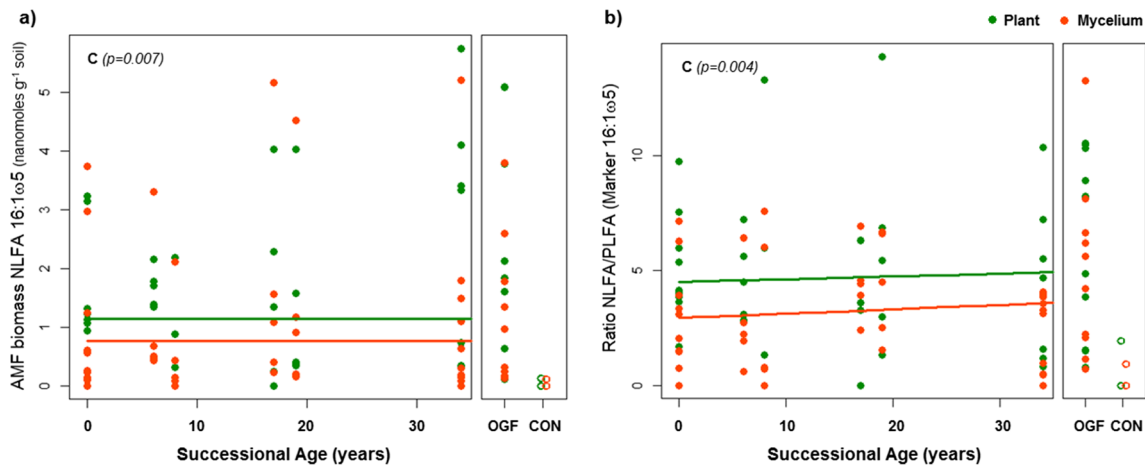


Fig. 4 **a** Biomass of arbuscular mycorrhizal fungi as moles of NLFA 16:1ω5, and **b** NLFA:PLFA ratio of the biomarker 16:1ω5. The righthand box shows the reference values for the old-growth forest

(OGF) AM fungal communities and the control (CON) with no AM fungal community. Significant successional age (A) and compartment (C) effects are indicated

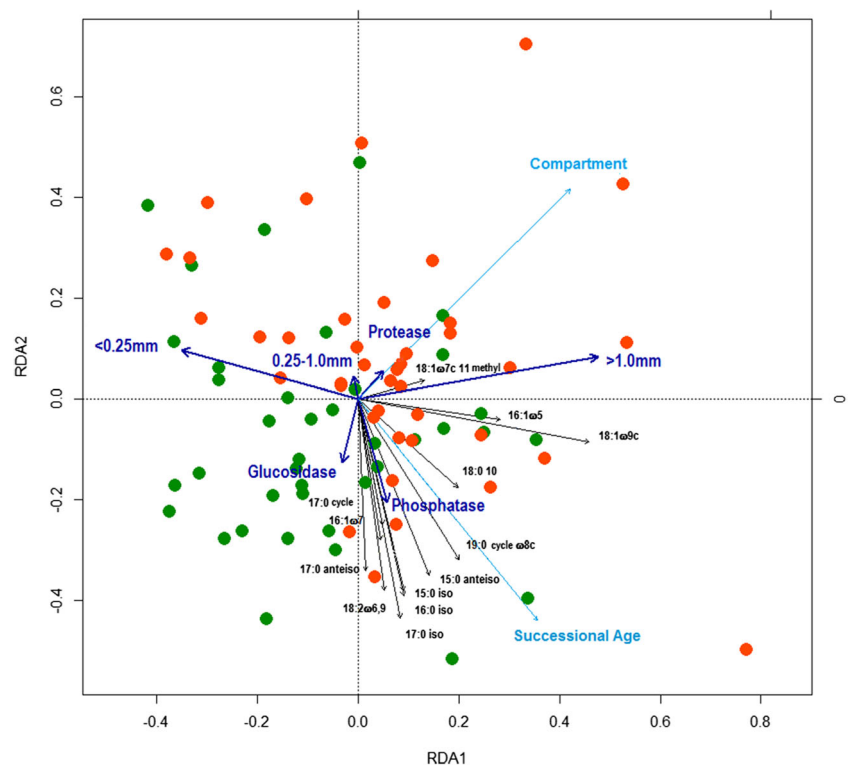
case, mostly by the successional age of the AM fungal communities and compartments (10%), only 4% by the abundance of microbial biomarkers, and 5% was shared.

Redundancy analysis showed that the abundance of many microbial biomarkers was positively related to the successional age of AM fungal communities and phosphatase activity (Fig. 5). The macroaggregate fraction ≥ 1.0 mm was related especially to the fungal biomarkers 16:1ω5 for AMF and 18:1ω9 for saprotrophic fungi. The fraction ≤ 0.25 mm showed no positive association with microbial biomarkers. Enzyme activities were more clearly associated with the plant

compartment than with the mycelium compartment. β -glucosidase activity was positively related to bacterial biomarkers. Phosphatase, in turn, was related to biomarkers for bacteria, saprotrophic fungi, and AMF. Casein-protease was related only to a biomarker for actinobacteria. The variation explained was 33%, and the first component explained 23% (adjusted $r^2 = 0.175$).

Microbial biomarkers did not correlate with aggregate fractions or enzyme activities, but the successional age of AM fungal communities correlated positively with phosphatase, β -glucosidase, and the two macroaggregate fractions

Fig. 5 Redundancy analysis including response variables (aggregate fractions and enzymatic activity) and factors (successional age of AM fungal communities and compartment labeled in light blue) in relation to the abundance of microbial fatty-acid markers. Green dots indicate plant compartments and red dots AM fungal mycelium compartments



(Table 3). Phosphatase was positively related to β -glucosidase and protease whereas protease and β -glucosidase were negatively related to the fraction ≤ 0.25 mm. Protease was positively related to the fraction ≥ 1.0 mm and β -glucosidase to the fraction 0.25–1.0 mm (Table S1).

Discussion

Both functions, soil aggregation and promotion of enzymatic activity, seemed remarkably similar and stable in magnitude in the soil exposed to the ten AM fungal communities examined. Contrary to our expectations, our results suggested that these communities had only slightly reduced some of their functional capabilities during the transformation from forest to cattle ranching and the subsequent years of management and thus were relatively resistant. Nevertheless, soil macroaggregates and especially phosphatase activity showed a recovery trajectory with increasing successional age. β -glucosidase showed also a positive trend with successional age and only protease seemed clearly resistant (i.e., similar along the successional age continuum).

Our prediction was based on the expectation that, given the recent history of land conversion from forest to pasture and pasture management in this region (< 50 y), slash and burn followed by grazing in the active pastures had likely been acting as a selection pressure and transforming AM fungal communities. However, although AM fungal communities and soil properties may change between particular sites (Allen et al. 1998; Gavito et al. 2008; Sandoval-Pérez et al. 2009), recent studies have shown that soil physical, chemical, and biological properties were highly stable across large areas with different land use or land cover in this region, and most of the soil and plant properties that changed with pasture use recovered rapidly during the first years under natural regeneration (Ayala-Orozco et al. 2017). Those authors measured soil aggregates and phosphatase from field samples along a successional gradient that included several of the sites used in this

study and found no significant differences in soil aggregates along the successional gradient (suggesting resistance) and a close to significant correlation (0.35) between successional age and phosphatase activity (suggesting no resistance but recovery). Resilience was attributed to the overall high plant diversity and plant cover present in most sites as a result of the low-input management prevalent after land conversion. In accordance with those observations, AM fungal communities appeared to have replaced some species but maintained the same basic phylogenetic composition in the sites used to obtain the AM fungal communities tested in our study (Carrillo-Saucedo et al. 2018). Our results suggest, therefore, that AM fungal communities had maintained the functional capabilities measured because they maintained their basic phylogenetic composition. However, other functional characteristics of AM fungal communities not explored in this study might change along succession. Gavito et al. (2008) found high compatibility between several plant species' growth and AM fungal communities from sites with different land cover in the Chamela region but Allen et al. (2003) found early-seral AM fungal communities to better promote plant establishment than late-seral communities in restoration plots in the tropical dry forest of the Yucatan Peninsula. Functional traits vary within some range at the fungus species level (Chagnon et al. 2015) but seem to be preserved at the family and order levels (Maherali and Klironomos 2012), although some species may be replaced by others under selection processes. Our experimental study thus supports the resistance to pasture management and the recovery trends along successional time found by Ayala-Orozco et al. (2017) in field measurements of soil aggregation and phosphatase activity that included some of the same sites used to collect the AM fungal communities used in the present study. Our results also support the theory that phylogenetic trait conservatism in AM fungal communities is important for the resilience of AMF diversity and of ecosystem functions to which AMF contribute (Maherali and Klironomos 2007).

Another relevant finding was that soil aggregation was higher in the mycelium compartment than in the plant compartment. Lehmann et al. (2017) as well reported that the ability of AMF alone to aggregate soil is comparable to that of roots, and discussed that hyphae, like roots, are able to provide the physical, chemical, and biological requirements for the formation of stable aggregates (Jastrow et al. 1998; Rillig and Mummey 2006; Hallet et al. 2009). Additionally, AMF may promote aggregate stability through their cementing and hydrophobic properties (Rillig et al. 2010). Successional age of the AM fungal communities had a minor but overall positive effect on the formation of stable aggregates, which we assume is related to the increasing plant diversity (Mora et al. 2014) and decreasing environmental heterogeneity (Lebrija-Trejos et al. 2011) observed during natural regeneration. Other studies in tropical regions suggest that soil

Table 3 Spearman correlations between successional age of the AM fungal communities and response variables measured in the two compartments

Variables	Root		Mycelium	
Fraction < 0.25 mm	-0.35	*	-0.30	
Fraction 0.25–1.0 mm	0.55	***	0.22	
Fraction > 1.0 mm	0.27		0.39	*
Acid phosphatase	0.51	***	0.50	***
Casein-protease	0.15		0.25	
β -Glucosidase	0.18		0.32	*

Bonferroni corrected values * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

aggregation usually recovers with natural regeneration (Duchicela et al. 2013). We assume our observations are explained by the historical legacy of the inoculated AM fungal communities (Teste and Dickie 2017), whose composition and function likely integrates the results of the selection and adaptation processes of the AM fungal species to the environmental biotic and abiotic conditions along succession (Koide et al. 2013). All other factors, pot, soil, plant, environmental conditions, and time were similar in our experiment.

Our long-term experiment performed with a native perennial as host plant growing under the seasonal, local environmental conditions also showed that soil aggregation proceeded very slowly, as opposed to the rapid changes observed in short-term experiments conducted with no nutrient, water, or temperature limitations and with annual plants producing numerous fine roots and exudates. Some field measurements performed in the same region (Cotler and Ortega-Larrocea 2005; Martínez-Trinidad et al. 2012; Murguía-Flores 2012; Cardona-Valadez 2013; Chávez-Macedo 2014; Ayala-Orozco et al. 2017) have found similar proportions of aggregate fractions to those reported in this study, in soils with and without experimental treatments. The predominantly young and sandy soils contain mainly < 0.25 mm microaggregates and other particles, followed by the 0.25–1.0 mm fraction and less than 10%, on average, of aggregates > 1 mm. In those studies, the fraction responding most rapidly and clearly to plant cover management also was the fraction > 1 mm. Only one study has reported a higher proportion of macroaggregates than microaggregates, in OGF soils from Chamela (García-Oliva et al. 2006).

For enzyme activities, in general, the plant compartment had the highest values, most likely associated with carbon and nutrient release from root exudates favoring aggregate formation-disintegration dynamics (Rillig et al. 2015) and microbial activity (Priyadharsini et al. 2016). Only protease, the enzyme least related to microbial biomarkers, had similar values in both compartments. Protease was only slightly related to 18:1 ω 7c 11-methyl, a marker for actinobacteria that seemed to be more abundant in the mycelium compartment than in the plant compartment. Phosphatase was the enzyme activity most positively related to the mycelium compartment, AM fungal community successional age, and abundance of AMF. Although phosphatase was also related to other bacterial (16:1 ω 7) and saprotrophic fungi (18:1 ω 9) biomarkers and can be produced by plant roots as well, its association with AMF was evident. β -glucosidase and protease, in turn, were more associated with aggregate fractions than with the mycelium compartment or AMF abundance. AMF-bacteria coupled activity to produce phosphatase and solubilize organic P sources has been demonstrated (Zhang et al. 2018), and likely other coupled enzymatic activities will follow in the future. Aggregate fractions are known to influence microbial activities (Waldrop et al. 2000, Huang et al. 2009). Unlike

phosphatase, an enzymatic activity attributed to AMF (Saito 1995; Feng et al. 2002), it is unknown if β -glucosidase and protease are produced directly by AMF or through a coupled mechanism with other microorganisms. To date, it is assumed that AMF have only weak enzymatic and decomposing capabilities (Joner et al. 2000; Read and Pérez-Moreno 2003), but evidence is growing for a greater contribution by AMF to decomposition and nutrient cycling (Tu et al. 2006; Gui et al. 2017). That the mycelium compartment could maintain very similar enzymatic values, either produced directly or through associations with other microorganisms (Smith and Smith 2011; Kaiser et al. 2015; Zhang et al. 2018), to those observed in the plant compartment has strong implications for the contribution of AMF to nutrient cycling because their influence extends far beyond the rhizosphere into the bulk soil and the litter (Bunn et al. 2019).

Phosphatase increased with successional age as observed by Chávez-Macedo (2014) in this region, in other tropical regions (Acosta-Martínez et al. 2007), and in other chronosequence studies (Welch et al. 2014). It also increased with soil C, N, and P availability, from pastures to successional forests and further to mature forests (Sandoval-Pérez et al. 2009) likely due to C and N limitation and scarcity of organic P sources for phosphatase activity in pastures. Phosphorus is the most limiting nutrient and phosphatase has been the most responsive enzyme to biotic and abiotic changes in the Chamela region because, after being lost in clearance burnings, erosion, and grazing, there are very few ways for return of this nutrient, so productivity is sustained by efficient recycling of organic P (Lawrence et al. 2007). Extensive pasture management rarely involves fertilization, either chemical or organic, so besides C and N that can be reincorporated through plant C assimilation and N fixation, the rest of nutrients often also are of low availability. The findings of Ayala-Orozco et al. (2017) with field measurements in a successional gradient of the Chamela region, support this theory and some of our observations. Soil C and available N increased rapidly with successional age, but available P and phosphatase increased very slowly and still remained lower than in OGF after 30 y of succession. Therefore, not surprisingly, the three enzymatic activities measured in these pots with no fertilization for 3 years were positively related to each other, suggesting that the nutrients released by their activities might have synergistically promoted one another, as multiple nutrient limitation can constrain enzyme production and activity (Allison and Vitousek 2005).

Promotion of soil aggregation and exocellular enzymatic activities, the two functional traits examined in the AM fungal communities of a successional gradient, was explained in different ways but with clear linkage to AMF performance. Soil aggregation was explained mainly by the abundance of certain microbial biomarkers, two fungal and one bacterial, whereas enzyme activity was explained by the compartment and

successional age of the AM fungal communities. In other words, soil aggregation was more dependent on the abundance of AMF, saprotrophic fungi, and actinobacteria than on the host or the different AM fungal communities, and nutrient cycling was more dependent on the plant and its interaction with the AMF present in the communities than on the abundances of microbial groups. Filamentous organisms like fungi and actinobacteria possess ideal traits to contribute to soil aggregate formation, stabilization, and disintegration (Lehmann et al. 2017), but few studies to date have provided evidence for the specific contribution of AMF and other soil biota to soil aggregation. Enzyme activities involved in nutrient cycling, in contrast, seem to be most dependent on the carbon input from the plant and on other differences present in AM fungal communities that are related to successional age. Our interpretation is that those differences likely arise from the AM fungal species present in the inocula and their associated biota, but definitively confirming that would require molecular characterization of the active soil biota present in both compartments.

In conclusion, our results suggest that functional traits of the AM fungal communities we studied are resilient to management as pastures mainly because they showed small reductions in response to the disturbance pressure and recovered through successional time. This study supports the theory that species may change with disturbance but, if the same phylogenetic composition is maintained, community functional traits also can be maintained, as has been proposed and is better understood for plant communities (Lavorel and Garnier 2002; Gross et al. 2008; Suding et al. 2008).

Acknowledgments S. M. Carrillo-Saucedo thanks Posgrado en Ciencias Biológicas at Universidad Nacional Autónoma de México as well as Consejo Nacional de Ciencia y Tecnología (CONACyT) for a scholarship during her PhD studies. This research was supported by Dirección General de Asuntos del Personal Académico (DGAPA) from Universidad Nacional Autónoma de México (UNAM) through project PAPIIT-IN224010 and CONACyT projects SEP-CONACyT 2009-129740 and 2015-255544. We thank Francisco Mora for statistical guidance and Emanuel García, Gustavo Verduzco Robles, Abel Verduzco Robles, Yolanda García and Ana Lidia Sandoval Pérez for technical assistance. We thank also Raúl Ahedo, Manuel Maass and Ma. Eugenia González for rainfall and temperature data.

Author contributions Conceived research: SMCS, MEG

Performed research: SMCS

Analyzed data: SMCS, MEG

Wrote the manuscript: SMCS, MEG

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