Fungal Ecology 70 (2024) 101354

Contents lists available at ScienceDirect

Fungal Ecology

journal homepage: www.elsevier.com/locate/funeco

# Impact of hurricane disturbance on mycorrhizal co-occurrence networks: Resilience and community dynamics in the Neotropics

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ARTICLE INFO

Handling Editor: Prof. Marie Davey

*Index descriptors:*
Arbuscular mycorrhiza
Cyclone
Ectomycorrhiza
Fungal guilds
Interspecific interactions

ABSTRACT

Extreme climatic events and related disturbances such as hurricanes are increasingly altering forest ecosystems. How these events impact forest fungal communities is poorly characterized. We examined the effect of a hurricane on mycorrhizal community structure and potential interspecific fungal interactions, inferred from OTU co-occurrences. We characterized the root fungal communities of dual-mycorrhizal plants from nine plots during two consecutive years after a category four hurricane impacted the coastal Mexican Pacific tropical forest in Jalisco. Presence-abundance matrices were used to calculate properties of mycorrhizal networks including nestedness and modularity, and to infer patterns of co-occurrence. One year after the hurricane there was a loss of links between plants and fungi. Increased network modularity and connectivity were observed after two years. We also found that disturbance changed arbuscular mycorrhizal fungal network structure more strongly than ectomycorrhizal fungal networks. Fungal guilds changed their putative interspecific interactions, from mutual exclusion in the first year to a significant increase in co-occurrence of plant pathogens, saprotrophs, and endophytes in the second year. Our results suggest that in the short term, rhizospheric interactions can be resilient to hurricanes, but fungal guilds may have divergent responses.

## 1. Introduction

Global change is increasing the frequency and severity of pulse disturbances across many ecosystems. Additionally, anthropogenic activity such as forest clearance enhances natural disturbance events (Banks et al., 2013). For example, higher temperature of the oceanic surface has a strong effect on the formation and strength of tropical storms and hurricanes (Henderson-Sellers et al., 1998). Climate warming will thus cause hurricanes to be more frequent and stronger in the second half of the 21st century (Knutson et al., 2015). As a result, there is a growing interest in the effect of more frequent and powerful hurricanes on natural communities. While studies have examined the response of plants, birds, insects, mammals, and other animals (e.g. Ameca et al., 2019; Bhattarai and Cronin, 2014; Jimenez-Rodríguez et al., 2018; Novais et al., 2018), few studies have examined the response of belowground communities to hurricanes (Alvarez-Manjarrez and Garibay-Orijel, 2021; Cantrell et al., 2014; Lodge et al., 2022; Vargas et al., 2010).

Fungi are a major component of soil microbial communities and play essential roles for soil functioning as decomposers and plant mutualists (Swift et al., 1979; Vincent and Declerck, 2021). Fungal lifestyles can be classified by functional guilds such as saprotrophs, pathogens, mycorrhizal-types, lichens, and endophytes. Soil fungal communities are highly susceptible to disturbances, especially fire, drought, and nitrogen deposition (Alvarez-Manjarrez and Garibay-Orijel, 2021; Banerjee et al., 2019; de Vries et al., 2018; Dean et al., 2014; Glassman et al., 2016; Jia et al., 2021; Phillips et al., 2019; Yuste et al., 2011). Each of the functional guilds varies in its response to biotic and abiotic factors due their different nutrient acquisition strategies (Schappe et al., 2020). These changes may be due to direct effects of disturbance on the soil environment, but they may also arise from cascading effects on aboveground communities.

Our study took place after the category four Hurricane Patricia, with wind speeds up to 345 km/h, impacted the Mexican Pacific tropical forest on the coast in Jalisco. Several studies described the effect of this

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https://doi.org/10.1016/j.funeco.2024.101354
Received 29 May 2023; Received in revised form 6 February 2024; Accepted 5 April 2024

hurricane disturbance on the vegetation of this tropical forest and its productivity (Martínez-Yrízar et al., 2018; Parker et al., 2018; Paz et al., 2018), animal community interactions (e.g. Novais et al., 2018; Sil-Berra et al., 2021), soil fungal communities (Alvarez-Manjarrez and Garibay-Orijel, 2021), biogeochemical processes (Jaramillo et al., 2018, 2022), and decomposition (Gavito et al., 2018). Particularly, the soil fungal communities underwent a turn-over, increasing their diversity immediately after the hurricane, but decreasing a year later. Basidiomycota, the phylum with the most species with white rot enzymes to break down lignin, was more abundant after the hurricane. After two years, the soil fungal composition showed resilience (Alvarez-Manjarrez and Garibay-Orijel, 2021). How the hurricane affected fungal-plant interactions remains an open question.

Most plants establish root mutualistic symbioses with fungi forming several mycorrhizal types: arbuscular mycorrhiza (AM) and ectomycorrhiza (ECM). AM are present in ~80% of terrestrial plants, while ECM are associated with 3% of plants (Brundrett and Tedersoo, 2018). Approximately 60% of trees associate with ECM, particularly those distributed in temperate and boreal forests (Steidinger et al., 2019). Mycorrhizal interactions are often context dependent as they rely on the exchange rate of soil resources (Bogar et al., 2022). Thus, environmental changes in soil resource availability after disturbance can modify these interactions even if they do not directly affect fungal physiology (Kennedy, 2010; Mahmood, 2003).

In general, work from non-perturbed systems has shown that mutualistic networks tend to be nested, i.e., arranged in a cohesive nucleus (Bascompte, 2009). For example, in plant-animal interactions, generalist plants interact more with generalist animals; this results in functional redundancy in the ecosystem (Bascompte, 2009). In contrast, modularity is a network property that indicates the compartmentalization of closely interacting species (Toju et al., 2014). It has been proposed that in the face of disturbance, highly modular networks insulate neighboring modules from cascading effects (Gilarranz et al., 2017). However, this topic is still open to debate. When they have been investigated, plant-fungal networks appear to have different responses according to their guild; particularly, AM networks tend to show nestedness (Põlme et al., 2018). It is unclear though how the structure of these mycorrhizal networks is affected by hurricane disturbances.

In this study we used high-throughput sequencing to gauge the effects of a severe disturbance on root fungal communities. We studied a tropical dry forest that has predominantly arbuscular mycorrhizal associations. Hurricane Patricia drastically modified vegetation structure and composition (Jimenez-Rodríguez et al., 2018; Parker et al., 2018). Large litter inputs impacted carbon and nutrient cycling, including N:P and C:P ratios in soil (Gavito et al., 2018; Jaramillo et al., 2022). We made use of this natural experiment to classify disturbance in three levels, then sample roots fungal communities one and two years after the hurricane to characterize changes in network properties, fungal community structure, and putative interspecific interactions inferred from co-occurrence patterns. We hypothesized that: 1) generalists would resist disturbance creating nestedness and low modularity in mycorrhizal networks; 2) the level of disturbance would generate different changes in the plant-mycorrhizal fungus relationship, losing putative interactions with greater disturbance; and 3) the hurricane disturbance would create a stress environment that would increase putative interspecific competition between guilds.

## 2. Materials and methods

The study was carried out in the Biological Station of Chamela, Jalisco, Mexico. We established nine 20 × 20 m plots in October 2016 (coordinates Table S1). All plots were randomly selected within the same soil type based on edaphic properties. For each plot, we identified, counted, and measured diameter at breast height (DBH) of all living trees and shrubs >3 cm (Table S2). Light and temperature were measured on the forest floor with a HOBO Pendant UA-002-08, and humidity with a Kestrel 5700 Weather Meter three times per plot. We used the slope at each site to calculate potential erosion for our analysis (Stone and Hilborn, 2000; Table S3). All ECM hosts – some of which also form AM associations (Álvarez-Manjarrez et al., 2021) – were identified and flagged (Fig. S1), and three root systems of 10 cm length were sampled per plant and pooled by host species for further analyses. In 2017, we re-sampled the root systems of the flagged trees; both samplings were done during the rainy season from August to October. The number of the sampled plants varied depending on the plot, from 31 plants to 136, with a total of 609 evaluated plants (Table S2). Our sampling began in October 2016, one year after Hurricane Patricia made landfall. Without data from before the hurricane, we acknowledge that the patterns we describe do not fully capture initial conditions and recovery. However, they do provide information on shifts in fungal community structure two years after a major hurricane event.

We selected roots with ectomycorrhizal root-tips under a stereomicroscope and these root-tips were preserved in 96% ethanol for further analyses. Additionally, we pooled three soil samples (5 × 5 cm cores) from each plot yearly and stored them at 4 °C to assess their physicochemical properties. Soil samples were analyzed by the “Laboratorio de Fertilidad de Suelos y Química Ambiental” at the Colegio de Posgraduados, Mexico. Total N and P were obtained by the Kjedahl method and quantified molybdenum blue colorimetry. Total C was determined by the Warkley and Black method. Electric conductivity and pH were analyzed by a conductivity bridge and pH meter, respectively. $PO_4$ was extracted by molybdenum blue colorimetry, and $NO_3$ and $NO_4$ were obtained by steam distillation (Fig. S2; Table S3). To determine the levels of disturbance, we performed a hierarchical cluster analysis with hclust package in R, using Ward distance including all the abiotic characteristics and the number of trees dead, fallen, and alive. The plots were classified in three levels: (1) “**low disturbance**” plots with high tree density, high number of fallen live trees, lowest slope and erosion, and high organic matter and total Carbon; (2) “**medium disturbance**” plots with high alive trees, moderate slope, and lower $NH_4$; (3) “**high disturbance**” plots with a low number of live standing trees, lowest density of trees, tendency to be eroded, and high content of $PO_4$ (Figs. S2 and S3; Table S2). There were 2 low, 5 medium, and 2 high disturbance plots used in the study.

Root-tip DNA extraction was performed with the PowerMax Soil DNA isolation kit according to manufacturer’s instructions (MoBio; USA). The internal transcribed spacer 2 (ITS2) of nuclear ribosomal DNA was amplified and bioinformatic analyses were conducted using the toolkit PipeCraft v1.0 (Anslan et al., 2017) reported previously in Alvarez-Manjarrez and Garibay-Orijel (2021). We used default values of vsearch (Rognes et al., 2016), demultiplexing with MOTHUR v1.36 (Schloss et al., 2009), filtering chimeras de novo using UNITE ITS2 v7.1 as a reference (Kõljalg et al., 2013); we then cut primers and removed primer artifacts using vsearch. We extracted ITS2 with ITSx v1.0.11 (Bengtsson-Palme et al., 2013) and clustered into OTUs with CD-HIT v4.6 (Li and Godzik, 2006) using a 97% of similarity as threshold (Li and Godzik, 2006). Singleton OTUs comprised of a single sequence were excluded from the analysis and taxonomy was assigned to the remaining OTUs using BLAST + v2.2.28 (Camacho et al., 2009) and UNITE v7.1. Fungal guilds were then assigned with FUNGuild (Nguyen et al., 2016).

We obtained 2,003,944 (9.82%) quality-filtered sequences from an initial 20,402,884 reads; after chimera filtering 1,268,036 sequences were left that clustered into 3763 OTUs; after the removal from control sequences, we obtained 3625 OTUs (42.7% were unidentified). GenBank accessions numbers: **SAMN33482969** to **SAMN33483034**. The number of sequences for each sample varied strongly (from millions to thousands), so we rarefied with the median (44294 number of sequences) using rrarefy in the vegan package of R (Oksanen et al., 2013); samples with less than the median were discarded for statistical analyses but not for mycorrhizal network analysis. The fungal community matrices were normalized using Hellinger transformation. We determined the significance of abiotic variables on fungal community composition using permutational analysis of variance (PERMANOVA) with adonis in the vegan package.

### 2.1. Mycorrhizal network analysis (bipartite networks)

Here we refer to mycorrhizal network as an ecological network of plant-fungal interactions identified taxonomically as mycorrhizal fungi. To test the effect of disturbance on the mycorrhizal network metrics, particularly modularity, we calculated nestedness and modularity of the overall mycorrhizal bipartite networks with a "co-occurrence" matrix of plants and fungi. This overall matrix included all mycorrhizal fungal species (i.e., AM, ECM, orchid and ericoid mycorrhiza) to compare the variation of the entire mycorrhizal network between years; however, orchid and ericoid mycorrhizal fungi were very rare so we just considered the AM and ECM for our analyses. Within guild assignation, we found 37 OTUs with ambiguous trophic mode between pathogen, saprotroph, and/or symbiont, such as *Entoloma* sp.; we interpret these as symbionts. Separate calculations for AM and ECM networks were performed by year, disturbance level, and plot. A nestedness index was calculated with the NODF function in the bipartite R package (Dormann et al., 2008) and its significance was tested comparing observed and 999 randomized matrices using quantitative swap and shuffle methods 'swsh_both' in the vegan R package (Oksanen et al., 2013). Non-parametric comparisons between network properties were performed with the gao function in the nparcomp R package (Gao et al., 2008) using zero values instead of missing data to run the test. Centrality, a measure to quantify the importance of the nodes, was calculated with igraph in R to make the network plots, which were visualized using the Kamada-Kawai algorithm with ggnetwork in the ggplot2 R package (Wickham, 2016), coloring by fungal guild.

### 2.2. Interspecific network analysis (unipartite networks)

Disturbance changes the environment and may change interactions between organisms within a community. To infer changes in interspecific interactions, we carried out a co-occurrence unipartite network (only fungi) analysis using the CoNet app of Cytoscape with data from the roots separated by years. The matrices contained only fungal OTUs with known guilds, excluding lichenized and fungal parasites of lichens because they are not considered common in the roots. The parameters used were minimum row sum of 20, with log standardization, using Pearson and Spearman correlation with Bray-Curtis dissimilarity distance. These interspecific network analyses are based on the presence or absence and abundance of species. According to Kennedy (2010) we used species abundance as a measure of competitiveness. We acknowledge that these co-occurrence patterns do not necessarily mean that fungi are directly interacting with one another. We use the term "putative interspecific interactions" throughout this article to describe potential interactions inferred from this analysis.

The analysis was performed using 100 bootstrap iterations with the Benajmin-Hochberg test correction for the P-value threshold 0.05. The graph was generated using the mean of multi-graph using the option "union" to merge networks, adding the guilds as attributes to compare co-occurrence between them.

## 3. Results

Plant richness in plots varied between 28 and 59 shrub and tree species. While most of the common plants form AM, there were some common ECM hosts such as *Achatocarpus gracilis, Apoplanesia paniculata, Guapira petenensis, Coccoloba liebmanii,* and *Lonchocarpus* spp. (Table S1).

Roots fungal communities showed evidence of shifts after hurricane Patricia. Mycorrhizal diversity was lower one year after the hurricane (2016), with few mycorrhizal species shared between hosts, but significantly increased two years after the hurricane (2017). In 2016 we found 31 OTUs from AM fungi and 46 OTUs of ECM fungi, and in 2017 the richness increased in both groups to 51 and 91, respectively; hence the structure of the mycorrhizal networks was more complex in 2017 (Fig. 1). In both years, Thelephoraceae species were common and abundant in host roots. Details of the community composition are in the supplementary information (Figs. S4–S10).

ECM fungi had more richness in plots with low and high disturbance, but not in medium disturbance plots (Fig. S5). Plots with high disturbance had abundant saprotrophs. AM (Glomeromycetes) varied considerably across years and disturbance levels (Fig. S6). We found significant differences in guild abundance between plots and years ($X^2 = 38$, P = 3.7e-7, df = 5). Ordination analysis showed that communities were structured by year and host (Fig. S11).

PERMANOVA results showed that root fungal community diversity was mainly predicted by light at ground level ($F_{1,\ 59} = 1.338$, $R^2 = 0.018$, P = 0.042), degree of disturbance in plots ($F_{2,\ 59} = 1.4$, $R^2 = 0.039$, P = 0.018), host ($F_{9,\ 59} = 1.689$, $R^2 = 0.214$, P = 0.001), year ($F_{1,\ 59} = 2.851$, R2 = 0.051, P = 0.001), and soil temperature ($F_{1,\ 59} = 2.858$, $R^2 = 0.04$, P = 0.001). Variation in fungal community structure across disturbances and hosts is plotted in Fig. 2. ECM community composition was mainly determined by host identity ($F_{8,\ 53} = 2.145$, $R^2 = 0.238$, P = 0.001), followed by year ($F_{1,53} = 5.388$, $R^2 = 0.075$, P = 0.01). Arbuscular community composition was only determined by soil pH ($F_{1,29} = 1.93$, $R^2 = 0.102$, P = 0.01) (see Fig. 3).

### 3.1. Network structure

*Guapira petenensis, Achatocarpus gracilis*, and *Apoplanesia paniculata* were the hosts with the most centrality in our plots, meaning we inferred they had the greatest number of fungi associated with them. The most generalist fungal species were *Tomentella* sp. (SH006884.07FU associated with *A. gracilis, G. petenensis, Coccoloba liebmanii*, and *Ruprechtia fusca*) and *Clavulina* sp. (SH629574.07FU associated with *G. petenensis, Apoplanesia paniculata*, and *Lonchocarpus eriocarinalis*). The same plants were sampled in the plots both years; however, the first year of sampling, when the hurricane was more recent, there were some plants without any mycorrhizal fungal sequences in their roots. The fungal composition in 2017 was similar to that found in soil before the hurricane when comparing with the data of Alvarez-Manjarrez and Garibay-Orijel (2021).

The plants we studied are dual mycorrhizal hosts, i.e., they associate with AM and ECM at the same time; we call this a dual mycorrhizal network. The plots that had a dual mycorrhizal network belong to the low disturbance and medium disturbance categories. While connectivity was greater in 2017, we found just one plot with significant nestedness (A250). *Guapira* and *Achatocarpus* often have dual mycorrhizal associations; however, their mycobionts changed in each plot. Four plots shared more than two AM or ECM species between host, and these plots were classified as low and medium disturbance.

When we analyzed the networks' characteristics separating by guilds (i.e., AM and ECM) we found that in 2016 the AM network was lost in almost all the plots. Only two had a measurable network, while in four plots we found ECM networks (Table 1). One of the plots, with high disturbance, presented AM and ECM networks at the same time. Plots with low disturbance had only ECM networks while one of the high disturbance plots did not recover any of the networks between hosts (Fig. 1; plot T2800).

### 3.2. Putative interspecific interactions within the rhizospheric fungal community

Roots fungal guilds changed interactions from highly competitive to co-habitation through forest recovery (see Fig. 4). During 2016, ECM fungi had negative occurrence interactions with saprotrophs, pathogens, endophytes, and other ECM species. Most of the abundant Glomeraceae species co-occurred with ECM, saprotrophs, and other arbuscular

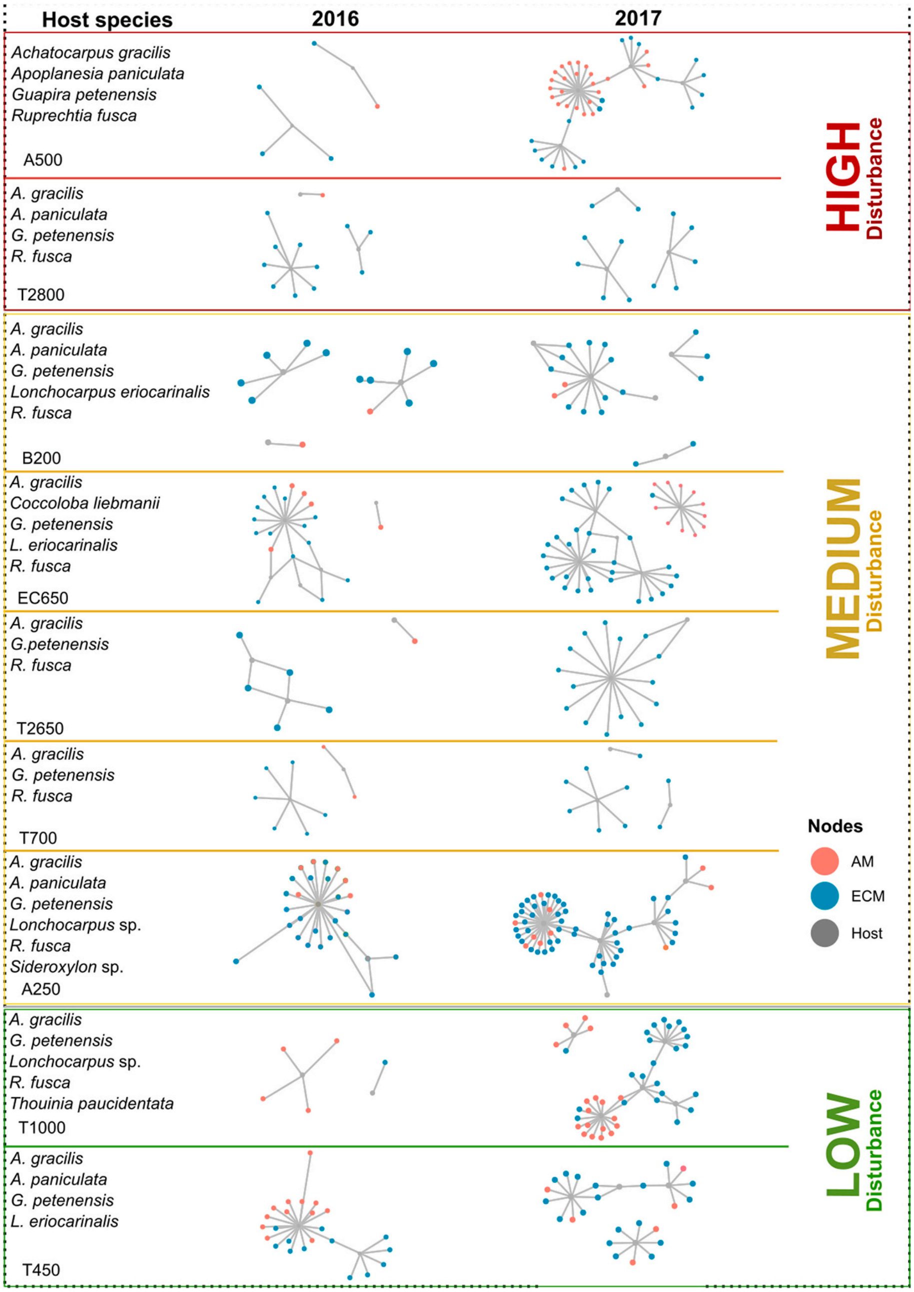

**Fig. 1.** Mycorrhizal networks across different sampling plots including all the mycorrhizal guilds in 2016 and 2017. Plots were made using the Kamada-Kawai algorithm and are arranged by disturbance plot classification. On the right is a list of hosts of each plot that were sampled both years In 2016, some hosts did not have mycorrhizal fungi in their roots, so they do not appear in the plots. Abbreviations: AM = Arbuscular mycorrhizal, ECM = ectomycorrhizal.

mycorrhizal fungi. Plant pathogens also demonstrated exclusion patterns with Glomeraceae (Fig. S12). In general, plant pathogens co-occurred with saprotrophs and endophyte species (Fig. 4a–S12). In 2017, higher fungal richness created more significant interactions in a more complex network. More OTUs of ECM fungi were identified, but with lower abundance compared to other guilds, demonstrating mainly intra-guild negative co-occurrence, especially with saprotrophs. Negative co-occurrences were rare between AM and saprotrophs/endophytes guilds. Endophytes were co-present with AM, plant pathogens, and some saprotrophs; however, there were some endophyte species that excluded saprotrophs (e.g., *Xylaria* excludes saprotrophs) and ECM fungi (Fig. 4b).

## 4. Discussion

In this initial analysis of dual mycorrhizal networks in a tropical forest, our results reveal a low number of putative associations between plants and fungi after the occurrence of a major hurricane. Our study commenced after the hurricane landing, and we lack data on the network's structure before the hurricane. However, our findings suggest that this natural event may have significantly decreased mycorrhizal network connections between plant species. These connections showed signs of recovery within two years after the major disturbance, indicating ongoing forest recovery processes. Despite the negative impact of the hurricane on the mycorrhizal community, our study highlights the potential resilience and ability of mycorrhizal fungi to change after such disturbances.

Additionally, our research indicates that the ECM network exhibited greater resilience to the hurricane compared to the arbuscular mycorrhizal network. The higher diversity observed in contributed to greater complexity in fungal interspecific interactions on roots. Importantly, it

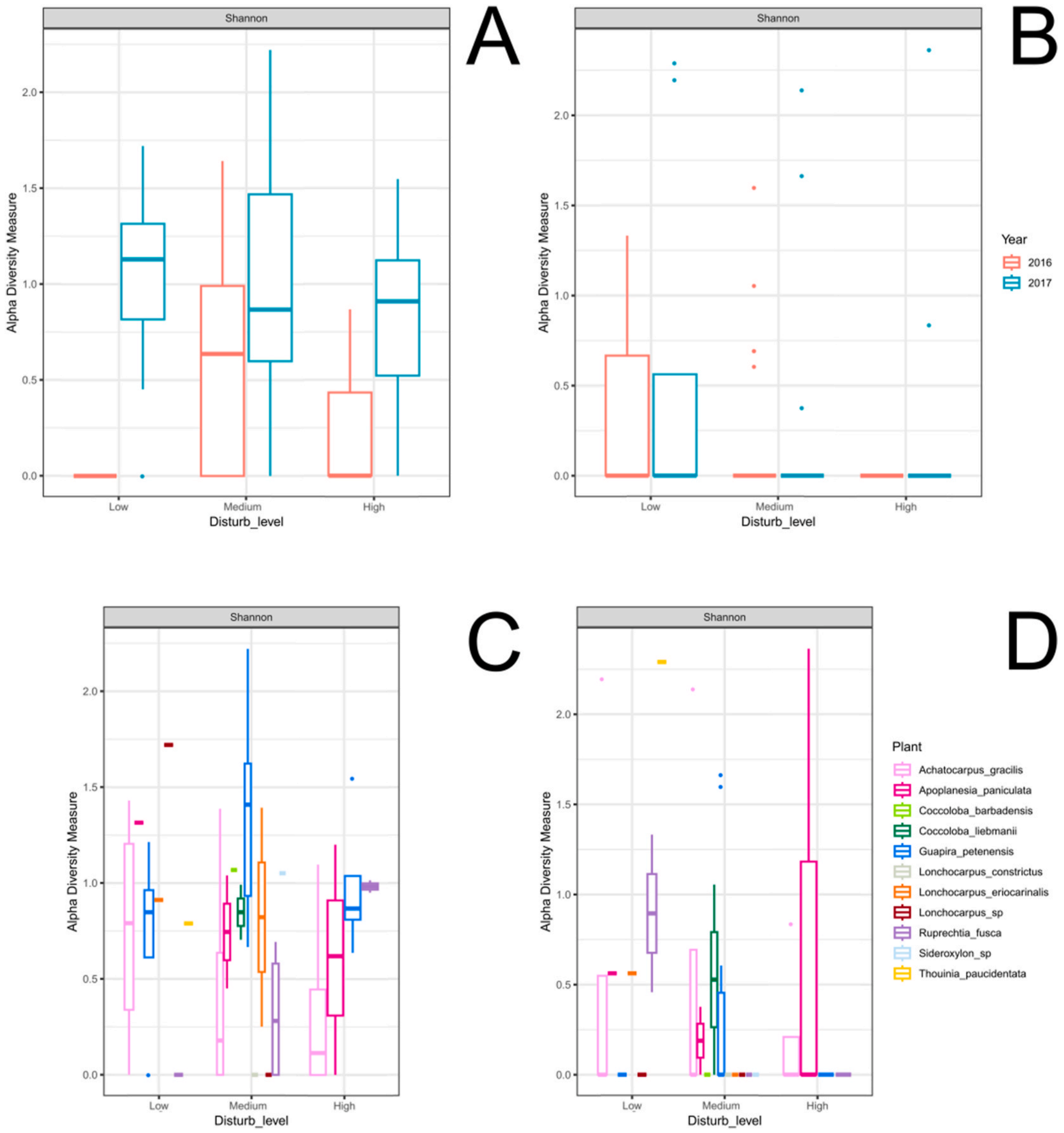

**Fig. 2.** Patterns of mycorrhizal diversity across disturbances and hosts. (A) Ectomycorrhizal and (B) arbuscular mycorrhizal diversity across different levels of disturbance in each year. (C) Ectomycorrhizal and D) arbuscular mycorrhizal diversity index by host.

appears that competition between fungal species was reduced in the aftermath of the hurricane, suggesting a dynamic response to environmental stressors.

When we analyzed ECM and AM network components separately, we observed both guilds suffer loss of connections with plant species in 2016, especially AM connections. This could be direct related to the hyphal growth rate, as ECM growth is three to seven times higher than AM hyphae (Jones et al., 1998), consequently, ECM recovery could occur more rapidly. Also, we found only one ECM network with very low modularity in a plot with a medium level of disturbance. Two years after the disturbance, modularity was a common feature in the ECM networks and we did not find nestedness. Ectomycorrhizal species presents higher specificity to their host which could explain the observed high modularity (Bahram et al., 2014). Specifically, in this tropical dry forest, the ECM community displayed a strong preference for low abundance hosts (Alvarez-Manjarrez et al., 2018) Specificity, together with modularity, can change with disturbance, e.g., comparison of plant-herbivore networks before and after a hurricane found a decrease in specificity and number of compartments (Luviano et al., 2018).

We hypothesized that after the disturbance, inhospitable conditions would be a filter and only generalist species would form mycorrhizal networks; two years after the hurricane and as the ecosystem recovered, links between plant species increased. However, the fungal symbionts were specialists of each host and the mycorrhizal network became more modular. This pattern can be ascribed to more specialized species, which are more common in undisturbed sites whereas generalists prevail in any conditions, particularly in high disturbance sites (López-Carretero et al., 2014). Also, highly modular networks could make the communities more resilient to disturbance (Gilarranz et al., 2017).

Plants in the tropical dry forest are predominantly associated with arbuscular mycorrhizal fungi (Carrillo-Saucedo et al., 2018; Gavito et al., 2008; Marinho et al., 2019). Interestingly, even hosts forming ectomycorrhizal relationships establish symbiosis with AM in this ecosystem (Álvarez-Manjarrez et al., 2021). Following a hurricane, there is an observed increase AM colonization in plant roots (Vargas et al., 2010). However, mere colonization data fails to unveil the connections between plants. Hurricane-induced organic matter decomposition, and in general decomposition heightened $CO_2$ release; the decomposition rates post-Hurricane Patricia increased (Gavito et al., 2018). Experiments with elevated $CO_2$ levels have demonstrated the promotion of AM fungal hyphae growth and spore germination (Bécard and Piché, 1989; Jin et al., 2011), potentially explaining the surge in AM colonization

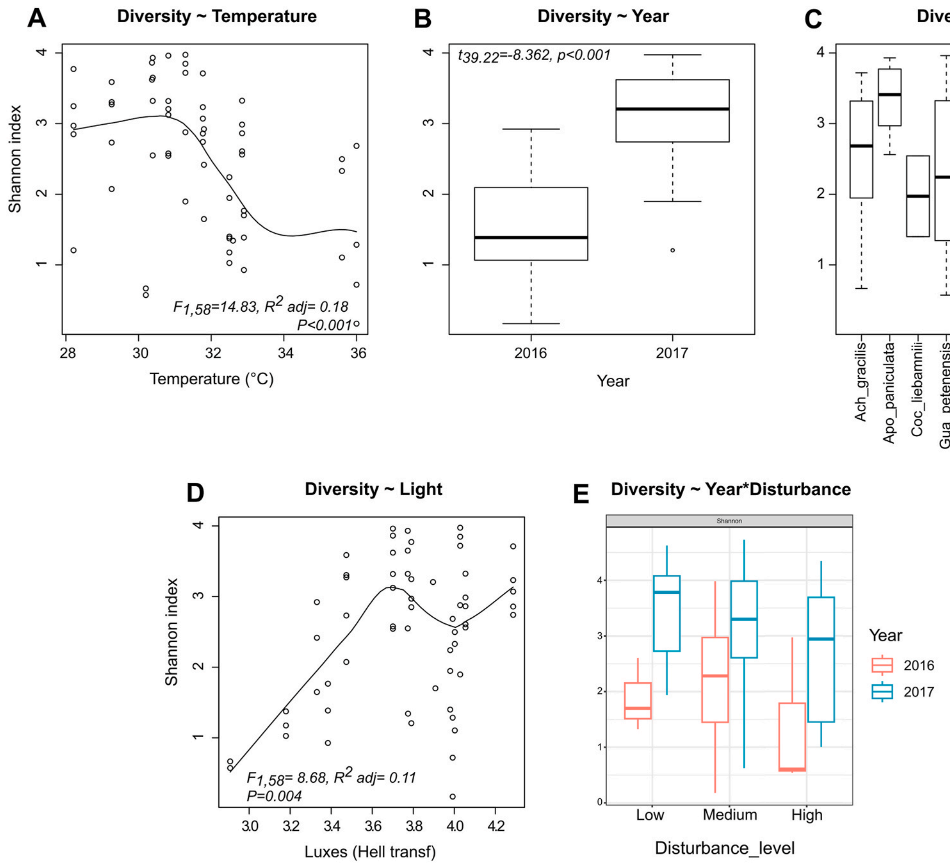

**Fig. 3.** Significant predictors of roots fungal community structure: (A) Soil temperature, (B) year of sampling, (C) plant species, (D) light at ground level, (E) plot level disturbance. Bold horizontal lines from boxplots represents mean values, and box margins are variance. Abbreviations: Ach_gracilis = *Achatocarpus gracilis,* Apo_paniculata = *Apoplanesia paniculata*, Coc_liebmanii = *Coccoloba liebmanii*, Gua_petenensis = *Guapira petenensis*, Lon_constrictus = *Lonchocarpus constrictus*, Lon_eriocarinalis = *Lonchocarpus eriocarinalis*, Lon_sp = *Lonchocarpus* sp., Rup_fusca = *Ruprechtia fusca*, Sid_sp = *Sideroxylon* sp., Tho_paucidentata = *Thouinia paucidentata.*

**Table 1**
Arbuscular and ectomycorrhizal networks properties two years (2016 and 2017) after hurricane Patricia.

| Plot - disturbance | Net | 2016 | | | | | | 2017 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Nestedness | | | | | Modularity | Nestedness | | | | | Modularity |
| | | NODF | Z-value | Mean | P-value | WNODF | | NODF | Z-value | Mean | P-value | WNODF | |
| T2800 high | **ECM** | 0 | 0 | 0 | 1 | 0 | NA | 0 | 0 | 0 | 1 | 0 | NA |
| | **AM** | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| A500 high | **ECM** | 0 | 0 | 0 | 1 | 0 | NA | 9.909 | 0.804 | 8.463 | 0.5 | 11.261 | 0.792 |
| | **AM** | NA | NA | NA | NA | NA | NA | 5.438 | 0.44 | 5.109 | 0.69 | 0.906 | 0.813 |
| B200 medium | **ECM** | 0 | 0 | 0 | 1 | 0 | NA | 9.23 | −0.73 | 10.82 | 0.38 | 8.461 | 0.765 |
| | **AM** | 0 | 0 | 0 | 1 | 0 | NA | 0 | 0 | 0 | 1 | 0 | NA |
| EC650 medium | **ECM** | 12.87 | 0.27 | 12.50 | 1 | 17.82 | 0.40 | 10.48 | 0.42 | 10.03 | 0.79 | 15.46 | 0.37 |
| | **AM** | 20 | 0.261 | 20 | 1 | 0 | NA | NA | NA | NA | NA | NA | NA |
| T2650 medium | **ECM** | 0 | 0 | 0 | 1 | 7.692 | NA | 5.66 | 0 | 5.66 | 1 | 0 | NA |
| | **AM** | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| T700 medium | **ECM** | 0 | 0 | 0 | 1 | 0 | NA | 0 | 0 | 0 | 1 | 0 | NA |
| | **AM** | 0 | 0 | 0 | 1 | NA | NA | NA | NA | NA | NA | NA | NA |
| A250 medium | **ECM** | 5.341 | 0 | 5.341 | 1 | 8.76 | NA | **2.204** | **−2.84** | **4.161** | **0.02** | 5.239 | 0.483 |
| | **AM** | 22.58 | 0 | 22.58 | 1 | 0 | NA | 0 | 0 | 0 | 1 | 0 | NA |
| T1000 low | **ECM** | NA | NA | NA | NA | NA | NA | 7.911 | 0.884 | 6.923 | 0.36 | 8.104 | 0.566 |
| | **AM** | NA | NA | NA | NA | NA | NA | 0 | 0 | 0 | 1 | 0 | NA |
| T450 low | **ECM** | 14.28 | 0 | 14.28 | 1 | 5.357 | NA | 5.031 | −1.583 | 7.109 | 0.15 | 5.87 | 0.641 |
| | **AM** | 0 | 0 | 0 | 1 | 0 | NA | 0 | 0 | 0 | 1 | 0 | NA |

after hurricanes. It is important to acknowledge the limitation of using the ITS2 metabarcoding region with ITS4ngs primers described by Tedersoo et al. (2014) for characterizing the AM communities. These primers predominantly target Ascomycota and Basidiomycota, resulting in low coverage of AM taxa during sequencing (Větrovský et al., 2023).

While we sequenced abundant AM fungi in plant roots, the AM network exhibited disconnection after Hurricane Patricia, with most AM species restricted to a single host. Our hypothesis posits that AM experienced physical damage due to their coenocytic mycelia, which can withstand more damage than ECM septate mycelia, leading to the disruption of

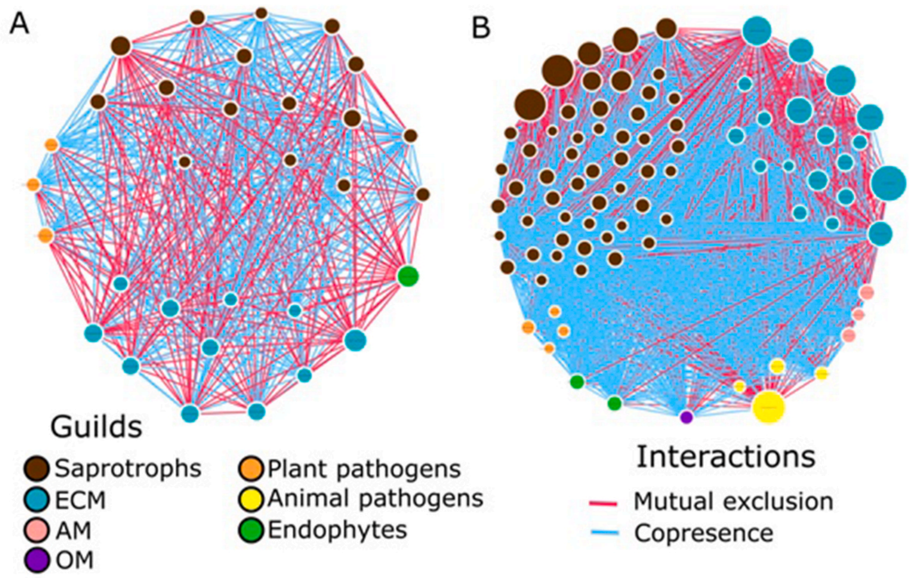

**Fig. 4.** Putative interspecific interactions inferred from co-occurrence patterns (A) one year (2016), (B) and two years after Hurricane Patricia (2017). The network in figure (A) was built with the 31 OTUs with more than 100 sequences that had a strong correlation in the interaction. The network in figure (B) was constructed with the 85 OTUs with more than 200 sequences. Size of the node indicates the frequency of negative interactions (mutual exclusion). Abbreviations: AM = Arbuscular mycorrhizal, ECM = ectomycorrhizal, OM = orchid mycorrhizal.

their associations with plants.

During hurricanes tall trees are more vulnerable to damage (Paz et al., 2018), and these mature trees are commonly network hubs (i.e., trees with more connectivity; Beiler et al., 2010; Cannon et al., 2022). The main ECM hosts of this forest are shrubs or small trees that suffered less wind impact than the tall trees. The mechanical damage to mature trees could explain the immediate disconnection between AM mycorrhizal components (Selosse et al., 2006). The disconnection of AM mycorrhizal network had never been reported because of disturbance. In a forest as dense with AM hosts it seems improbable to lose the connection between plants, at least for a long time. Some of the ECM hosts also form arbuscular mycorrhizal interactions (Álvarez-Manjarrez et al., 2021), so it is probable that even as the AM network loses links, the ECM network maintains connections between plants –forming a common network. Those hosts that have dual mycorrhiza, such as *Achatocarpus* and *Guapira*, are mycorrhizal hubs in this forest and should be consider essential for post-disturbance recovery.

According to our unipartite network analysis, interspecific interactions among fungi underwent significant changes from one year to another following the hurricane. In 2016, we observed several mutual exclusions, whereas one year later, with increased richness and abundance, fungal guilds had greater co-occurrence. Our 2016 results indicated that ECM fungi excluded AM, saprotrophic, pathogenic and other ECM fungal species. Conversely, in 2017, AM fungi were more abundant than ECM and co-occurred more with pathogens. Notably, ECM fungal species were found to inhibit pathogen establishment (Mohan et al., 2015) and saprotrophs through the Gadgil effect (Fernandez and Kennedy, 2016; Gadgil and Gadgil, 1971). Furthermore, they influenced AM colonization (Chen et al., 2000). AM fungi, while competing for root resources, could either exclude or facilitate the establishment of other fungal and promote the mycelial growth of others (Bennett and Bever, 2009). It is crucial to acknowledge that our analysis indicated probable correlations between species, not necessarily implying interspecific interactions, as these correlations could also be attributed to the effects of the abiotic conditions generated by the hurricane. Overall, we observed that antagonistic relationships were unbalanced and prone to change with environmental alterations (Kennedy, 2010; Mack and Rudgers, 2008). Importantly, plant mortality and the presence of unrooted plants may intensify competition for the remaining live roots that remain one year after a hurricane.

There is growing evidence that a regime of environmental disturbance has different effects on plant communities depending on frequency, intensity, and spatial and temporal scales of the disturbance event. The main disturbance effect of a hurricane is the mortality and loss of plant biomass (e.g., Parker et al., 2018; Zimmerman et al., 1994), which has cascading effects on the rest of the biotic communities. Our comparison between years suggests that, similarly to plants, root fungal communities show great changes following a major hurricane. As these fungal communities play critical roles in the establishment the recruitment of plants, this disruption in fungal community dynamics could have important repercussions for ecosystem structure and function. Our findings support the hypothesis that mycorrhizal network recovery depends on the level of disturbance. Further research will be required to determine whether the establishment of the mycorrhizal fungal species could accelerate recovery of the forests after disturbance.

Extreme climatic events such as hurricanes are becoming more frequent and severe as a result of global warming (Walsh et al., 2016). Both, man-made and naturally occurring extreme climatic events, create disturbance and, in turn, shape secondary successional forests (Lewis et al., 2015; Salazar et al., 2015). Disturbance complexity creates a multidirectional effect on fungal communities (García de León et al., 2018). Particularly, Hurricane Patricia disrupted fungal communities and their interaction networks (i.e., mycorrhizal networks and interspecific symbioses). These results highlight how critical disturbance will likely shape fungal communities and their ecosystems dynamics, especially in response to unprecedented global change.

## 5. Conclusions

This study marks the first investigation into the impact of a hurricane on root-associated fungal networks and their interactions. It is important to note that the effects of each hurricane impact the local environmental differently depending on its strength, plant community assembly, and local conditions. Our findings suggest that arbuscular mycorrhizal networks are more susceptible to disturbance than ectomycorrhizal networks. Generally, roots fungal communities may experience vulnerability to hurricane disturbance in the short term, but our data suggest a recovery occurring within two years. Throughout this recovery period, mycorrhizal dual plants may play a pivotal role in maintaining connections between plants. Given the escalating frequency and severity of climate change-associated disturbances, further studies are imperative to elucidate the functional implications of such changes.

## Conflicts of interest

Neither parties holding a conflict of interest or competing interest.

## Author contributions

JAM and RGO designed the study; JAM carried out the fieldwork, data analyses, and manuscript writing; MB and SP contributed with the data analysis and manuscript, RGO supervised the study, managed financial resources, and edited the manuscript.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Roberto Garibay-Orijel reports financial support was provided by National Council on Science and Technology.

## Acknowledgments

We thank CONACYT for funding the project Ciencia Básica 239266, for the PhD scholarship 404413 and for “beca mixta”. We thank the program “Posgrado en Ciencias Biológicas” of the Universidad Nacional Autónoma de México for JAM’s graduate studies. We thank our field assistants Abel Domínguez Pompa, Jorge Blanco, Rodolfo Ángeles-Argáiz, Sergio Vidal, Lorenzo Vásquez, Diego Flores, and the staff at the Biological Station of Chamela. We also thank Andrés Argüelles-Moyao for helping in the laboratory and Saleh Rahimlou for his assistance in bioinformatics. We thank Alfonso Delgado Salinas, Alfonso Valiente Banuet, Mariana Benítez Keinrad, Patricia Vélez, Margarita Villegas Ríos, Claire Elizabeth Willing, Kabir Gabriel Peay, and David Gernandt for their valuable comments and corrections.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2024.101354.

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