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Efecto del huracán Patricia en el ensamble de las comunidades de hongos del suelo y de la red micorrízica en el bosque Neotropical caducifolio

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Me permito informar a usted que en la reunión ordinaria del Subcomité de Biología Experimental y Biomedicina del Posgrado en Ciencias Biológicas, celebrada el día **7 de octubre de 2019** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **ALVAREZ MANJARREZ JULIETA** con número de cuenta **513014583** con la tesis titulada **"Efecto del huracán Patricia en el ensamble de las comunidades de hongos del suelo y de la red micorrízica en el bosque Neotropical caducifolio"**, realizada bajo la dirección del **DR. ROBERTO GARIBAY ORIJEL**, quedando integrado de la siguiente manera:

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"POR MI RAZA HABLARA EL ESPÍRITU"
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“Si la lluvia viene del cielo… entonces los hongos son divinos”

José de Jesús Preciado de León.

Yekwaate metá wixaritari Tateikietari. Hongos y Wixaritari de Tateikie

CONTENIDO

RESUMEN

Los escenarios del cambio climático predicen que habrá un aumento en frecuencia e intensidad en la incidencia de fenómenos extremos como los huracanes, por lo que estudiar sus efectos ecológicos se vuelve cada vez más relevante. En octubre del 2015, el huracán Patricia categoría 4 Saffir-Simpson, azotó el bosque tropical caducifolio (BTC) de la costa de Jalisco. Este evento catastrófico aportó 17.8 Megagramos por hectárea (Mg ha^{-1}) de biomasa al suelo, lo que aumentó el C, N y P del suelo de la Estación de Biología de Chamela. Además, durante el 2015 aumentaron la temperatura (de 25.1 a 25.6 ºC 1980-2015) y la precipitación media anual (de 765 mm a 800.4 mm 1983-2015).

Los hongos y bacterias son los principales descomponedores de la materia orgánica y su actividad se ve favorecida por altas temperaturas y humedad. Debido a la materia orgánica, y a las variables ambientales que modificó el huracán en el bosque, se propuso estudiar las interacciones de los hongos ectomicorrízicos con las plantas del BTC, el efecto del huracán Patricia en el ensamble de las comunidades de hongos del suelo, de la rizósfera y la red micorrízica en el BTC.

La tesis se dividió en tres capítulos y dos anexos: 1) la simbiosis ectomicorrízica del BTC previa al huracán; 2) efecto del huracán Patricia en la diversidad de hongos del suelo; 3) diversidad de hongos de la rizósfera y efecto del huracán en la red micorrízica. Adicionalmente, los dos anexos incluyen las descripciones de nuevas especies: el anexo 1 contiene la descripción de *Tomentella brunneoincrustata,* hongo ectomicorrízico asociado a Nyctaginaceae subfamilia Pisonieae; en el anexo 2 se encuentra la descripción de *Scytinopogon minisporus*, hongo saprótrofro común de la hojarasca del BTC.

En el capítulo 1 se realizaron muestreos de raíces con 91 núcleos de suelo del 2012 al 2014. Este muestreo fue realizado antes del huracán Patricia. Todas las raíces fueron revisadas con un microscopio estereoscópico para identificar morfotipos de ectomicorrizas. Las ectomicorrizas fueron separadas, descritas y se extrajo su DNA. Se amplificó la región ITS rDNA y se secuenció con Sanger. Los resul-

tados arrojaron que 20 especies de plantas –no monodominantes, principalmente del orden Caryophyllales– son los hospederos ectomicorrízicos de 19 especies de hongos ectomicorrízicos (ECM). *Achatocarpus* y *Guapira* fueron los principales hospederos. Los resultados sentaron las bases para poder estudiar a los hospederos ectomicorrízicos y la red micorrízica después del huracán.

En el capítulo 2 se estudiaron a las comunidades de hongos del suelo a través del tiempo. Se tomaron muestras de suelo en noviembre del 2014, mayo y octubre del 2016, y abril y septiembre del 2017 de un mismo sitio. Del suelo se extrajo el DNA y se realizó PCR multiplex para la región ITS2 con *primers* específicos para hongos; las librerías se secuenciaron usando Illumina Miseq. Se asignaron nombres taxonómicos a los OTUs comparando las secuencias contra UNITE y usamos FUNGuild para determinar los gremios. La riqueza y abundancia incrementaron después del huracán mientras la dominancia decrecía; esto se invirtió progresivamente con el paso del tiempo. Los hongos más comunes fueron basidiomicetos saprótrofos y formaron parte de la comunidad persistente. Además, se observó sucesión ecológica sin remplazo.

Para el capítulo 3, a un año después del huracán (octubre del 2016), se montaron nueve cuadrantes en el BTC para estudiar el efecto del huracán en los hongos rizosféricos y específicamente en la red micorrízica. Dentro de las parcelas se marcó a todos los hospederos ectomicorrízicos, se tomaron raíces secundarias de cada individuo y se juntaron por especie; en el 2017 se re-muestrearon las plantas marcadas. Las raíces se revisaron con microscopio estereoscópico apartando únicamente a las ectomicorrizas; se utilizó la misma metodología molecular del capítulo 1. La diversidad fue menor a un año después del huracán e incrementó al siguiente año. Se encontró que la diversidad rizosférica tiene una correlación positiva con la luz y negativa con la temperatura del suelo; la identidad del hospedero determina la comunidad rizosférica. Los Ascomycota fueron el grupo más diverso, y los Glomeromycota tuvieron baja diversidad en 2016. La red micorrízica perdió conectividad en 2016 produciendo alta modularidad, y las conexiones se recuperaron en el 2017 en la mayoría de las parcelas.

La alta diversidad fúngica encontrada en el bosque ayuda a la rápida recuperación del ecosistema. Los datos de las comunidades fúngicas mostraron resiliencia, es decir, a pesar del disturbio los hongos tuvieron la capacidad de regresar al estado previo al huracán. La perturbación es un resultado no linear de naturaleza compleja, que tiene impacto a diferentes escalas. Los cambios en los ecosistemas ponen a prueba la capacidad inherente de los organismos a soportar nuevas condiciones y la diversidad fúngica colabora a que el BTC sea resiliente a los huracanes.

ABSTRACT

Climate change scenarios predict that there will be an increase in frequency and intensity in hurricane formation, so studying their ecological effects becomes increasingly relevant. In October 2015, hurricane Patricia category 4 Saffir-Simpson made landfall in the tropical dry forest (TDF) of Jalisco's coast. This catastrophic event contributed 17.8 Mg ha^{-1} of biomass to the soil, which increased the C, N and P of the soil of the Chamela Biology Station. In addition, during 2015 the temperature increased (25.1 to 25.6 ºC 1980-2015) and the average annual rainfall (765 mm to 800.4 mm 1983-2015).

Fungi and bacteria are the main decomposers of organic matter and their activity is favored by high humidity and warm temperatures. Due to the organic matter, and environmental variables that modified the hurricane in the forest, it was proposed to study the effect of hurricane Patricia on the assembly of the fungal communities of the soil, the rhizosphere and the mycorrhizal network in the BTC.

The thesis was divided into three chapters and two supplementary files: 1) the ectomycorrhizal symbiosis of the TDF prior to the hurricane; 2) effect of Hurricane Patricia on the diversity of soil fungi; 3) diversity of rhizosphere fungi and effect of the hurricane in the mycorrhizal network. Additionally, the two annexes include descriptions of new species: Supplementary 1 contains the description of *Tomentella brunneoincrustata* associated Nyctaginaceae subfamily Pisonieae; Supplementary 2 contains the description of *Scytinopogon minisporus*, saprotroph from TDF.

In Chapter 1, root samples were sampled with 91 soil cores from 2012 to 201; Sampling done before Patricia. All roots were checked with stereoscopic microscope to identify morphotypes of ectomycorrhizae. The ectomycorrhizae were separated, described and their DNA was extracted. The ITS rDNA region was amplified and sequenced with Sanger. The results showed that 20 species of non-monodominant plants, mainly from order Caryophyllales, are the ectomycorrhizal hosts of 19 species of ectomycorrhizal fungi (ECM). *Achatocarpus* and *Guapira*

were the main hosts. The results laid the foundations for studying the ectomycorrhizal hosts and the mycorrhizal network after the hurricane.

In Chapter 2, soil fungal communities were studied over time. Soil samples were taken in November 2014, May and October 2016, and April and September 2017 from the same site. DNA was extracted from the soil and multiplex PCR was performed for the ITS2 region with fungal specific primers; the libraries were sequenced using Illumina Miseq. Taxonomic names were assigned to the OTUs by comparing the sequences against UNITE and using FUNGuild to determine the guilds. Diversity increased after the hurricane while its dominance decreased; This was reversed over time. The most common fungi were saprotrophic basidiomycetes and were part of the resistant community. In addition, ecological succession was observed without replacement.

For Chapter 3, we settled nine permanent plots in October 2016 were all ectomycorhizal hosts were tagged. From there plants, we took secondary roots and the roots of each individual were pooled by species; In 2017, marked plants roots were re-sampled. We only processed roots with ectomycorrhizae and followed the same molecular methodology of Chapter 1. We found that rhizospheric diversity had a positive correlation with light and negative to soil temperature; also host identity determines the fungal community. Diversity was lesser one year after hurricane and increased two years after. Ascomycota was the most diverse group; Glomeromycota had low diversity in 2016. Saprotrophs were the most common guild in high disturbance plots. ECM had higher richness in plots with low and high disturbance. The mycorrhizal network lost connectivity in 2016 producing high modularity, while connections recovered in 2017.

The high fungal diversity found in the forest helps the rapid recovery of the ecosystem. Data from the fungal communities showed resilience*, i.e*., despite the disturbance, the fungi had the ability to return to the pre-hurricane state. The disturbance is a non-linear result of a complex nature, which has an impact on different scales. Changes in ecosystems test the inherent ability of organisms to withstand new conditions and fungal diversity helps to make the TDF resilient to hurricanes.

INTRODUCCIÓN

Los eventos climáticos extremos son cada vez más frecuentes y se asume que tiene una conexión de ellos con el calentamiento global (Diffenbaugh et al., 2017). El aumento en la temperatura global está provocando el derretimiento del permafrost liberando reservorios de carbono y aumentando los gases invernadero (Schuur et al., 2015). El CO_2 reacciona con el agua acidificando los océanos (Hoegh-Guldberg et al., 2007), las épocas de secas y lluvias se están viendo magnificadas, y en consecuencia los fenómenos del Niño y la Niña se presentan con mayor severidad (Cai et al., 2014; Miralles et al., 2014). Así mismo, los cambios en los ciclos biogeoquímicos están teniendo un efecto en los nutrientes, propiedades físicas y la humedad del suelo (Seidel et al., 2008), y el aumento en la temperatura oceánica está promoviendo la formación e intensidad de huracanes (Knutson et al., 2015).

De manera particular, los huracanes también llamados ciclones o tifones, son eventos climáticos extremos formados por grandes cantidades de agua caliente y su energía proviene de la evaporación de la superficie del océano. El agua condensada forma nubes y lluvia; las nubes se concentran alrededor de un núcleo caliente de baja presión, conocido como el ojo del huracán (Henderson-Sellers et al., 1998). Alrededor del ojo del huracán los vientos circulan como resultado del momento angular que le proporciona la rotación de la Tierra a medida que el aire fluye hacia el eje de rotación. Los huracanes se clasifican del 1 al 5, de acuerdo con la velocidad de sus vientos en la escala Saffir-Simpson, donde 1 va de 110-153 km/h, hasta la catastrófica categoría 5 con ≥252 km/h (NOAA 2019). Después del impacto del huracán se presentan lluvias intensas durante varios días. La cantidad de precipitación depende de la humedad del aire, el tamaño y la velocidad del huracán (Regmi et al., 2013). Para el 2075 se predice que la temperatura oceánica aumentará 4.5°C, y habrá 338% más de ciclones tropicales de categorías 4 y 5. También habrá un aumento del 17% en la intensidad de las tormentas tropicales y lluvia traída por huracanes (Knutson et al., 2015). La posición geográ-

fica de México vuelve vulnerable al país ante estos eventos, por lo que entender el efecto de los huracanes es cada vez más relevante.

Los eventos climáticos extremos junto con las actividades antropogénicas son perturbaciones que modelan los sistemas forestales influyendo en su composición, estructura y funcionamiento. Cada perturbación tiene efectos diferentes en los bosques, dependiendo de su severidad, frecuencia y magnitud (Holden & Treseder, 2013). Los eventos de mayor magnitud y severidad solían ser menos frecuentes antes del cambio climático (Figura 1); sin embargo, se pronostica un aumento en frecuencia y magnitud de algunos de ellos (Knutson et al., 2015; Diffenbaugh et al., 2017). Los disturbios crean efectos en cascada en las propiedades abióticas y bióticas del sistema. Además, los ecosistemas pueden experimentar más de una perturbación, lo que tiene efectos compuestos que pueden llevar al ecosistema a nuevas composiciones o cambios sin precedentes (Dale et al., 2001).

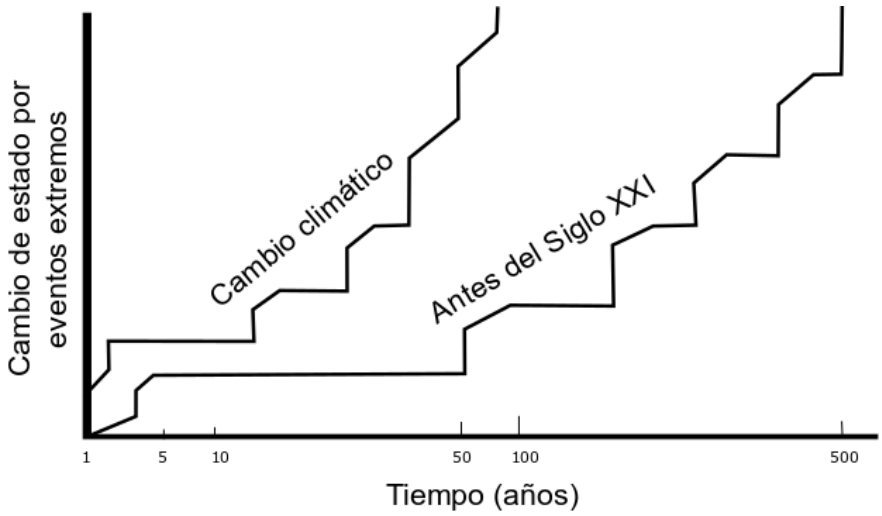

Figura 1. Modelo hipotético de la frecuencia con que suceden los eventos climáticos de gran magnitud (eventos extremos) a partir del cambio climático (idea modificada de Selby 1982).

Los cambios en los ecosistemas ponen a prueba la capacidad inherente de los organismos para soportar nuevas condiciones. Incluso hay especies que se ven beneficiadas por los cambios, al tener un ambiente más idóneo para produc-

ción de biomasa, por ejemplo el aumento de CO_2 y de la temperatura beneficiará a algunas especies de plantas (Bellard et al., 2012). Las especies cuya capacidad intrínseca a variar (e.g. en su fisiología, fenología o distribución) y a persistir en la perturbación, confieren resistencia a las funciones del ecosistema (Bellard et al., 2012; Oliver et al., 2015). La respuesta plástica de las especies es importante para su persistencia a corto plazo pero esto también puede tener un costo y ser insuficiente para evadir su extinción (Gienapp et al., 2008; Moritz & Agudo, 2013).

Los efectos de los eventos extremos que propicia el cambio climático pueden medirse a diferentes escalas. Estas escalas pueden ser en espacio, tiempo o inherente a sus características biológicas-fisiológicas, y pueden tener efecto en los diferentes niveles de la biodiversidad (desde individuos hasta biomasa). En la escala de individuos un evento extremo puede hacer variar su fecundidad, susceptibilidad a enfermedades, sobrevivencia, tasa de actividad, crecimiento, etc; a nivel de poblaciones puede variar el reclutamiento, la estructura de edades, la abundancia, rango de su distribución, etc; en comunidades puede tener efecto en nuevas interacciones interespecíficas, desequilibrio, desincronización, etc; en ecosistemas puede variar el flujo de energía, la cantidad de biomasa, la producción de servicios ecosistémicos, etc. (Bellard et al., 2012).

A escala de comunidad, si la composición biológica tiende a la redundancia ecológica –diferentes especies desempeñan el mismo papel ecológico– al experimentar perturbación, la comunidad tiene mayor propensión a mostrar resiliencia (Standish et al., 2014). La alta biodiversidad incrementa la resiliencia del ecosistema (Mori, 2016). Las especies que tienen alta tolerancia a la alteración de las condiciones (i.e. temperatura, pH, nutrientes, entre otros) son las especies que conforman las comunidades de ambientes con alto disturbio.

Existe un debate sobre el concepto de resiliencia. Holling (1973) propuso el término para referirse a la habilidad del sistema para resistir el cambio y hacer frente al disturbio o para regresar después de la perturbación a un estado estable similar al incial. Con el tiempo, el concepto derivó en el proceso de recuperarse después del disturbio (Pimm 1994; Grimm & Wissel, 1997). Actualmente existen

términos que han sido derivados del estudio de la perturbación y que se han confundido con resiliencia. Por ejemplo, ‘resistencia’ se puede definir como el grado en el que una variable cambia después de un disturbio (Pimm 1994), como la inmutación de la comunidad al disturbio (de Vries & Shade, 2013), o como la capacidad de regresar rápidamente al estado previo al disturbio (Oliver et al., 2015). Por otro lado, también el concepto ‘recuperación’, que invloucra los procesos endógenos que llevan al sistema al equilibrio, suele tomarse como resiliencia. Mientras que la ‘elasticidad’ es la tasa en la que un sistema se recupera del disturbio (Hodgson et al., 2015). En esta tesis se empleará el término resiliencia como la capacidad regresar a un estado estable similar al incial, de Holling (1973).

Las comunidades microbianas, compuesta por archeas, bacterias, hongos, protozoarios, entre otros, habitan en prácticamente cualquier ecosistema o sustrato del planeta. En el suelo las comunidades microbianas son altamente diversas y generalmente presentan redundancia ecológica. La alta diversidad del edafón (i.e. organismos que habitan en el suelo) puede llevar al ecosistema a la estabilidad. La estabilidad se manifiesta en la resistencia y de la resiliencia, por lo que la estabilidad de la comunidad microbiana serán resistentes y resilientes dependiendo de su diversidad y su fisiología (Cantrell et al., 2014). El edafón se compone de bacterias, artrópodos, nematodos, anélidos, mamíferos, reptiles, protozoos, hongos, etc. Particularmente los hongos, uno de los grupos más biodiversos del planeta (Blackwell, 2011), tienen papeles ecosistémicos importantes como la descomposición de la materia orgánica, participando activamente en los ciclos biogeoquímicos del C, N y P (Bueé et al., 2009; Jaramillo et al., 2018). En el grupo de los hongos se encuentran especies con estilos de vida muy variados, como los saprótrofos, que son degradadores de la materia orgánica; los micorrízicos, que se establecen de manera mutualista con las raíces de las plantas; los parásitos y patógenos de animales, plantas y hongos; los endófitos, que pueden llegar a ser mutualistas o parásitos; los liquénicos, que tienen asociaciones mutualistas con cianobacterias y algas, etc.

Particularmente, los hongos micorrízicos tienen una relación mutualista con las plantas al haber intercambio de nutrimentos entre ambos (Trappe 2005). De acuerdo con su morfología y fitobionte participante se diferencían siete tipos de micorrizas (Smith & Read, 2008), dentro de las cuales las ectomicorrizas (ECM) son constituidas por hongos de los phyla Ascomycota y Basidiomycota, mientras que las micorrizas arbusculares (AM) están conformadas por hongos del subphylum Glomeromycotina. Éstas dos son las interacciones micorrízicas más comunes en los ecosistemas terrestres (Smith & Read, 2008). Los hongos ectomicorrízicos, tienen la capacidad de oxidar materia orgánica del suelo para obtener C, aunque en menor proporción que los hongos saprótrofos (Shah et al., 2016). Estos hongos reciben C de los fotosintatos de su planta hospedera y le transfieren hasta el 80% del N y el 70% del P adquirido del suelo. Los hongos micorrízicos arbusculares son simbiontes obligados pues dependen de su hospedero vegetal para la obtención del C; a cambio, estos hongos extraen del suelo N y P, y los transfieren a la planta (trasfieren a la planta hasta el 20% del N y el 90% del P adquirido del suelo; van der Heijden et al., 2015).

Existen algunos trabajos donde refieren el efecto de las perturbaciones en las comunidades de hongos, como en incendios o deforestaciones (*e.g.* Holden et al., 2013) y en particular de los hongos micorrízicos (e.g. Rincón et al., 2014; Glassman et al., 2015). No obstante, poco se conoce sobre el efecto de los huracanes en la estructura de las comunidades de hongos. Cantrell y colaboradores (2014) realizaron simulaciones de un huracán en parcelas experimentales en Puerto Rico, tratando de conocer el efecto en las comunidades de hongos y bacterias. Ellos encontraron que la apertura del dosel y la variación interanual de la precipitación tienen un fuerte efecto en la actividad microbiana. Por otro lado, Vargas y colaboradores (2010) estudiaron el efecto del huracán Wilma en las comunidades de hongos micorrízico arbusculares de Yucatán, donde encontraron que existe mayor porcentaje de colonización en las raíces de las plantas después del huracán; además de haber un enriquecimiento de N en el suelo, al aumentar la humedad y temperatura del suelo, lo que ayudó a la rápida descomposición. Ellos hipo-

tetizan que las plantas adoptan la estrategia de invertir más C en sus micorrizas, en vez de formar nuevas raíces, por lo que encuentran mayor colonización.

Los hongos micorrízicos habitan en el suelo, donde llegan a completar su ciclo de vida formando propágulos sexuales o asexuales. Estos hongos necesariamente deben estar asociados a sus hospederos, ya que algunos pueden obtener C de la descomposición de la materia orgánica, pero necesitan el aporte de sus simbiontes vegetales (Shah et al., 2016). En algunos bosques tropicales se ha visto que los hongos ectomicorrízicos tienen alta especificidad hacia sus hospederos (Tedersoo et al., 2010). Por ejemplo, en el bosque tropical caducifolio, que está compuesto principalmente de leguminosas, la mayoría de sus plantas no forma esta interacción (Alvarez-Manjarrez, 2014; Waring et al., 2016), por lo que las plantas ectomicorrízicas representan islas por colonizar. Es decir, a pesar de que en el suelo se encuentren todos los propágulos de estos hongos, sólo algunos de ellos llegarán a establecerse en las raíces.

Cuando los hongos micorrízicos logran establecerse con su hospedero, colonizan todas las raíces posibles, ya sean de la misma planta, de la misma especie o de otras especies adyacentes. Por lo tanto, diferentes especies de plantas pueden estar micorrizadas por el mismo hongo, interconectadas entre sí por micelio en común. A esta conexión planta-planta vía hongo se le conoce como red micorrízica. A través de la red micorrízica, se transfieren compuestos de planta a planta (e.g. agua, carbono, nitrógeno, fósforo, etc.) y se ayuda al establecimiento, crecimiento y sobrevivencia de plántulas (Simard et al., 2012).

Las propiedades de las redes micorrízicas han sido analizadas desde la teoría de redes (Beiler et al., 2010; Montesinos-Navarro et al., 2012; Bahram et al., 2014; Põlme et al., 2018). La teoría de redes nos ayuda a comprender las interacciones ecológicas de las especies que componen una comunidad. Las propiedades estadísticas y topológicas de las redes nos permiten entender la robustez (resiliencia) de las comunidades ante la afectación de las comunidades por eventos climáticos extremos. Estas modificaciones de las comunidades son perturbaciones a la red de interacciones. Entiéndase perturbación de las redes como la pérdida de

nodos o enlaces entre nodos. No obstante, el estudio sobre la perturbación en las redes micorrízicas y su cambio en el tiempo todavía no ha sido explorada.

En la presente tesis se realizó un estudio sobre el efecto del huracán Patricia en el bosque tropical caducifolio de Chamela, Jalisco. El huracán Patricia golpeó las costas de Jalisco el 24 de octubre del 2015, alcanzó vientos máximos de 345 km/h y antes de tocar tierra redujo su velocidad a 240 km/h (categoría 4); impuso un récord en el Pacífico, al alcanzar vientos de 190 km/h en 24 h. La fase cálida propiciada por el fenómeno de El Niño asociada a la Oscilación del Sur provocó la formación de tan poderoso huracán. Este huracán causó daños en la vegetación, provocando un aporte de troncos, ramas y árboles desenraizados; especialmente de fracciones finas de lignina (Martínez-Yrízar et al., 2018). El dosel dañado aportó 17.8 Mg ha^{-1} de biomasa al suelo (Parker et al., 2018) engrosando el mantillo con hojas y ramas, lo cual generó una ganancia de nutrientes en el suelo (Gavito et al., 2018).

La principal vegetación de la costa de Jalisco es el bosque tropical caducifolio (BTC), donde la familia Fabaceae tiene la mayor diversidad y densidad. Esta tesis hipotetizó que ya que algunas especies de leguminosas han sido reportadas como hospederos ectomicorrízicos en otras partes del mundo (e.g. Henkel et al., 2002) los hospederos ectomicorrízicos del BTC pertenecerán a la familia de las leguminosas.

El BTC se caracteriza por un periodo de lluvias muy estacional; durante la época de secas, los árboles caducifolios reabsorben nutrientes antes de tirar sus hojas dando lugar a la acumulación de mantillo (Rentería et al., 2005). Mientras la sequía persiste, la actividad microbiana se ve reducida por la falta de agua, y la transformación y descomposición del N se detiene. La degradación del mantillo está en función de la disponibilidad y variación en la precipitación anual (Anaya et al., 2012). El huracán Patricia incrementó la cantidad de nutrientes en la materia orgánica, la temperatura (de 25.1 a 25.6 ºC 1980-2015) y la precipitación media anual (de 765 mm a 800.4 mm 1983-2015; Maass et al., 2018), la descomposición del mantillo (Gavito et al., 2018) pero se desconoce el efecto en las comunidades

fúngicas. Por lo que se propusieron las hipótesis: 1) el aumento de nutrientes en el suelo, principalmente C, N y P, incrementará la diversidad de hongos del suelo, principalmente saprótrofos del phylum Basidiomycota; 2) el aumento en la cantidad total de nitrógeno y fósforo provocará la reducción de la interacción micorrízica, por lo que se reducirá la diversidad de hongos micorrízicos en el suelo.

El suelo funciona como sustrato de muchos hongos, mas no explica toda la biología de los hongos micorrízicos, por lo que también se estudió la rizósfera. La rizósfera es la estrecha región del suelo en contacto con las raíces de las plantas. La diversidad fúngica de la rizósfera está fuertemente influenciada por su hospedero y el suelo que lo rodea (Grayston et al., 1998). Por lo que se esperó que: 1) el aumento de nutrientes en el suelo propiciará un aumento en la diversidad fúngica de la rizósfera; 2) los hongos rizosféricos compiten por la interacción con la raíz, por lo que un sistema perturbado generará un cambio en las interacciones interespecíficas; 3) las redes micorrízicas suelen tener alta modularidad –propiedad de la red que experimentalmente reduce el impacto de la perturbación– por lo que los sitios donde la perturbación del huracán Patricia fue mayor, se espera que la modularidad sea más alta.

La presente tesis estudió el efecto del huracán Patricia en las comunidades de hongos del suelo y, específicamente en las comunidades rizosféricas. Para entender cómo se modifica la comunidad de hongos del suelo tendiendo a volver a la estabilidad previa al huracán, además de modelar la red micorrízica; y con ello se contribuyó al conocimiento de la ecología de los hongos durante la perturbación. El documento está dividido en tres capítulos y dos anexos:

Capítulo 1. Tuvo como objetivo deteminar a los simbiontes ectomicorrízicos, tanto plantas como hongos, del bosque tropical caducifolio antes del huracán Patricia.

Capítulo 2. Sus objetivos fueron conocer la comunidad de hongos saprótrofos, micorrízicos, parásitos, patógenos y otros estilos de vida del suelo; y comparar el ensamble de las comunidades de hongos del suelo antes y después del hura-

cán para conocer el efecto de la perturbación de acuerdo con datos ambientales y cantidad de nutrientes en el suelo.

Capítulo 3. Los objetivos fueron identificar las especies de hongos ectomicorrízicos que se establecen en las rizósferas a pesar de la perturbación causada por el huracán; determinar cuáles son las variables ambientales o nutrimentales que benefician a los hongos ectomicorrízicos para que se establezcan en las raíces después de un huracán; comparar las interacciones interespecíficas de los diferentes gremios fúngicos en los dos años después del huracán; y evaluar el efecto de la perturbación del huracán Patricia en la estructura de la red micorrízica.

Anexo 1. Descripción la nueva especie *Tomentella brunneoincrustata,* hongo ectomicorrízico que se establece exclusivamente con raíces de Nyctaginaceae en el BTC de Chamela, Jalisco. Adicionalmente se realizó un análisis filogenético para todos los representantes del género *Tomentella* en México.

Anexo 2. Descripción la nueva especie *Scytinopogon minisporus*, hongo saprótrofo común en los residuos del mantillo en el BTC de Chamela, Jalisco.

MARCO TEÓRICO

Los microorganismos del suelo y su papel ecológico

El suelo, constructo de la alteración física y química de las rocas por la actividad biológica, es la corteza terrestre más superficial. El suelo contiene materia orgánica, minerales, gases, líquidos y organismos; es un ecosistema hiperdiverso donde se establecen las plantas, habitan bacterias, hongos, artrópodos, mamíferos, reptiles, etc (Voroney & Heck, 2015). En una hectárea de suelo en buen estado de conservación hay 1000 kg de lombrices, artrópodos, 150 kg de protozoarios, algas, 1700 kg de bacterias y 2700 kg de hongos (Pimentel et al., 1980; Lee & Foster, 1991; Barget & ven der Putten, 2014). Esta cantidad de biomasa corresponde en gran medida a la materia orgánica encontrada en el suelo.

La materia orgánica del suelo proviene de las plantas, animales y microorganismos que en él habitan. Esta materia orgánica es la que determina los nutrientes que tendrá el suelo, puesto que de la descomposición de la materia orgánica se reciclarán todos los elementos que la componían. La materia orgánica puede contener polisacáridos (celulosa, hemicelulosa, almidón, pectina), proteínas, quitina, lignina –compuesto más recalcitrante de la materia orgánica–, entre otras; dependiendo de su composición química podrán ser fácilmente adquiribles por los organismos del suelo o necesitarán de procesos enzimáticos u oxidativos para descomponerse (Chenu et al., 2015).

Al finalizar la descomposición de la materia orgánica se pueden obtener diferentes elementos que son esenciales para todos los organismos: carbono, nitrógeno, fósforo, potasio, calcio, azúfre, entre otros. Los nutrientes disponibles del suelo –iones asimilables por las plantas y microorganismos, por ejemplo el ion amonio (NH_4)– se agotan rápidamente, por lo que el proceso de descomposición es constante. Los encargados de llevar a cabo la descomposición son los microorganismos del suelo, que incluye a los microartrópodos, nematodos, hongos y bacterias. Los microartrópodos ayudan a romper mecánicamente el mantillo que apor-

tan las plantas en el suelo. Mientras que las bacterias y los hongos rompen las moléculas que conforman a la materia orgánica dejando nutrientes disponibles (Berg, 1999).

Los hongos y las bacterias del suelo tienen un papel fundamental en la descomposición de la materia orgánica y el reciclaje de nutrientes por lo que regulan y equilibran a los ciclos biogeoquímicos (Bahram et al., 2018). Las bacterias son los organismos más abundantes del planeta y se encuetran habitando todo tipo de ambientes, incluso en condiciones extremas de temperatura o presión (Bargett & van der Putten, 2014). Tanto bacterias como hongos son diversos y sus roles ecológicos no se restringen a la descomposición de la materia orgánica. Por ejemplo, las bacterias del género *Rhizobium* pueden asociarse a las raíces de algunas leguminosas y fijar nitrógeno atomsférico gracias a sus enzimas nitrogenasas (Zahran 2001); los hongos también pueden asociarse a las raíces del 96 % de las plantas y proveerlas de nitrógeno, fósforo y agua (van der Heidjen et al., 2015).

Los hongos y sus gremios nutricionales

El reino de los hongos se estima que es uno de los grupos más diversos del planeta, con una estimación aproximada de 1.5 - 5.1 millones de especies (Blackwell, 2011). Se han secuenciado 44,563 OTUs de hongos que habitan en los suelos de alrededor del mundo (Tedersoo et al., 2014b). Todos estos hongos pueden ser categorizados en los diferentes gremios, grupos de especies que usan estrategias ecológicas similares para explotar el mismo recurso (Peay et al., 2016). Estos gremios son los hongos saprótrofos, micorrízicos, liquénicos, endófitos, patógenos y parásitos de animales o plantas. Es importante mencionar que aunque los podemos clasificar de este forma, existen muchas especies que no pertenecen toda su vida a un gremio exclusivamente (e.g. hongos endófitos que pueden ser saprótrofos; hongos ectomicorrízicos que pueden ser saprótrofos; hongos saprótrofos que pueden ser parásitos, etc.; Thomas et al., 2016; Shah et al., 2016; Lanver et al., 2018).

Los hongos saprótrofos obtienen su carbono de la descomposición de la materia orgánica inherte. Estos hongos pueden tener la capacidad enzimática para

descomponer la pared celular de las plantas (hongos de pudrición café y blanda) y lignina (hongos de pudrición blanca). Principalmente los hongos del pylum Basidiomycota, y alguas especies de Ascomycota, contiene especies con capacidad de desarrollar pudrición blanca (Voriskova & Baldrian, 2013). Dependiendo de la composición de la materia orgánica es la sucesión de especies fúngicas; las especies pioneras de hongos son los que tienen preferencia por moléculas sencillas de obtener, como glucosa y celulosa, hasta que llegan las especies con la capacidad de romper moléculas recalcitrantes, como la lignina (Talbot et al., 2015).

Los hongos micorrízicos, endófitos y liquénicos mantienen una relación mutualista con sus simbiontes. Los hongos micorrízicos obtienen el carbono de sus simbiontes, mientras que pueden proporcionar nutrientes, metabolitos, protección contra patógenos, humedad, etc. Los hongos endófitos tienen una relación estrecha con sus plantas hospederas, pues prácticamente pueden habitar toda su vida dentro de los tejidos vegetales. Estos hongos se transmiten de manera vertical a través de las semillas de las plantas, o de manera horizontal y al penetrar al hospedero suelen ser asintomáticos (Busby et al., 2016). Los hongos endófitos también tienen un papel importante en la descomposición de la materia orgánica, puesto que son los primeros hongos presentes en la materia en descomposición. La mayoría de los hongos endófitos son Ascomycota (Promputtha et al., 2007; Song et al., 2017). De igual forma, el 90% de los líquenes son asociaciones de ascomicetos (y 10% basidiomicetos) con cianobacterias o algas verdes. El hongo necesita de la interacción con los fotobiontes para poder formar un talo. Los líquenes representan el 8% de la biomasa terrestre (Asplund & Wardle, 2017). En el siguiente apartado se hablará con más detalle de los hongos micorrízicos.

Los hongos patógenos y parásitos de animales y de plantas son hongos antagónicos de sus hospderos, pues se alimentan de sus tejidos causándoles necrosis y otras enfermedades. Estos hongos fitopatógenos suelen ser agentes infecciosos que colonizan tallos, hojas, raíces, flores y frutos. Su infección se puede dar por los estomas de las hojas, flores o por daño directo al tejido infectado (Garrett et al., 2015). Mientras que los hongos que atacan a los animales también

pueden atacar tejidos específicos, e incluso algunos de ellos son comensales, los cuales pueden ser patógenos oportunistas (Gauthier et al., 2015).

Los hongos micorrízicos

Los hongos micorrízicos son todos aquellos que tienen simbiosis con las raíces de las plantas, generalmente mutualistas. Cuando la asociación es mutualsita, las plantas transfieren fotosintatos –principalmente glucosa– a sus simbiontes fúngicos, mientras que los hongos por medio de procesos enzimáticos u oxidativos (Shah et al., 2016), obtienen nitrógeno (NH_4, NO_3) y fósforo (PO_4) del suelo y lo translocan a la raíz (van der Heidjen et al., 2015).

Smith & Read (2008) propusieron clasificar a las micorrizas en siete tipos de acuerdo a su morfología y familia de planta que coloniza: ectomicorriza, endomicorriza –también llamada micorriza arbuscular–, ectendomicorriza, micorriza ericoide, monotropoide, arbutoide y orquideoide. Las ectomicorrizas (ECM) y las micorrizas arbusculares (AM) son los dos tipos más estudiados por su importancia ecológica. Las ECM se forman con 2% de las plantas terrestres (Brundrett & Tedersoo, 2018) principalmente coníferas aunque también se pueden encontrar en angiospermas (Corrales et al., 2018); fuera de los trópicos se estima que el 80% de los árboles forman ECM (Steidinger et al., 2019). Los phyla de hongos que forman esta asociación son Ascomycota, Basidiomycota y Mucoromycota (Brundrett & Tedersoo, 2018). Mientras que las AM se con el 80% de las plantas terrestres, siendo más dominantes en los ecosistemas tropicales (van der Heijden et al., 2015; Steidinger et al., 2019). Esta asociación es formada por el phylum Mucoromycota subphylum Glomeromycotina (Spatafora et al., 2016).

Los bosques tropicales cada vez han sido más explorados por los micólogos, lo cual ha generado el descubrimiento de plantas que forman la asociación ectomicorrízica, e.g., los bosques de leguminosas en Guyana (Smith et al., 2011). Adicionalmente se han descrito nuevas especies de hongos ectomicorrízicos (e.g. Ramírez-López et al., 2015; Sánchez-García et al., 2016; Sukarno et al., 2019) Estas exploraciones han ayudado a entender que la diversidad de hongos ectomicorrízicos en los tropicos están fuertemente influenciados por la identidad y abun-

dancia de su hospedero puesto que son altamente específicos (Tedersoo et al., 2010; Alvarez-Manjarrez et al., 2018; Corrales et al., 2018). Los hospederos tropicales conocidos hasta el momento pertenecen a las familias Achatocarpaceae, Dipterocarpaceae, Fabaceae, Fagaceae, Junglandaceae, Myrtaceae, Nyctaginaceae, Polygonaceae, Phyllantaceae, Pinaceae, Salicaceae, Sarcolanaceae (Alvarez-Manjarrez 2014; Corrales et al., 2018) El patrón mundial indica que la diversidad de hongos ectomicorrízicos es menor en los trópicos, en comparación con las zonas templadas y boreales (Bahram et al., 2013), probablemente por la abundancia de sus hospederos (Steidinger et al., 2019). En los bosques donde la abundancia de los hospederos ectomicorrízicos es baja, los hongos ectomicorrízicos se encuentran restringidos en área; tal es el caso de los bosques tropicales caducifolios.

Algunas plantas pueden presentar varios tipos de micorriza. Aunque poco se sabe de la importancia de la dualidad de las interacciones micorrízicas, es probable que le confiera mayor beneficio (Teste et al., 2019). Por ejemplo, las coníferas presentan micorrizas arbusculares y ectendomicorrizas cuando están en estadíos muy tempranos de desarrollo; conforme el árbol envejece, va asociándose mayoritariamente con hongos ectomicorrízicos. Que las plantas puedan tener en sus raíces a diferentes especies de hongos les confiere versatilidad en la adquisición de nutrientes y agua, pero además pueden establecer conexión con otras plantas –de la misma o de diferente especie– a través de los hongos (Simard 2018).

La red micorrízica

Las conexiones que existen entre las raíces de las plantas a través de los hongos se conocen como redes micorrízicas. Estas conexiones les permiten compartirse nutrientes y señales químicas entre plantas de la misma preferentemente a su descendencia, o de diferente especie (Simard et al., 2012; 2015; Simard 2018).

Las redes micorrízicas se pueden dividir dependiendo del grupo de hongos que las forman: la red micorrízica arbuscular y la red ectomicorrízica. Esta di-

ferencia se basa en las diferentes estrategias que tiene cada grupo de micorriza, pero además por su ecología. Las redes micorrízicas arbusculares son formadas por un bajo número de especies fúngicas que pueden asociarse a un gran número de plantas (Montesinos-Navarro et al., 2012). Mientras que las redes ectomicorrízicas, tienen alta especificidad hacia la identidad del hospedero, por lo cual pueden llegar a ser más restringidas e.g. en los bosques tropicales (Bahram et al., 2014).

En estas redes se ha comprobado el paso de carbohidratos entre plantas, lo cual se puede ver como un proceso de facilitación, lo que a su vez ayuda al establecimiento del bosque. De igual forma, se ha descubierto que en los bosques caducifolios de Francia, los encinos no tienen suficientes reservas de carbono para rebrotar durante la primavera. Existe flujo de carbono de la red ectomicorrízica hacia sus hospederos, lo cual les ayuda a formar nuevo material fotosíntetico y volver a pagar el carbono a los hongos (Bernard et al., 2012). Adicionalmente, a través de la red micorrízico arbuscular, las plantas pueden alertar a las plantas aledañas de formar metabolitos secundarios así evitando el ataque por herbívoros (Babikova et al., 2013).

Todas estas maravillas que pasan debajo de nuestros pies, han sido objeto de estudio en modelos matemáticos, como lo son los modelos de redes (e.g. Simard 2018).

Propiedades de las redes ecológicas

Las redes ecológicas son modelos de interacciones de dos o más organismos. Nos ayudan a representar, enumerar o catalogar las interacciones de una comunidad (Jordano et al., 2009). En estos modelos existen nodos que representan a las especies interactuantes, y enlaces que son las interacciones que hay entre ambos. Estas interacciones pueden ser mutualistas o antagonistas. Un grupo de nodos conectados a cierto nodo constituye el vecindario, y el número de tales conexiones es el grado. El grado nos ayuda a saber la generalización-especialización de cada especie (Jordano et al., 2009). Las redes ecológicas se

han ayudado de la teoría de grafos para generar modelos de redes. Dichos modelos pueden ayudar a entender estructura y propiedades de las redes.

Cuando las redes se construyen con nodos de la misma naturaleza se le llama red unipartita (e.g., interacción entre ardillas, gatos, cacomixtles, perros de mi colonia; aunque son elementos heterogéneos todos son animales). Cuando las redes se contruyen con dos clases distintas de elementos, entonces son redes bipartitas (Figura 2), tal es el caso de la interacción de las plantas con los hongos micorrízicos (Mariani et al., 2019).

Existen diferentes propiedades que se miden de las redes. A continuación se dará una breve explicación de cada una de las métricas de las redes.

La conectividad es el número de interacciones con respecto al total posible; generalmente es baja a medida que la riqueza de especies de una comunidad aumenta. Topología se refiere a distribución de los enlaces entre especies, es decir la distribución del grado o de conectividad. Saber la topología nos ayuda a entender cómo se entrelazan los nuevos nodos y qué tan sensible es la red cuando los nodos se pierden. En general, las redes reales tienen gran número de nodos con pocos enlaces, y nodos superenlazados –también llamados *hubs*– (Jordano et al., 2009). Los nodos que tienen pocas conexiones se les puede considerar especialistas, mientras que los nodos más conectados serían los generalistas. Existen algunas ecuaciones para poder medir el grado de especialización de cada especie (d') o de una red bipartita (H_2' ; Blüthgen et al., 2006).

Al comparar las topologías de las redes ecológicas se pueden encontrar similitudes de cómo se distribuyen las conexiones. Uno de esos patrones es el anidamiento o encajamiento (*nestedness*). El anidamiento es la conexión de nodos *i* y *j* donde el grado de *i* es más pequeño que el grado de *j*, siempre y cuando tengan este conjunto de nodos se encuentren en el mismo vecindario (Figura 2; Mariani et al., 2019). Dicho de otro modo, las especies especialistas interactúan exclusivamente con las generalistas, y éstas a su vez interactúan entre ellas (Jordano et al., 2009).

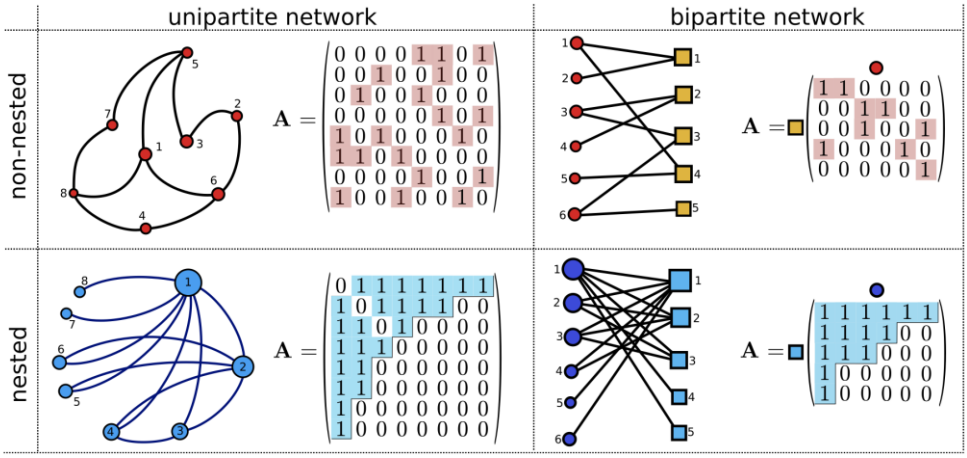

Figura 2. Ejemplos de redes unipartitas y bipartitas con y sin anidamiento. Tomada de Mariani et al., 2019.

Por otro lado, hay especies dentro de la red que interactúan con mayor intensidad y frecuencia entre sí, formando módulos o compartimentos, a esta característica se le llama modularidad (Jordano et al., 2009). Estos subgrupos con mayor especificidad pueden funcionar como subredes (Lewinsohn et al., 2006).

Las redes mutualistas y redes tróficas, pueden ser modulares (Raffaeli & Hall, 1992; Dicks et al., 2002); las redes con más de 50 polinizadores suelen ser significativamente modulares, y hay correlación entre el anidamiento y la modularidad. Las redes con menor número grado tienden a ser altamente modulares, mientras que al haber más conexiones tiende al anidamiento. Existen redes que pueden ser tanto anidadas como modulares, ya que se interconectan los módulos generando anidamiento (Fortuna et al., 2010). Las redes ectomicorrízicas presentan alta modularidad y no-anidamiento (Bahram et al., 2014). Mientras que las redes micorrízicas arbusculares suelen ser anidadas (Montesinos-Navarro et al., 2012).

Existen el debate acerca de que tanto anidamiento como la modularidad indican que la red al ser perturbada puede ser robusta y resiliente. El anidamiento, al estar compuesto por especies generalistas con alto grado, la pérdida de alguno de los nodos puede no colapsar la red; sin embargo, la consecuencia en la red depende del nodo que se pierda, pues al eliminarse un nodo con pocas conexio-

nes tiene menor impacto (Burgos et al., 2007). En contraparte, se sugiere que el anidamiento puede ser un indicador de comunidades menos estables en comparación con redes sin estructura; y al ser redes mutualistas puede demeritar su persistencia (Suweis et al., 2013). Mientras que la modularidad de la red también se ha observado que puede tener un efecto en el módulo afectado pero impide la afección a todos los demás miembros de la red (Gilarranz et al., 2017).

Perturbación y sus efectos en los microorganismos

Los ecosistemas se encuentran en constante perturbación, principalmente por actividades antropogénicas y por los eventos climáticos, cada vez más frecuentes. La perturbación crea heterogeneidad en el paisaje, así como cambio en las poblaciones de especies; lo cual a su vez tiene repercusión en el ensamble de las comunidades. Las especies que tengan mayor tolerancia al estrés o al ser modificado su ambiente se vean favorecidas son las que formarán parte de la comunidad después de la perturbación (Oliver et al., 2015).

La habilidad de una comunidad de sobrellevar el estrés ambiental o a la perturbación y tender al estado previo, se le conoce como estabilidad (Harrison, 1979). Orians (1975) menciona que la estabilidad lo conforman siete propiedades: constancia, persistencia, inercia, elasticidad, amplitud, estabilidad cíclica y trayectoria de la estabilidad. A la constancia también se le puede llamar resistencia, pues es la falta de cambios de algún parámetro del sistema, número de especies, composición taxonómica, etc. después de la perturbación. La persistencia es la sobrevivencia en el tiempo de alguno de los elementos del sistema. La inercia es la habilidad del sistema a resistir perturbaciones, lo cual corresponde a la definición de resiliencia de Holling (1973). La elasticidad es la velocidad a la que el sistema regresa al estado previo a la perturbación. La amplitud es el área en donde el sistema permanece estable. Actualmente la estabilidad se describe comúnmente por su resiliencia y resistencia; para esta tesis se utilizó el término resiliencia como la habilidad del sistema de absorber la perturbación mientras se mantienen la función y estructura (Meyer et al., 2016).

Los hongos y las bacterias presentan redundancia ecológica por ser principalmente descomponedores (Purahong *et al*., 2016). Sin embargo, tienen diferencias biológicas importantes que generan distintas reacciones de respuesta a los cambios ambientales. Una de las diferencias radica en el cociente C:N de ambos organismos. El cociente C:N correlaciona con la tasa intrínseca de crecimiento de las comunidades microbianas. Los hongos tienen en promedio un cociente C:N de ~5-15 y las bacterias ~3-6. Por lo tanto, los hongos pueden crecer en sitios donde hay menor cantidad de N en comparación con el C, y en los sustratos ricos en N crecen rápidamente bacterias (Steren y Elser, 2002). Además, la tasa de crecimiento de las bacterias es exponencial en horas, mientras que los hongos crecen con menor velocidad. Los hongos, en general, pueden considerarse como una comunidad con estrategia *K*, en comparación con las bacterias (de Vries y Shade, 2013).

Hemos aceptado ampliamanete que la riqueza y composición de las comunindades vegetales afectan procesos ecosistémicos y su influencia es incorporada en modelos de escalas globales. Los microorganismos, que desempeñan papeles ecológicos igualmente importantes, fueron la caja negra durante mucho tiempo (Allison & Martiny, 2008). El desarrollo de la biología molecular nos armó de herramientas para poder entender mejor la ecología de las comunidades microbianas. Recientemente, la actividad de las comunidades microbianas, e.g. la descomposición ha sido modelada para escalas globales (Steidinger et al., 2019), y cada vez se sabe más de los efectos de la composición de las comunidades microbianas. Al igual que en los macroorganismos, las comunidades microbianas pueden ser resistentes y resilientes después de la perturbación (Allison & Martiny, 2008).

El impacto de la perturbación en las comunidades microbianas depende de la naturaleza del disturbio. Por ejemplo, la biomasa de los microorganismos se reduce después de un incendio hasta un 48.7%, después de la cosecha hasta 19.1% y de tormentas hasta 41.7%. Las diferencias en los efectos de las perturbaciones abióticas y bióticas sobre las comunidades microbianas, varían dependien-

do de la disrupción del suelo y la remoción de la materia orgánica (Holden & Treseder, 2013).

Generalmente la perturbación provoca sucesión de especies, es decir cambios locales en la composición de especies (Ellner & Fussmann, 2003). Ha habido gran seguimiento sobre las comunidades de hongos ectomicorrízicos después de incendios (e.g. Stendell et al., 1999; Dahlberg, 2002; Rincón et al., 2014), donde encuentran que la riqueza decrece dependiendo del tiempo en que duró el incendio. Adicionalmente, hay hongos pirófilos que son propiciados por los incendios y colonizan las plántulas (Rincón et al., 2014). Así como este estudio, se han encontrado más sobre otros eventos climatológicos y actividades antropogénicas (e.g. Kalucka & Jagodzinski, 2017; Krug Vieira et al., 2018; Smith et al., 2018; Wang et al., 2019). Aunque cada vez toma más relevancia el estudio de las comunidades microbianas después de la perturbación, todavía falta mucho por saber.

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Julieta 27/11/19

CAPÍTULO 1. CARYOPHYLLALES ARE THE MAIN HOST OF A UNIQUE SET OF ECTOMYCORRHIZAL FUNGI IN A NEOTROPICAL DRY FOREST

Resumen

Durante mucho tiempo se pensó que la simbiosis ectomicorrízica estaba restringida a los bosques templados. Sin embargo, a medida que se han explorado los bosques tropicales, ha quedado claro que estos hábitats albergan hongos ectomicorrízicos (ECM) únicos. Hemos estado explorando los bosques tropicales caducifolios, que son ecosistemas terrestres en peligro de extinción y puntos calientes de endemismo. Debido a que Fabaceae es la principal familia de plantas en este entorno, planteamos la hipótesis de que los árboles en este linaje serían los principales huéspedes ectomicorrízicos. Hemos secuenciado la región de ITS rDNA de los hongos, y para plantas rbcL y trnL cDNA de para identificar a ambos simbiontes de las puntas micorrizadas. La posición sistemática de cada simbionte fue confirmada por inferencia filogenética bayesiana. Identificamos 20 especies de plantas pertenecientes a 10 familias que hospedaron 19 especies únicas de hongos ECM de 5 linajes. La mayoría de los hongos ECM se asociaron con plantas del orden Caryophyllales, no con Fabaceae. *Achatocarpus* y *Guapira*, los hospederos principales, están dispersos por todo el bosque y no están en parches monodominantes. La baja diversidad de hongos ECM puede explicarse por la baja densidad de las plantas hospederas y su alta especificidad. Nuestros resultados indican que Caryophyllales es un orden importante de hospederos ectomicorrízicos tropicales con al menos cuatro linajes independientes que en su proceso evolutivo desarrollaron la capacidad de formar ectomicorrizas.

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ORIGINAL ARTICLE

Caryophyllales are the main hosts of a unique set of ectomycorrhizal fungi in a Neotropical dry forest

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Abstract The ectomycorrhizal symbiosis was long thought to be restricted to temperate forests. However, as tropical forests have been explored, it has become clear that these habitats host unique ectomycorrhizal (ECM) fungi. We have been exploring tropical dry forests (TDF), which are endangered terrestrial ecosystems and hotspots of endemism. Since Fabaceae is the main plant family in this environment, we hypothesized that trees in this lineage would be the main ECM hosts. We sequenced the ITS rDNA region from fungi and both *rbcL* and *trn*L cpDNA from plants to identify both symbiotic partners from root tips. The systematic position of each symbiont was confirmed by Bayesian phylogenetic inference. We identified 20 plant species belonging to 10 families that hosted 19 unique ECM fungal species from 5 lineages. Most ECM fungi were associated with Caryophyllales, not with Fabaceae. *Achatocarpus* and *Guapira*, the main hosts, are scattered throughout the forest and are not in monodominant patches. The low ECM fungal diversity can be explained by the low density of host plants and their high specificity. Our results indicate that Caryophyllales is an important order of tropical ECM hosts with at least four independent evolutionary lineages that have evolved the ability to form ectomycorrhizae.

Keywords *Achatocarpus* · Caryophyllales · Chamela · ECM fungal community · ECM hosts · *Guapira* · Neotropical dry forest

Introduction

Nearly 90% of terrestrial plants acquire nutrients from soil via symbioses with mycorrhizal fungi. Mycorrhizal diversity is estimated to involve as many as 50,000 fungal species associated with 250,000 plant species (van der Heijden et al. 2015). Arbuscular mycorrhiza and ectomycorrhiza are the most common interactions. While much is known about taxa involved in arbuscular mycorrhizal relationships, there is less information concerning ectomycorrhizae, particularly in tropical ecosystems. Recently, there has been a growing interest in understanding both the biogeography and the diversity of the ectomycorrhizal (ECM) symbionts in temperate versus tropical habitats (Bahram et al. 2013; Tedersoo et al. 2014a; Looney et al. 2016). It is known that ECM fungal diversity is higher in temperate forests compared to tropical forests, opposite to the trend for plant diversity (Tedersoo et al. 2014b) and other organisms.

In those tropical forests where ECM plants are monodominant, ECM associations prevail (Fukami et al. 2017). Monodominance refers to a single plant species occupying large territories and allowing the establishment of highly diverse ECM fungi communities; this was observed in forests dominated by Dipterocarpaceae and some Fabaceae species. For example, the *Dipterocarpus* tropical rainforest of Thailand hosts 57 ECM fungal species (Dell et al. 2005),

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and the Malaysian dipterocarp rainforest hosts more than 90 species (Peay et al. 2010). Additionally, five leguminous species associated with 39 ECM fungi were found in the tropical rainforest in Guinea (Diédhiou et al. 2010). Similarly, in the Guiana Shield, species of *Dicymbe* and *Aldina* (Fabaceae) host a diverse community of more than 172 ECM fungal species (Smith et al. 2011, 2017). In contrast, most tropical forests are characterized by plant hyperdiversity and ECM hosts are scattered so that ECM associations are rare (Alexander 2006; Brundrett 2009; Peay 2016). In these ecosystems, few studies have been conducted on the ecology and diversity of ECM associations (e.g., Haug et al. 2005; Tedersoo et al. 2007, 2010). The ECM fungal richness in these forests is low compared to the richness of ECM monodominant tropical forests (Tedersoo et al. 2010). Accordingly, ECM fungal richness in the tropics can generally be predicted by the abundance (e.g., basal area) of ECM hosts and their diversity (Tedersoo et al. 2014b).

The ECM symbiosis evolved independently in 145 genera from 24 families of plants (Wang and Qiu 2006; Brundrett 2009). Tropical ecosystems have revealed new evidence of phylogenetically disparate plants that form ECM associations. The symbiosis of *Asteropeia* (Asteropeiaceae), *Guapira*, *Neea* and *Pisonia* (Nyctaginaceae), *Coccoloba* (Polygonaceae), *Uapaca* (Phyllantaceae), *Gnetum* (Gnetaceae), *Aldina* (Fabaceae subfamily Papilionoideae), and *Oreomunnea* (Junglandaceae) has only recently been documented or verified (Wang and Qiu 2006; Tedersoo et al. 2007; Smith et al. 2011; Bâ et al. 2012; Hayward and Horton 2012; Séne et al. 2015; Alvarez-Manjarrez et al. 2016; Corrales et al. 2016). Asteropeiaceae, Nyctaginaceae, and Polygonaceae belong to Caryophyllales, a plant order that is assumed to develop arbuscular mycorrhizas. Considering that tropical trees are hyperdiverse and that many tropical habitats remain unexplored, it seems highly probable that many novel ECM associations still await discovery in the tropics. Neotropical forests may not only harbor unknown ECM hosts, but they also could be sites of origin and diversification for different ECM fungal lineages (e.g., *Clavulina,* Inocybaceae; Matheny et al. 2009; Kennedy et al. 2012).

Most of this knowledge comes from rainforests; however, tropical dry forests (TDF) still remain largely unexplored. These forests are hyperdiverse (DRYFLOR 2016) and no monodominant plant taxa are known from TDFs. Fabaceae is one of the most extensive families in this ecosystem, with high richness and endemism (Linares-Palomino et al. 2006). TDFs are among the most imperiled ecosystems on the planet because land-use change has been accelerated by agricultural practices or grazing over large expanses of habitat (DRYFLOR 2016). TDFs are unique and globally important habitats, covering a total of 1,048,700 km^2 distributed throughout northern Australia, Southeast Asia, Africa, and the Americas (Miles et al. 2006). In the Neotropics, TDF comprise about 519,597 km^2, 51% of them are in South America, 39% in North and Central America, and 9% in the Caribbean (Portillo-Quintero and Sánchez-Azofeifa 2010). Even when the aboveground plant ecology is well understood in TDFs, information of soil symbiotic interactions is scarce. This knowledge is urgently needed in order to understand the contribution of ECM fungi to the nutrient cycling and rhizosphere processes in this ecosystem.

In this research, we examined the diversity and community structure of ECM fungi associated with several plant species in a Mexican TDF. Our main questions were as follows: (1) Is Fabaceae the main ECM host lineage in TDF? (2) Who are the ECM fungi associated with the plant hosts and what are their phylogenetic relationships? (3) What is the morpho-anatomy of these associations? and (4) Are the fungal-plant interactions in the TDF dominated by generalists or specialists?

Materials and methods

Study site

This study took place in the biological research station of Chamela, Jalisco, Mexico (N 19° 30′, W 105° 03′). The site occupies 3319 ha of TDF and tropical sub-deciduous forest. The most dominant plant family is Fabaceae with 160 species, of which 57 species are trees. Besides legumes, other common families harboring trees are Euphorbiaceae (26 species), Anacardiaceae (3), Annonaceae (5), Nyctaginaceae (3), and Polygonaceae (9) (Lott and Atkinson 2002). The mean annual precipitation is 784 mm, approximately 85% of annual precipitation is concentrated between July to October; the rest of the year is dry. However, precipitation is heterogeneous depending on the hurricane season. The mean annual temperature is 24.6 °C with a maximum of 30.3 °C and minimum of 19.5 °C (García-Oliva et al. 1995). Soils of the region are young Entisols which are poorly developed with low organic matter and pH of 6–7 (Martínez-Yrízar and Sarukhán 1993). We performed four visits for sampling during the rainy season: July–August 2012, October–November 2012, October 2013 and November 2014.

Root sampling

We used the published flora of the region (Lott 1993) to identify putative ECM host plants in the Fabaceae, Nyctaginaceae, and Polygonaceae to conduct directed root sampling, focused on Fabaceae hosts. We collected both rhizosphere and soil core samples. Rhizosphere samples were extracted directly from suspected ECM hosts by tracking their roots. Soil samples consisted of four pooled soil cores (2.5 cm diameter × 30 cm deep) taken under suspected ECM hosts or ECM sporocarps (Fig. S1). In total, we sampled 13

rhizospheres and 91 soil cores (~53,508 cm^3), 61 under suspected ECM plants and 30 under putative ECM fruit bodies. We sieved each sample to isolate fine roots and dissected roots that had a fungal mantle under a stereomicroscope. We further characterized clean root tips according to Agerer and Rambold (2004–2017) and preserved root tip vouchers in 96% ethanol at 4 °C until processed.

Plant identification and phylogenetic analysis

We identified the plant host of root tip samples using molecular techniques. We extracted DNA from leaves and roots with the REDExtract-N-Amp Plant kit (Sigma-Aldrich, St. Louis, MO, USA). We PCR-amplified the chloroplast *rbcL* region using *rbcL-a*_F and *rbcL-a*_R primers following Kress and Erickson (2007); we amplified the *trn*L region using *trn*C, *trn*D, *trn*E, and *trn*F primers following Taberlet et al. (1991). Amplicons were managed and sequenced as in Ángeles-Argáiz et al. (2016). We edited sequences, assembled, and clustered into MOTUs at 100% similarity with Geneious v.6.1.4 (Biomatters Ltd.). We compared sequences with GenBank and/or the BOLD database (www.boldsystems.org/) using MEGABlast (Zhang et al. 2000).

We produced sequences from MEXU herbarium vouchers (Instituto de Biología, UNAM) of the families that were most commonly associated with the root tip samples. A small leaf portion (2 mm) was taken from plant species of Achatocarpaceae, Nyctaginaceae, and Polygonaceae. From these tissues, we extracted DNA and sequenced the *trn*L and *rbcL* regions. Accession numbers from MEXU and GenBank of each species is presented in Table S1.

We generated a Bayesian phylogenetic analysis for the order Caryophyllales using the *rbcL* region, including vouchers and root tip sequences, BOLD Systems, and GenBank sequences. The alignment was performed using MAFFT v7 (http://mafft.cbcr.jp/alignment/server/) and revised manually with PhyDE. The substitution model was selected by jModelTest v2.1.3 (Darriba et al. 2012) using BIC calculations. Mr. Bayes (Ronquist and Huelsenbeck 2003) was used for phylogenetic analyses. The model used was HKY + I + G for 10,000,000 generations with 4 MCMC chains and a sampling frequency of 100 with a print frequency was 500. The branch support was computed by posterior probabilities and we generated a consensus majority rule tree.

Fungal identification and phylogenetic analysis

All terrestrial sporocarps in the study site were collected using plastic boxes and wax paper. From all materials, we made macroscopic descriptions including fresh colors coded with Kornerup and Wanscher (1978). A small piece of each fruit body was preserved in 96% ethanol for DNA extraction. Sporocarps were dehydrated with hot air (~60 °C) and deposited in the MEXU herbarium.

We extracted DNA from the fruit bodies with the REDExtract-N-Amp Plant kit (Sigma-Aldrich, St. Louis, MO, USA). The fungal internal transcribed spacer (ITS) region was PCR-amplified with ITS1F and ITS4 primers following Garibay Orijel et al. (2013) using the RubyTaq PCR master mix (Affymetrix, CA, USA). Amplicons were manipulated and sequenced with the same protocols we reported in the plant identification section. Sequences were edited, assembled, and clustered into MOTUs with Geneious v.6.1.4 (Biomatters Ltd.). Fungal MOTUs were assembled at 97% nucleotide similarity (Smith et al. 2007). Consensus sequences were compared with GenBank and UNITE using MEGABlast (Zhang et al. 2000).

We conducted fungal identification (root tips and fruit bodies) by phylogenetic analyses of the /clavulina, /inocybe, /lactarius-russula, /thelephora-tomentella and /sebacina lineages. For this, we downloaded the close relatives that resulted from MEGABlast searches from GenBank and UNITE and aligned them with our sequences using MAFFT v7 (http://mafft.cbcr.jp/alignment/server/) and PhyDE. Bayesian analysis was run in Mr. Bayes v3.2.2, over 5,000,000 generations with 4 MCMC chains and three partitions (ITS1, 5.8S, ITS2). To generate a consensus majority rule tree with the posterior probabilities, we used the GTR + I + G substitution model, sampling frequency of 100, and printing frequency of 500.

Characterization of mycorrhizae

Samples with abundant root tips were fixed in FAA or Navashin for several hours and then later washed with tap water and preserved in 70% ethanol. We observed the fixed samples with a stereoscope microscope to characterize their morphology, using DEEMY as a reference (Agerer and Rambold 2004–2017). To characterize the mantle, Hartig net and external mycelium for each sample, we made anatomical slices, which were dyed with safranin and fast green FCF following the protocol from Sandoval-Zapotitla (2005).

Results

Ectomycorrhizal host plants

We identified 98 root samples either by *rbcL* or *trn*L cpDNA regions from 201 roots (48.75% success rate). The *rbcL* region was inconclusive to approximate the genera of several ECM hosts. For instance, *Guapira petenensis* was grouped with *Neea* and *Pisonia* GenBank accessions. When we added the *trn*L of voucher sequences, the root tip sequences matched at 100% with *G. petenensis*.

Despite the fact that the sampling was targeted to Fabaceae (i.e., *Caesalpinia* spp., *Cynometra oaxacana*, *Haematoxylum brasiletto*, *Lonchocarpus* spp.), the most common plants amplified from root tips with a fungal mantle were *Achatocarpus gracilis* (Achatocarpaceae) and *G. petenensis* (Nyctaginaceae), with 53 and 13% of the root tips, respectively. *Achatocarpus gracilis* shrubs were identified based on morphological comparisons between field observations and herbarium specimens. Moreover, the *rbcL* sequences from root tips were identical with leaf voucher sequences and with GenBank sequences of *Achatocarpus* and *Phaulothamnus* species (Fig. 1).

The main ECM host species belonged to Caryophyllales: *A. gracilis*, *Coccoloba* sp., *G. petenensis*, *Pisonia* sp., Pisonieae sp., *Ruprechtia* sp. and five more unidentified Nyctaginaceae species. Despite the fact that *Achatocarpus* and *Ruprechtia* were commonly colonized by ECM fungi and were clearly covered by a mantle of ECM fungal hyphae, we were unable to observe the Hartig net in the mycorrhizas. We also found typically non-ECM plant lineages whose roots were colonized by ECM fungi but without Hartig net: Apocynaceae, Araliaceae (*Aralia excelsa*), Caesalpinoideae, Papilionoideae (*Apoplanesia paniculata, Lonchocarpus* sp.), Moraceae (*Ficus* sp.), Sapindaceae, Sapotaceae, and Surinaceae (*Recchia mexicana*). All of these had low colonization by ECM fungi in their roots and they represent only 20.6% of the samples (Table 1).

Fungal diversity

In three sampling years, 26 ECM fruit bodies were found corresponding to: 18 of *Thelephora versatilis*, 6 of *Tremelloscypha* sp., 1 of *Tomentella brunneoincrustata,* and 1 of *Thelephora pseudoversatilis*. Similarly, ectomycorrhizae were seldom found in the soil cores: in *c.* 53,600 cm^3 of soil, we found 209 root tips with a fungal mantle. In fact, some of the soil cores did not have any ectomycorrhizae, whereas nearly all roots were ECM in a few soil cores. On average, there were 2.2 ECM root tips per soil core, with the maximum being 21 root tips in one soil core below *Guapira*. The ectomycorrhizae were located in restricted places, distributed in patches according to their host plant distribution.

We successfully sequenced the ITS region of 115 from 209 roots samples, belonging to ECM and saprotrophic fungi. Most samples (109 root tips) belonged to ECM fungi and corresponded to 19 species (Table 2). Only ECM Basidiomycota species were found on the roots but one unidentified Ascomycota species (Dothideomycetes) was also sequenced (Table S2). ECM species belonged to five distinct lineages of fungi: /clavulina, /inocybe, /russula-lactarius, /sebacina, /thelephora-tomentella (Tedersoo and Smith 2013).

The /sebacina lineage was present in 39% of root tips and was represented by *Tremelloscypha* sp. and *Sebacina* sp. (Figs. S2, S3). *Tremelloscypha* sp. was resolved in a Neotropical clade with samples from Mexico to Venezuela with posterior probability (PP) of 1; *Sebacina* sp. was related to Neartic species from Mexico with low support. The /thelephora-tomentella lineage corresponded to 32% of the total samples and was represented by two *Thelephora* species and six *Tomentella* species. All the Thelephoraceae belonged to tropical clades: *Th. versatilis*, *Th. pseudoversatilis*, *Tomentella brunneoincrustata*, *Tomentella* sp. 1, *Tomentella* sp. 4, *Tomentella* sp. 5 belong to a clade supported by 0.98 PP; *Tomentella* sp. 2 and *Tomentella* sp. 3 belong to two different tropical clades with 0.88 and 1 PP, respectively (Fig. S4). The /clavulina lineage was also common and diverse (20% of root tips) with five different species, four *Clavulina* and one *Membranomyces*. The *Membranomyces* species was related with a clade from temperate forests with 0.98 PP. *Clavulina* spp. were closely related each other; there was no PP support for this relationship (Fig. S5). The lineages /inocybe and /russula-lactarius were each represented by just one or two species. The sequences from /russula-lactarius belonged to two independent tropical clades that also included Ecuadorian species, each with a PP of 1 (Fig. S6). Also /inocybe formed two independent clades with long branches, *Inocybe* sp. 2 was related with Australian species with low support (Fig. S7).

Mycorrhizal morphotypes

The mycorrhizal systems established with TDF plants were small in size (i.e., length of ~1–3 mm). They usually were unbranched and showed different patterns of soil exploration depending on fungal species.

Guapira morphotypes had all of the typical ectomycorrhiza characteristics including the mantle, Hartig net and external mycelia (Fig. 2). These morphotypes were evident, almost observable without magnification, and they varied depending on the mycobiont. *Clavulina* sp. 2 (Fig. 2a, b) presented a beige mantle formed by hyphae with refracting incrustations, with a mantle of 13–16 μm, and the Hartig net was paraepidermal. The ECM of *Membranomyces* sp. (Fig. 2c, d) had a white mantle with a smooth surface contact exploration type, a paraepidermal Hartig net with infrequent lobules, and was present in the first cortical layer of the root cells. This species also had extensive intraradical hyphae (Fig. 2d).

On the other hand, *Tomentella* sp. 1 associated with Pisonieae sp. (Fig. 2e, f) had a sinuous mycorrhiza with a dark brown mantle and a few emergent hyphae. Its mantle did not cover the tip and the Hartig net was paraepidermal with lobed septa. Meanwhile, when *Tomentella* sp.1 was associated with Polygonaceae, it had a copper colored mantle, with sinuous tips and a completely smooth surface.

We found some morphotypes with very particular and unusual characteristics. In the *Th. versatilis* ectomycorrhizae, the hairy mantle with medium-distance exploration did not cover the root tip, with partial mantle zones on the roots. Also, *Achatocarpus* and /sebacina have a very thin, hyaline, and

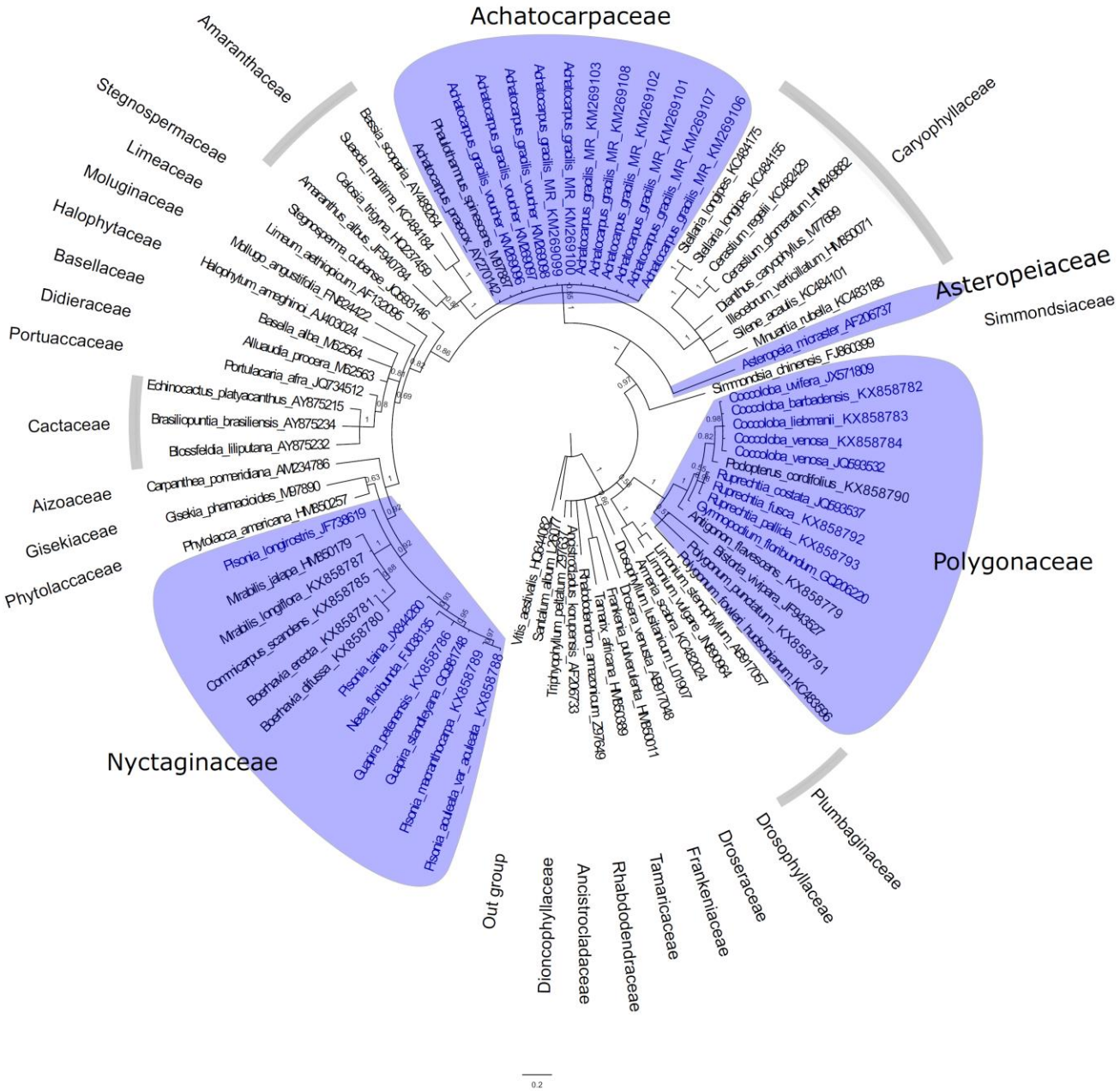

Fig. 1 Bayesian phylogenetic analysis of the Caryophyllales based on *rbcL*. The four clades that are known to contain ectomycorrhizal plants are highlighted by blue boxes. The Achatocarpaceae clade includes sequences from the BOLD database as well as those from mycorrhizal roots (MR) and fresh leaves (voucher) collected at Chamela

almost imperceptible to white mantle, with short-distance exploration type. The mantle was composed by 3–4 hyphae layers (< 12 μm) with some emergent clamped hyphae that aggregate the nearby soil. *Achatocarpus* does not form an evident Hartig net with any of the ECM fungi that we examined (Fig. 2g, h).

Fungal-host interaction

We found 19 ECM fungal species associated in different proportions with 10 plant families (Table 1). In general, the /sebacina lineage (*Tremelloscypha* sp. and *Sebacina* sp.) exhibited a preferential association with *A. gracilis*. Although *Tremelloscypha* sp. was found forming a fungal mantle on roots of *Achatocarpus*, *Ficus* sp. and Sapotaceae sp., a Hartig net was not observed. The /clavulina lineage was strongly associated with Nyctaginaceae members, except for *Clavulina* sp. 1, which was associated with *Achatocarpus* (Fig. 3).

Achatocarpus and *Guapira*, the two main ECM hosts, shared only two fungal species: *T. dichroa* and *Tomentella* sp. 1. Some plant species were found hosting only one ECM fungal

Table 1 Ectomycorrhizal symbionts in the tropical dry forest of Chamela, Mexico

Order	Family	Plant species	No. RT	Fungal species	Hartig net
Apiales	Araliaceae	*Aralia excelsa*	1	*Thelephora versatilis*	?
Caryophyllales	Achatocarpaceae	*Achatocarpus gracilis*	25	*Tremelloscypha* sp.	No
			15	*Sebacina* sp.	No
			3	*Clavulina* sp. 1	?
			3	*Tomentella* sp. 2	?
			1	*Inocybe* sp. 2	?
			1	*Russula* sp. 1	?
			1	*Th. versatilis*	?
			1	*Tomentella* sp. 1	?
Caryophyllales	Nyctaginaceae	*Guapira petenensis*	6	*Membranomyces* sp.	Yes
			4	*Tomentella* sp. 1	?
			1	*Clavulina* sp. 2	?
			1	*Tomentella brunneoincrustata*	Yes
			1	*Tremelloscypha* sp.	?
Caryophyllales	Nyctaginaceae	Nyctaginaceae sp. 1	4	*Membranomyces* sp.	Yes
			2	*Tomentella* sp. 1	?
Caryophyllales	Nyctaginaceae subfam. Pisonieae	Pisonieae sp.	3	*To. brunneoincrustata*	Yes
			1	*Tomentella* sp. 1	Yes
Caryophyllales	Nyctaginaceae	*Pisonia* sp.	1	*To. brunneoincrustata*	Yes
			1	*Inocybe* sp. 1	?
Caryophyllales	Nyctaginaceae	Nyctaginaceae sp. 2	1	*Clavulina* sp. 4	?
Caryophyllales	Nyctaginaceae	Nyctaginaceae sp. 3	1	*Clavulina* sp. 3	?
Caryophyllales	Nyctaginaceae	Nyctaginaceae sp. 4	1	*Russula* sp. 1	?
Caryophyllales	Nyctaginaceae	Nyctaginaceae sp. 5	1	*Tomentella* sp. 4	?
Caryophyllales	Polygonaceae	*Coccoloba* sp.	3	*Th. versatilis*	?
Caryophyllales	Polygonaceae	*Ruprechtia* sp.	2	*Th. versatilis*	?
Ericales	Sapotaceae	Sapotaceae sp.	1	*Tremelloscypha* sp.	?
Fabales	Fabaceae subfam. Caesalpinoideae	Caesalpinoideae sp.	1	*Tomentella* sp. 3	?
Fabales	Fabaceae subfam. Papilionoideae	Papilionoideae sp.	1	*Tomentella* sp. 5	?
Fabales	Fabaceae subfam. Papilionoideae	*Lonchocarpus* sp.	1	*Tomentella* sp. 1	?
Fabales	Fabaceae subfam. Papilionoideae	*Apoplanesia paniculata*	1	Russulaceae sp.	?
Fabales	Surianaceae	*Recchia mexicana*	1	*Th. versatilis*	?
Gentianales	Apocynaceae	Apocynaceae sp.	1	*Tomentella* sp. 1	?
Rosales	Moraceae	*Ficus* sp.	1	*Tremelloscypha* sp.	?

No. RT Number on root tips, *?* unknown

species that was not associated with any other tree. For instance, *A. paniculata* was associated with Russulaceae sp., Caesalpinioideae sp. with *Tomentella* sp. 3, and Papilionoideae sp. with *Tomentella* sp. 5.

Certain species of *Tomentella* and *Thelephora* were the most generalist in this ecosystem. *Thelephora versatilis* was associated with *A. gracilis*, *A. excelsa*, *R. mexicana*, and *Ruprechtia* sp. Similarly, *Tomentella* sp. 1 interacted with roots of *A. gracilis*, *Coccoloba* sp., *G. petenensis*, *Lonchocarpus* sp., and other Nyctaginaceae species.

We also found saprotrophic fungi and species with unknown function on roots (Table S2), including Agaricales sp. on *G. petenensis*, Agaricales sp. on Caesalpinioideae, Dothidiomycetes sp. on Polygonaceae, and *Entoloma* sp. on Sapindaceae.

Discussion

The Caryophyllales as the main ectomycorrhizal hosts in the tropical dry forest

Although Fabaceae is the most species-rich family in the study site (155 species; Lott 1993), our results demonstrate that

Table 2 Taxonomic identity and root tip abundance of ectomycorrhizal fungi

Taxon name	N	Accession number	UNITE SH| DOI	Best BLAST match	Percent similarity
Tremelloscypha sp.	29	KM269089	SH016792.07FU| 10.15156/BIO/SH016792.07FU	*Tremelloscypha* sp. (KF061282)	98% (649/660)
Membranomyces sp.	15	KU175675	SH487941.07FU	*Clavulina cinerea* (JN228228)	83% (753/910)
Sebacina sp.	15	KP896286	SH488205.07FU	*Sebacina* sp. (FJ378741)	97% (641/660)
Tomentella sp. 1	12	KM269095	SH495677.07FU	*Tomentella* sp. (EU625861)	93% (641/689)
*Thelephora versatilis**	9	KM269094	SH490448.07FU	*Thelephora versatilis* (KJ462494)	100% (665/665)
*Tomentella brunneo-incrustata**	6	KP896288	SH489022.07FU	*Tomentella brunneoincrustata* (KP896288)	100% (628/628)
Tomentella sp. 2	4	KM269090	SH496760.07FU	Uncultured *Tomentella* (EU625861)	93% (641/689)
Clavulina sp. 1	3	KM269091	SH493124.07FU	*Clavulina* sp. (JX287358)	93% (676/730)
Russulaceae sp.	3	KM269093	SH489887.07FU	*Russula nigricans* (EU819428)	84% (618/733)
*Thelephora pseudoversatilis**	2	KU175679	SH010135.07FU| 10.15156/BIO/SH010135.07FU	*Thelephora pseudoversatilis* (JX075890)	99% (635/642)
Inocybe sp. 1	2	KP896287	SH493665.07FU	*Inocybe* sp. (GQ469526)	81% (569/702)
Clavulina sp. 2	1	KP896290	SH488204.07FU	*Clavulina* sp. (JX287358)	93% (669/717)
Clavulina sp. 3	1	KP896291	SH495009.07FU	*Clavulina* cf. *amethystina* (GU550110)	90% (581/640)
Clavulina sp. 4	1	KU175676	SH496187.07FU	*Clavulina* sp. (KF359593)	92% (612/668)
Inocybe sp. 2	1	KM269092	–	*Inocybe calospora* (HQ586852)	81% (566/702)
Russula sp. 1	1	KU175680	SH491260.07FU	*Russula acrifolia* (UDB002470)	91% (679/746)
Tomentella sp. 3	1	KU175681	SH009960.07FU| 10.15156/BIO/SH009960.07FU	*Tomentella* sp. (KF472143)	97% (634/683)
Tomentella sp. 4	1	KP896289	SH492685.07FU	*Tomentella ellisii* (AB634268)	94% (541/570)
Tomentella sp. 5	1	KU175682	SH493257.07FU	Uncultured Thelephoraceae (KF836018)	95% (599/630)

N: Number of root tips. *Sequences are 100% similar to those of *Thelephora versatilis*, *Thelephora pseudoversatilis*, and *Tomentella brunneoincrustata* sporocarps collected at the same site (Ramirez-Lopez et al. 2015; Alvarez-Manjarrez et al. 2016)

legumes were not frequent ECM hosts in the TDF (Table 1). This is in contrast to other tropical ecosystems around the world where leguminous plants are confirmed as common ECM hosts (e.g., Tedersoo et al. 2007; McGuire et al. 2008; Diédhiou et al. 2010; Smith et al. 2011). *Achatocarpus gracilis*, *G. petenensis*, *Pisonia* sp., Pisonieae sp., Nyctaginaceae spp., *Coccoloba* sp., and *Ruprechtia* sp., all from Caryophyllales, were the most important ECM hosts in these TDF (16 of the 19 fungal species were associated with this group). *Achatocarpus gracilis* and *G. petenensis* are the host plants most frequently associated with ECM fungi. These species of trees (*Coccoloba*, *Guapira* and *Ruprechtia*) or shrubs (*Achatocarpus* and *Pisonia*) have low density at the study site and are also typically found at low density in other tropical forests (e.g., Tedersoo et al. 2010, 2012).

Achatocarpus gracilis belongs to a monophyletic clade that includes Caryophyllaceae and Amaranthaceae (Schäferhoff et al. 2009; Crawley and Hilu 2012) but there are no members from this clade that have thus far been reported as ECM (Wang and Qiu 2006). This suggests that the symbiosis with ECM fungi probably evolved independently in the *Achatocarpus* lineage, and it may be found in other members of Achatocarpaceae. This host species forms a "pisonioid" mycorrhizal type whereby none of the ECM fungi associated with *Achatocarpus* roots forms a conspicuous Hartig net (Ashford and Allaway 1982; Imhof 2009). At the Chamela site, *A. gracilis* does not occupy an extensive basal area, but it is widely distributed and found in all successional stages of TDF (Alvarez-Añorve et al. 2012). To understand the importance of the symbiosis with ECM fungi in this lineage, it would be necessary to answer the following questions: Do other species of the genus also develop this regular association with ECM fungi? Despite the lack of a Hartig net, is there nutrient transfer between *A. gracilis* and its associated ECM fungi? How do interactions with ECM fungi contribute to the fitness of this shrub in the successional forests?

Nyctaginaceae was the family with the highest number of ECM host species. In this family, we were unable to identify 10.3% of the plants at the species level even after comparison to voucher sequences, because of the low resolution of the chloroplast markers. Within this family, putative ECM hosts present in the study site could be species of *Abromia*, *Boerhavia*, *Commicarpus*, *Mirabilis*, *Okenia* or *Salpianthus* (Lott 1993). However, none of these genera are known to form ECM associations. The Nyctaginaceae species with the most frequent ectomycorrhizae was *G. petenensis*, which is an abundant tree in the study site (almost 80 individuals per ha) occupying a basal area around 1 m^2/ha (Durán et al. 2002). *Guapira* and Nyctaginaceae in general are known as ECM

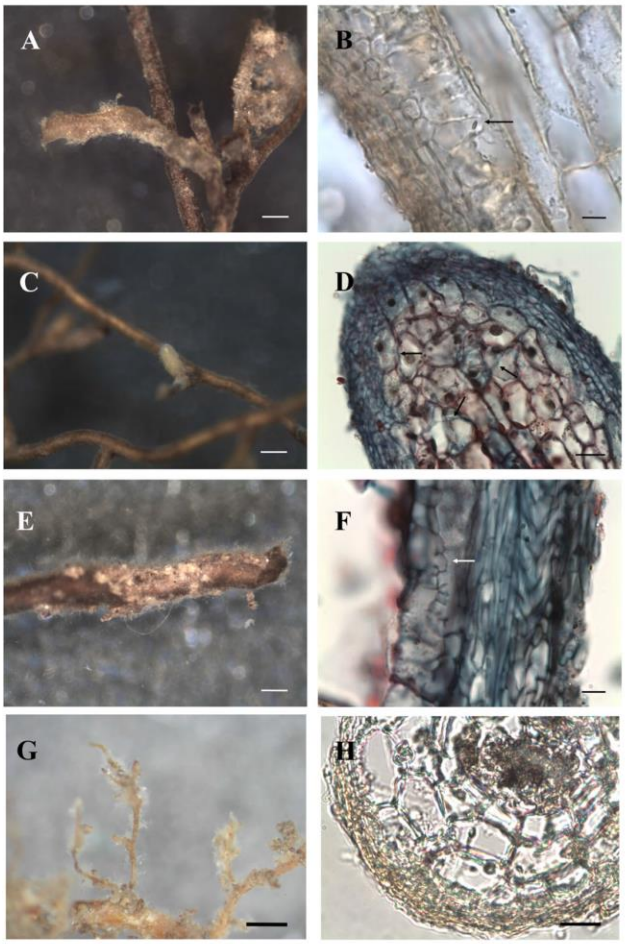

Fig. 2 **a** Ectomycorrhiza of *Clavulina* sp. 2 + *Guapira petenensis*. **b** Ectomycorrhiza of *Clavulina* sp. 2 + *G. petenensis* in longitudinal which shows the mantle and a detail of the Hartig net. **c** Ectomycorrhiza of *Membranomyces* sp. + *Guapira pentensis*. **d** Longitudinal view of *Membranomyces* sp. + *G. petenensis* ECM showing the mantle, the Hartig net, and numerous intraradical hyphae (arrows). **e** Ectomycorrhiza of *Tomentella* sp. 1 + Pisonieae sp. **f** Transversal slice that shows a dense mantle and a paraepidermal Hartig net (arrows). **g** *Sebacina* sp. + *Achatocarpus gracilis* root tips. **h** *Sebacina* sp. + *Achatocarpus gracilis* in transversal view, it shows the mantle and lack of Hartig net. Bars: **a**, **c**, **e** 0.25 mm; **b**, **f** 4.5 μm; **d** 75 μm; **g** 0.5 mm; **h** 6.6 μm

hosts throughout the tropics (Ashford and Allaway 1982; Chambers et al. 2005; Haug et al. 2005; Tedersoo et al. 2010; Hayward and Horton 2012).

Another recognized ECM host family is Polygonaceae, especially the genus *Coccoloba* (e.g., Bandou et al. 2006; Séne et al. 2015). There have been recent new reports of Polygonaceae species with ECM associations, for example *Gymnopodium floribundum* (Bandala et al. 2011). Our results showed that *Coccoloba* sp. and *Ruprechtia* sp. were associated with ECM fungi. We were not able to observe a Hartig net on *Ruprechtia* roots but this plant associated with *Th. versatilis*, a common ECM fungus in Chamela. *Ruprechtia* is a genus of Neotropical trees that primarily inhabits TDFs and is distributed from Mexico to Argentina and Uruguay (Pendry 2004). *Ruprechtia* (Triplarideae tribe), *Coccoloba* (Coccolobaeae), and *Gymnopodium* (Gymnopodieae) constitute the subfamily Eriogonoideae (Burke and Sanchez 2011), so it is likely that all of the plants in this subfamily may form ECM associations. The Eriogonoideae represents another distinct ECM lineage within Caryophyllales.

Interestingly, all the ECM Caryophyllales lineages except *Bistorta* are primarily found in tropical and subtropical forests. Caryophyllales is one of the orders with the highest speciation rate in angiosperms (Magallón and Castillo 2009). Most Caryophyllales species are assumed to develop arbuscular mycorrhizas or are non-mycorrhizal (Maherali et al. 2016). However, available data suggest that this group is an important lineage of ECM tropical hosts with at least four independent evolutionary lineages of ECM symbiosis in the families Achatocarpaceae (*Achatocarpus*), Asteropeiaceae (*Asteropeia*), Nyctaginaceae (*Guapira*, *Neea*, *Pisonia*), and Polygonaceae (*Bistorta*, *Coccoloba*, *Gymnopodium, Ruprechtia*) (Haug et al. 2005; Wang and Qiu 2006; Ducousso et al. 2008; Bandala et al. 2011; this study).

The hyperdiverse tropical dry forest harbors a unique set of ectomycorrhizal fungi

Previously the Neotropical dry forest in the Pacific coast was considered to be an exclusive arbuscular mycorrhizal ecosystem but our data suggest this habitat is home to a unique ECM fungal community. When including ectomycorrhizae and fruit bodies, we found 19 species of ECM fungi despite the fact that ectomycorrhizae were rare. We found 209 root tips in 91 soil samples (~53,600 cm^3 of soil); this is 0.003 ECM root tips/cm^3 soil. Fruit bodies of ECM fungi were even less frequent; in approximately 60 field days, we obtained only 28 collections of ECM sporocarps. Although scarcely found, all the ECM fungal species, except *Tremelloscypha* sp., are unique lineages and are only known from the TDF on the Pacific coast of Mexico. The ITS sequences of these taxa share only approximately 90% nucleotide similarity with any of the records in public databases. Thus, ca. 95% of species we collected are likely new to science and our research group has recently described some of these taxa as new species (*Tomentella brunneoincrustata*, *Thelephora pseudoversatilis*, *Th. versatilis*) (Ramirez-Lopez et al. 2015; Alvarez-Manjarrez et al. 2016). In spite of the recent studies on soil diversity in the TDF, our identified fungal taxa did not match those from Costa Rica based on sequence comparisons (data not shown; Waring et al. 2016). These mismatches contrast with the high number of shared plant species between Mexico and Central America-northern South America (DRYFLOR 2016). Nonetheless, the fungal lineages found here are common lineages in many forests worldwide: /clavulina, /inocybe, /russula-lactarius, /sebacina, and /tomentella-thelephora.

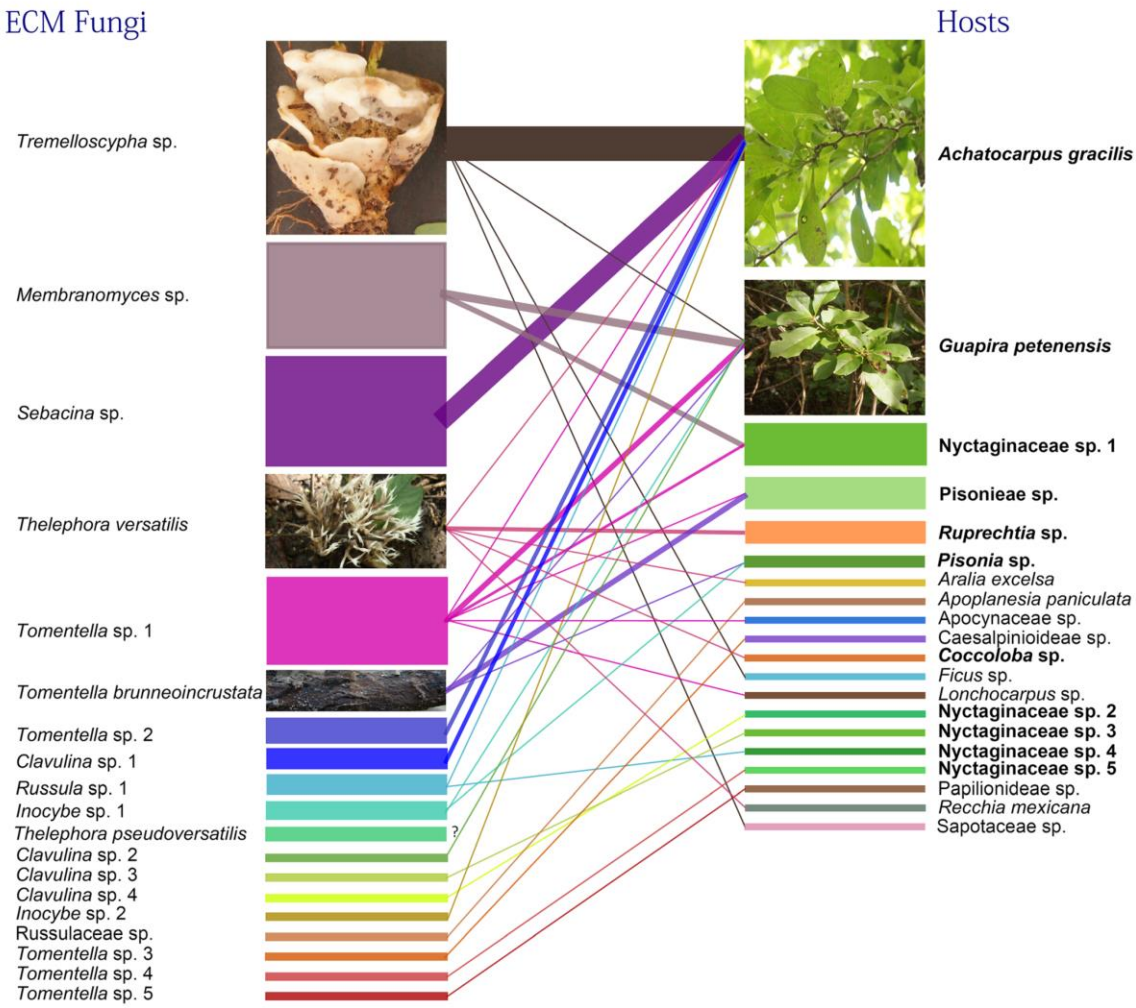

Fig. 3 Relationships between ectomycorrhizal fungi and plant hosts in the tropical dry forest of Chamela. The size of the square height represents the frequency of each species, the lines represent the interaction between plant and fungi and the width of the line is the frequency of that symbiosis. All the hosts in bold belong to Caryophyllales

The diversity of the ECM fungi at the local scale is related to the identity of the host plants and their density (Ishida et al. 2007; Tedersoo et al. 2010, 2012). The TDF on the Pacific coast of Mexico is considered a site with a distinctive and hyperdiverse vegetation (Lott and Atkinson 2002). Despite the fact that Chamela and nearby forests are among the driest known TDF habitats (Bullock 1986), the plant diversity is nonetheless similar to many tropical rainforests (Gentry 1988; Janzen 1988). The Mexican TDF is particularly rich in endemic species (Trejo and Dirzo 2002) and it has been estimated that 11% of the endemic species in Mexico are distributed in this ecosystem (Rzedowski 1991). Assuming that the TDFs have high plant endemism and that the high seasonality and drought stress are powerful physiological filters, it is likely that the ECM fungi from TDFs have adaptations to the extreme conditions and that some fungi might be endemics as well. To test this hypothesis, a wider sampling in the TDFs of the Neotropical Pacific coast will be necessary.

The hyperdiverse TDF in Chamela is comparable in diversity and abundance of ECM hosts with those in the Ecuadorian Amazon, white-sand forests in Brazil, and French Guiana where the ECM hosts are dispersed across the forest (Tedersoo et al. 2010; Roy et al. 2016). The low ECM fungal diversity in tropical forests with hyperdiverse host plants (Table S3) can be explained by the strong host filter, widely dispersed and relatively small host plants, and also perhaps the microbial mineralization during the short rainy season in the TDFs (Anaya et al. 2007).

Unusual morphotypes in the tropical dry forest

We report here the first evidence of a common occurrence of ECM fungi on the roots of *Achatocarpus gracilis*. The roots of *Achatocarpus* formed typical ECM morphotypes with several hyphal layers forming a distinct mantle. All of the fungi that we sequenced from these ECM roots are typical ECM

lineages, including members of the /sebacina, /clavulina, /tomentella-thelephora, /inocybe, and /russula-lactarius lineages (Table 1). The combination of the phylogenetic placement of *A. gracilis* along with the common occurrence of fungal mantles and the regular occurrence of a diverse array of ECM fungi suggests that this shrub species forms an ECM symbiosis. However, despite our morphological analysis, we did not find evidence of a Hartig net. This species can therefore be assigned to the "Pisonioid" mycorrhiza type, which has a mantle and an underdeveloped or nonexistent Hartig net (Ashford and Allaway 1982; Imhof 2009). The Pisonioid type has been documented on the roots of *Pisonia grandis*, also an ECM-forming member of Caryophyllales.

Guapira morphotypes from the /clavulina lineage presented typical characters of an ectomycorrhiza: mantle, Hartig net, extraradical mycelia, but they also have intraradical hyphae. The same observation has been made previously for *Guapira* and *Neea,* where the ECM fungi formed intraradical hyphae (Haug et al. 2005). These features suggest that *Guapira* may form a kind of ectendomycorrhiza instead of the typical ectomycorrhiza.

The /tomentella-thelephora lineage ectomycorrhizae had a mantle zoned by discontinuous colonization along the roots with all of their hosts. This morphotype formed short exploration to medium-distance fringe exploration morphotypes. This was also reported by Haug et al. (2005) in the /tomentella-thelephora—*Guapira* ectomycorrhizas in Ecuador.

Specific plant ectomycorrhizal fungal interactions in the tropical dry forest

Until now, all the ECM fungal communities are characterized by a small number of plant host lineages and a large number of ECM fungal lineages. For instance, a mixed temperate forest in Japan showed that a large number of ECM fungal lineages were found on eight hosts from three different plant families: Betulaceae, Pinaceae, and Fagaceae (Ishida et al. 2007). The TDF is a hyperdiverse forest where we found 20 hosts from 10 different families (i.e., Achatocarpaceae, Apocynaceae, Araliaceae, Fabaceae, Moraceae, Nytaginaceae, Polygonaceae, Sapotaceae, and Surianaceae). None of these plants form monodominant patches and their fungal symbionts showed strong host preferences. Although the ECM fungi from Chamela are associated with several host lineages, many of their hosts are still unknown. Some of the ECM fungi were found with low frequency on the roots of *Aralia excelsa*, *Apoplanesia paniculata*, Apocynaceae sp., Caesalpinioideae sp., *Coccoloba* sp., *Ficus* sp., *Lonchocarpus* sp., Papilionoideae sp., *Recchia mexicana*, and Sapotaceae sp. It is probable that these associations are opportunistic and could be compared to Singer's concept of "cicatrizing mycorrhiza" (Singer 1988).

In tropical forests where the ECM hosts are integrated among a matrix of arbuscular mycorrhizal trees, there is an inverse pattern between ECM fungal diversity and the plant diversity (e.g., Tedersoo et al. 2010). The monodominant forests, including temperate zones, have a high ECM fungal diversity. This is in contrast with the hyperdiverse tropical forests where the ECM fungal diversity is lower (Fig. 4). In the TDF of Chamela, 80% of ECM fungal species are specialists (associated with one host lineage) but we did find four generalists (associated with more than one host lineage). For example, *Th. versatilis* and *Tomentella* sp. 1 were able to interact with five and six plant lineages, respectively. Specifically, *Th. versatilis* is associated with two endemic species, *Recchia mexicana* and *Ruprechtia* sp. These results confirmed the pattern that in sites with ECM hosts at low frequency, there is more specialization in ECM fungal species (Tedersoo et al. 2008, 2010).

The host preferences in ECM fungal associations are defined by host selection and also by environmental factors (Dickie 2007); both factors together determine the mutualistic niche (Peay 2016). In an environment dominated by hyperdiverse non-ECM plants, ECM fungi face three challenges: (1) to find their dispersed hosts, they must either have

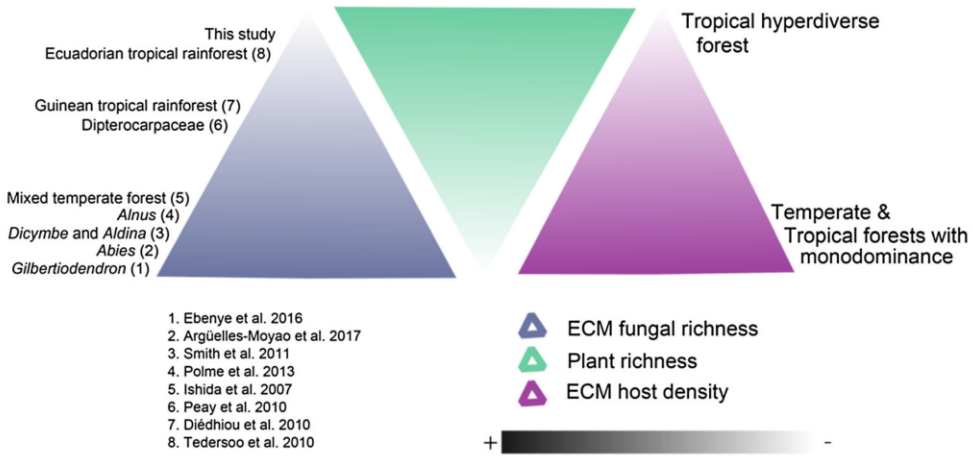

Fig. 4 Pattern between ectomycorrhizal fungal richness, plant richness, and ectomycorrhizal host density in different ecosystems. In the left side, there are some examples of studies about plant-ECM fungal diversity. Data from Ebenye et al. 2016; Argüelles-Moyao et al. 2017; Smith et al. 2011; Põlme et al. 2013; Ishida et al. 2007; Peay et al. 2010; Diédhiou et al. 2010; Tedersoo et al. 2010

long-lived spores or have excellent wind or vegetative dispersal; (2) to survive in such a restricted niche, they have to be highly competitive with saprotrophic, pathogenic, and other ECM fungi; (3) to widen their mutualistic niche by developing new opportunistic symbiosis or to specialize on only one plant lineage. The hyperdiverse TDFs represent a case of strong environmental filtering created by seasonality, intermittent drought stress, and pulses of high decomposition that result in edaphic heterogeneity (Campo et al. 1998, 2000), especially N mineralization (Anaya et al. 2007; Waring et al. 2016). All these represent biotic and abiotic filters that shape the ECM fungal community and also its specific interactions with plant hosts.

In conclusion, in the hyperdiverse Neotropical dry forest the Caryophyllales is the most important ECM plant host lineage with four independent origins of this symbiosis. These forests have a unique set of specialized ECM fungi. In order to understand the ecological importance of these unique ECM interactions, it will be necessary to focus on the adaptive advantages that the ECM symbiosis confers to plant hosts.

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Author contributions J.A.M. and R.G.O. were responsible for the experimental design. J.A.M. made the field work, laboratory proceedings, and the data analysis. J.A.M., R.G.O., and M.E.S. wrote the manuscript.

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Julieta 11/19

CAPÍTULO 2. SOIL FUNGAL COMMUNITY WAS PERSISTENT AND RESILIENT TO PATRICIA HURRICANE

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Resumen

El cambio climático producirá eventos catastróficos cada vez más comunes, en particular los huracanes. Los huracanes incrementan la precipitación y el mantillo en consecuencia de la destrucción de la vegetación. Estas condiciones son ideales para los organismos saprótrofos, tales como hongos y bacterias, mas no para los simbiontes obligados. Nuestro objetivo fue entender cómo el huracán Patricia (categoría 4) cambió la diversidad y el ensamble de la comunidad de hongos del suelo en un bosque tropical caducifolio. Las secuencias de ITS2 de DNA de hongos del suelo en una serie de tiempo de dos años (un año antes del huracán y cuatro de después) mostraron que antes de Patricia había 519 OTUs, donde Ascomycota era el phylum más diverso. Inmediatamente después del huracán, la riqueza de incrementó a 1358 OTUs, los basidiomicetos saprótrofos fueron los más abundantes, y la dominancia de la comunidad decayó. Después de uno y dos años del paso de Patricia, la diversidad decreció y la dominancia se recuperó gradualmente a través del tiempo. La diversidad de los hongos micorrízicos fue más alta después de Patricia y así permaneció durante dos años. Los hongos patógenos de plantas y parásitos incrementaron inmediatamente después de Patricia y con el tiempo decrecieron incluso más que antes del huracán. La comunidad persistente de todos los muestreos se conformó por 105 OTUs, principalmente sapro-

trofos. La heterogeneidad ambiental creada por el huracán explica el incremento de la diversidad, y la pérdida de la dominancia; las condiciones estresantes pudieron haber filtrado la diversidad a través del tiempo. La comunidad de hongos del suelo casi se recuperó después de dos años al estado previo al huracán; por lo que la comunidad de hongos del suelo fue resiliente al huracán Patricia. La resiliencia fúngica directamente aporta a la recuperación de las propiedades ecosistémicas, tales como la descomposición de la materia orgánica que impacta en la disponibilidad de nutrientes para la vegetación, la pedogénesis o la estabilidad de agregados del suelo que tienen un efecto en la erosión del suelo.

Abstract

Climate change will make catastrophic events more common, in particular hurricanes. Hurricanes increase rainfall, and litterfall through vegetation destruction. These are ideal conditions for saprotrophs organisms –such as fungi and bacteria– but inadeccuate for obligate symbionts. Our aim was to understand how hurricane Patricia (category 4) changed the diversity and community assembly of soil fungi in a tropical dry forest. ITS2 rDNA sequences from faungal soil of a two year-time series (one sampling before hurricane and four samplings after it) showed that before Patricia were 519 OTUs; Ascomycota was the most diverse phylum. Immediately after the hurricane, fungal richness increased to 1358 OTUs, Basidiomycota saprotrophs were more abundant; the community dominance decayed. After Patricia, fungal diversity decreased and dominance recovered gradually through time. Mycorrhizal fungi diversity was higher after Patricia and kept high after two years. Plant pathogens and parasites increased immediately after Patricia and decreased through time even more than before the hurricane. We found 105 OTUs, mainly saprobes, formed the persistent community during all the study. The diversity increased because hurricane created environmental heterogeneity, and the loss of dominance match with intermediate-disturbance hypothesis; these new conditions considered as harsh, could filter diversity through time. Soil fungal community almost recovered the previous hurricane state two years after the hurricane; hence soil fungal community was resilient to Patricia hurricane. Probably fungal resilience

directly helped to recover ecosystemic properties, such as decomposition of organic matter.

Keywords

Chamela, disturbance, high dominance, fungi, recovery, resistant community, tropical dry forest

Introduction

Climate change produces catastrophic events in short-intervals of time, such as hurricanes, even if they were considered infrequent events (Buma 2015). Catastrophic events, along with anthropogenic disturbance, affect the environmental conditions and create complexity in ecosystems (e.g. Hodgson et al., 2015; Riutta et al., 2018; Martínez-Yrízar et al., 2018). Disturbance tests the survival capacity to new conditions of each species, produces succession and loss of species in communities. After disturbance, some species resist and they could help to return quickly to the state prior the disturbance, giving resistance to the community (de Vries & Shade, 2013; Oliver et al., 2015). Whether the biological diversity is high it produces ecological redundancy that mitigates the disturbance and this in turn generates resilience (Standish et al., 2014; Mori 2016). Climate change will affect biological communities (Moritz & Agudo, 2013); however, the question remains as how species will change after the increasing disturbance.

Microbial communities, particularly fungi and bacteria, are the main soil decomposers (Tedersoo et al., 2014; Bahram et al., 2018). Their enzymes break the recalcitrant elements from the litter and soil, changing the availability of nutrients (Berg 2000). Also, soil available nutrients or organic matter changes the microbial communities through time (Grandy et al., 2009; Purahong et al., 2016). Their participation involves mineralization additionally with immobilization of elements in their own biomass (Hobbie 2015). Despite the great role of soil microorganisms, we continue to ignore the effect of catastrophic events in their communities.

Tropical forests are niche of hiperdiversity from several groups, and fungal communities are well represented (Tedersoo et al., 2014). In America, tropical dry for-

est (TDF) is distributed from Mexico to Argentina, and the Caribbean. Nowadays it has less than 10% of its original extent and is highly threatened by human activity (DRYFLOR 2016) and catastrophic events, such as hurricanes and fires. TDF goes through 3-6 months with less than 100 mm of rainfall (DRYFLOR 2016). During dry season, plants reabsorb nutrients from photosynthetic material and throw the leaves to prevent water loss (Rentería et al., 2005), and litterfall increases (Anaya et al., 2012). Water availability controls decomposition rate and mineralization (Anaya et al., 2012). Hurricanes in TDF increase soil organic matter, nutrients, and annual average precipitation (Gavito et al., 2018; Jaramillo et al., 2018). Hurricanes bring more rain and decomposition rate could modify depending on the hurricane (Gavito et al., 2018).

High-throughput sequencing has helped to understand the complex response of fungal communities' assembly to disturbance (e.g. Lekberg et al., 2011; García de León et al., 2018; Castillo et al., 2018). We used these methods to study the assembly of soil fungal communities before and after a hurricane. The studied hurricane was Patricia, category 4 Saffir-Simpson scale, made landfall in October 2015 in a tropical dry forest in the Mexican Pacific coast. Our aim was to understand how soil fungal communities' assembly was before and after hurricane in a time-lapse sampling. Our hypotheses were: 1) that due the increase of soil organic matter nutrient enriched, mainly C, N and P, we would find more diversity of species after hurricane, and an increase on the saprotroph guilds, mainly Basidiomycota – phylum with great enzymatic capacity– due the amount of lignin litter input; 2) the increase of soil nutrients will affect considerably mycorrhizal fungal community.

Methodology

Study site

This study was conducted on the Biological Station of Chamela, Jalisco, Mexico (19°30' N, 105°03' W) that has a warm subhumid weather (Aw0(x')i) on summer and warm dry (Bshw) in winter. This forest passes by a long dry period (8 months) so 84% of mean annual precipitation (1007.9 mm; 2007-2017) happens between July to October. Precipitation is variable depending on hurricane season in Sep-

tember-October (e.g. in 2011 with Jova hurricane increased to 1215 mm). The main vegetation type is tropical dry forest (TDF) and next to streams the vegetation is tropical moist forest.

The major land relief that we sampled was summit surface with Regosol eutric soil (Cotler *et al.*, 2002) on granite (Martínez-Trinidad *et al.*, 2008). This soil type along with the land relief is the driest place of the forest, shallow, with low organic matter accumulation, and without horizon B (Cotler *et al.*, 2002). The organic phosphorus is the main form of P in the TDF soil (Álvarez-Santiago 2002), however available phosphorus is the most limited nutrient (Jaramillo & Sanford, 1995).

Sampling

We sampled two soil cores (10 x 5 cm diameter) in a 200 m transect, every 20 m in both sides of transect; the 20 soil cores were pooled in a same sample. The soil was dried with silica gel at environmental temperature, and then stored in a plastic bag. The first sampling was done on the rainy season in November 2014 just before Patricia hurricane. After the hurricane, we sampled on dry and rainy season of two years: May and October 2016, April and September 2017. All the samplings were in the same transect (19°30’19.6’’ N, 105°02’30.3’’ W).

Soil chemical analysis

Total N and P were obtained by Kjedahl method and quantified by molybdate yellow colorimetric. Total C was determined by the Walkley-Black method. Electric conductivity and pH were analyzed by a conductivity bridge and pHmeter, respectively. These analyses were done by "Laboratorio de Fertilidad de Suelos y Química" from Colegio de Posgraduados, Mexico. We calculated the C:N, C:P ratio per sample. We plotted the results of soil characteristics with ggplot2 package in R (Wickham et al., 2016).

Molecular biology and bioinformatics

We extracted total DNA from 2 g of the finest part of soil with PowerMax Soil DNA isolation kit (MoBio; USA). After, ITS2 rDNA was amplified with the mix of fungal primers reported in Tedersoo et al. (2014) coupled with NextEra adapters at 2.5

μM. We used the Taq Platinum Multiplex PCR Master Mix (Life technologies; USA) protocol and made three multiplex PCR replicates per DNA extraction. The three PCR products of each DNA sample were pooled and sequenced by Illumina Miseq in "Instituto de Medicina Genómica", Mexico.

We filtered sequences by quality with default values using vsearch (minovlen=15; maxdiffs=99; minlength=150; maxee=1; truncqual=0; maxns=0). Sequences were demultiplexed with MOTHUR v1.36.1 (Schloss et al., 2009). Chimera filtering was done *de novo* using UNITE ITS2 v7.1 as a reference base filtering, cutting primers, and removing primer artefacts by vsearch. ITS2 region was extracted with ITSx v1.0.11 (Bengtsson-Palme et al., 2013). The OTU table was clustered using CD-HIT v4.6 (parameters: threshold similarity=0.97, min length=50, memory=400, min size=2, length cutoff=0, threads=1, storing=0, algorithm=0). Taxonomy of the most abundant read per cluster was assigned using BLAST+ v2.2.28 and UNITE v7.1 (Kõljalg et al. 2013). All these tools were performed in PipeCraft toolkit v1.0 (Anslan et al. 2017). We subtracted the number of sequences found in controls from each sample (Nguyen et al., 2014). The fungal guilds of each species were determined by FUNGuild (Nguyen et al., 2016).

Statistical analysis

We analyzed the diversity from all the soil samples determining richness and frequency. Matrix was rarefied; rarefaction curve was plotted by vegan package in R (Oksanen et al., 2016). Then, the matrix was normalized by Hellinger transformation with vegan package of R (Oksanen et al., 2016). All graphics were done in ggplot2 package in R (Wickham et al., 2016). We compared diversity data per each sampling with one-way ANOVA in PAST. We calculated a multiple rank-abundance curves to determine dominance with goeveg package in R.

Results

Soil characteristics

Soil analysis showed that electric conductivity (EC; Fig. S1a) increased during May 2016 (dry season) just after the hurricane, and in April 2017 decreased dramatical-

ly. The same response was observed in total C (Fig. S1b) and again it increased on September 2017 (rainy season). Organic matter increased after hurricane and it was maintained high during the April 2017; in September 2017, organic matter decreased (Fig. S1c). Besides, total N increased after hurricane and it was maintained high during next seasons (Fig. S1d). After hurricane, soil pH was acid, with the lowest pH in September 2017 (Fig. S1E). Total P had a peak on May 2016 after hurricane and the next seasons decreased (Fig. S1f). Ratios C:N and C:P decreased before hurricane, nonetheless they both reacted different on the next seasons: C:N was lower than before the hurricane; meanwhile C:P increased dramatically after hurricane having the maximum measure on April 2017 (Fig. S1g, h).

Soil fungal diversity

Rarefaction curves showed that immediately after the hurricane richness increased, and in the posterior samplings decreased (Figure 1a). When data was normalized, Simpson diversity index (1-D) increased immediately after hurricane, and in consecutive samplings diversity diminished; however, diversity was kept higher than before hurricane (Figure 1b). Fungal diversity between samplings was significantly different ($F_{4,10225}$=274.5; P<0.001) but not between rainy and dry seasons. In November 2014, before hurricane three species (*Acrocalymma vagum*, *Calvatia fragilis* and Tremellomycetes sp.) dominated with >500 sequences, and community abundance changed after hurricane to became more evenly distributed. Over time, the fungal community tended to recover dominance of few species (Figure 1c).

Before Patricia hurricane, we sequenced 519 OTUs, and after Patricia fungal richness increased to 1358 OTUs, in October 2016 (Table 1). This increment caused that some taxonomic groups appeared, e.g. the phyla Calcarisporiellomycota and Rozellomcyota (classification of Wiljayawardene et al., 2018) were not present before hurricane (Fig. 2a-b). In general, Basidiomycota and Ascomycota were the most diverse phyla of any of the seasons of sampling. However, Basidiomycota abundance was higher immediately after Patricia (Figure 2b); Agaricomycetes were the 27% of all Basidiomycota, and Agaricales order was the most diverse or-

der in any sample. Most of Ascomycota belong to Sordariomycetes, Dothideomycetes, Eurotiomycetes, Leotiomycetes, Orbiliomycetes class, (Figure 2c-d). Pleosporales, Eurotiales, Xylariales, and Hypocreales were also diverse. In general, several new orders appear after hurricane with low diversity, e.g. Archaeosporales, Corticiales, Dothideales, Paraglomerales, and Diversisporales (Figure S2).

After hurricane 839 new OTUs appeared, and in consecutive samples the number of exclusive OTUs in each sample decreased. For example, in May 2016 we found 425 OTUs not shared with another season, while in October 2016 we found 189 exclusive OTUs. All the species found in November 2014 were present in the posterior samples with different abundance (Figure 1d). Besides, we found that 105 OTUs that were present in all samples, thus they conform the resistant soil fungal community. The resistant community is mostly integrated by fungi with unknown taxonomical identity, so that unknown fungal guild (62.85%), and the rest were saprotrophs (20%), plant pathogens (8.57%), and mycorrhizal fungi (5.71%) (Figure S3).

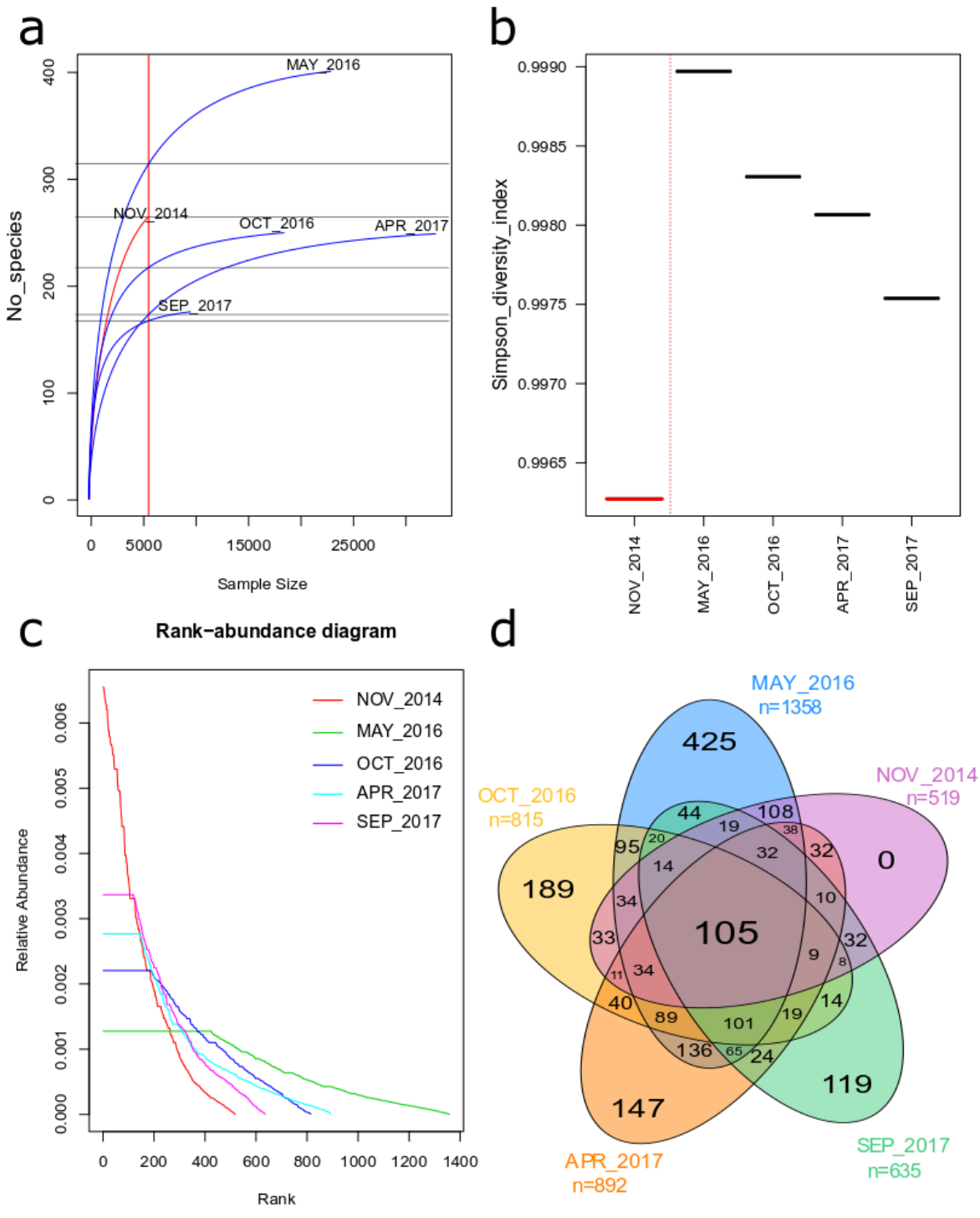
Table 1. Richness and abundance of each sampling season. November 2014 is the community before hurricane Patricia.

Sampling	Phy	Cla	Ord	Fam	Gen	OTUs	Unk	No. seq
Nov 2014	6	17	40	76	101	519	233	17258
May 2016	7	29	68	147	204	1358	599	54576
Oct 2016	7	24	50	96	114	815	365	44424
Apr 2017	6	21	55	102	130	892	391	49608
Sep 2017	7	23	50	87	101	635	296	32959

Phy=Phylum, Cla=Class, Ord=Order, Fam=Family, Gen=Genus, Unk=Unkown, No. seq= Number of sequences.

227 Before hurricane Patricia, arbuscular mycorrhizal fungi (AM) were rare and in the
228 posterior samples its diversity increased. Animal pathogens were less abundant
229 during May 2016 and more abundant in September 2017. Ectomycorrhizal fungi
230 had almost the same richness in each sample, however after Patricia their abun-
231 dance increased, especially in dry seasons (April and May). Parasites had higher
232 richness before hurricane however their abundance was less compared with the
233 posterior seasons; plant pathogens and saprotrophs presented the same pattern.
234 However, in saprotrophs, we found an increase in abundance during dry seasons
235 (Figure 2e-f).

236 In the study site, the first five most abundant species through time were Euroti-
237 omycetes sp. (OTU 2394), *Membranomyces* sp. (OTU 102; SH522097.07FU),
238 *Latorua caligans* (OTU 2724), Thelephoraceae sp. (OTU 516), *Geastrum* sp. (OTU
239 1901; SH025433.07FU); however, not all of them were present in all samplings,
240 for example, *Membranomyces* sp. was absent before Patricia (Figure S4).



241

242 Figure 1. A) Species rarefaction curves from each sampling, labels correspond to
243 sampling season. Vertical line belongs to sample before hurricane. B) Simpson
244 diversity index of each season of sampling. Red lines belong to sample before hur-
245 ricane. C) Rank-abundance curves of each sample. D) Venn diagram show the

number of share species between seasons. Abbreviations: NOV_2014= November 2014, MAY_2016= May 2016, OCT_2016= October 2016, APR_2017= April 2017, SEP_2017= September 2017.

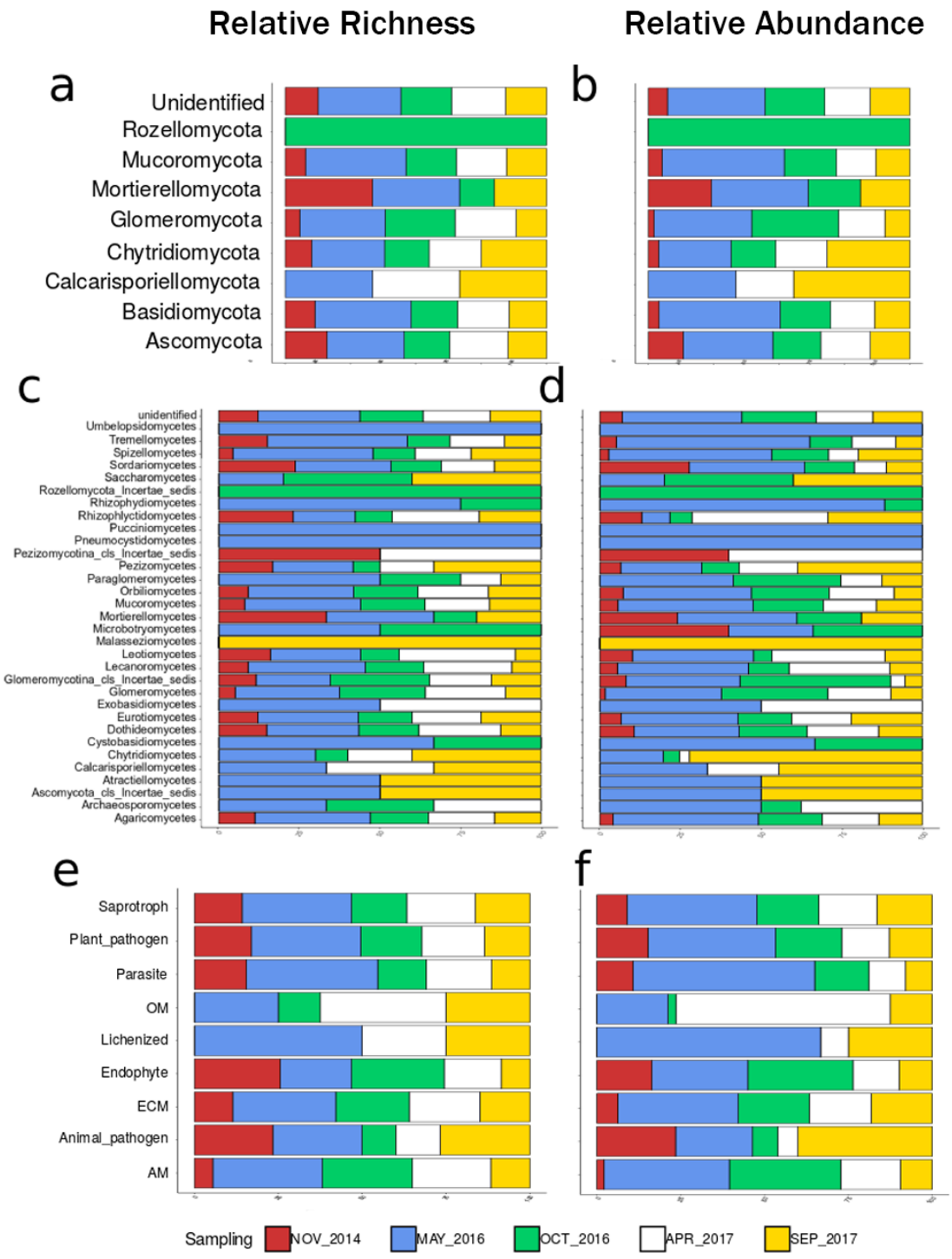


Figure 2. a, b) Relative richness and relative abundance of phyla, c, d) class, and e, f) guilds. Abbreviations: Sap= saprotrophs, Plant_path= plant pathogens, OM= orchid mycorrhiza, Lich= lichenized, Endo= endophytes, EM= ericoid mycorrhiza, ECM= ectomycorrhizal, Anim_path= animal pathogens, AM= arbuscular mycorrhiza.

Discussion

Our results tracked the succession of the fungal community after hurricane Patricia made landfall, and how soil fungi community was persistant and resilient in more than two years. We observed the fungal succession through time, with the highest diversity immediately after hurricane (1358 OTUs) and decreasing later. The high dominance before Patricia decayed and recovered slowly, showing resilience. The high diversity was a consequence of the appearance of 839 new OTUs after hurricane. Before Patricia hurricane, Ascomycota was the phylum more abundant, after hurricane Basidiomycota saprotrophs was the guild with highest diversity, followed by plant pathogens.

We highlight that before the disturbance there was high dominance of few species, but immediately after Patricia it disappeared. The low dominance fostered high fungal diversity after hurricane. This result is completely opposite to disturbed forests where some species become dominant over the community (Prieto et al., 2017). Disturbance can have a positive effect on richness, while undisturbed sites limit the establishment of new species (Wohlgemuth et al., 2002; Farrior et al., 2016). Through time, dominance recovered in more than two years after hurricane.

Tropical dry forest had high turnover because on each sample we found exclusive fungal species through time. We found no replacement from any of the initial species of 2014. The succession is non-directional replacement, i.e. harsh environment is a strong filter for a successful establishment (Svoboda & Henry, 1987), and diversity recovers slowly. However, fungi recover quicker compared to other organisms e.g. arbuscular mycorrhizal fungi have a quicker recovery than plant communities (Mao et al., 2019). Despite fungi recovered slowly, it seems to be resilient. Fungal resilience results from high fungal diversity which has ecological redundan-

281 cy (Peršoh 2015). An evidence of fungal redundancy was decomposition rate in-
282 creased after hurricane Patricia (Gavito et al., 2018).

283 Throughout two years, 105 fungal species persisted in all soil samples. We identi-
284 fied them as the soil resistant community since these species persisted thru a hur-
285 ricane category 4 and the seasonality of this ecosystem. These species are mainly
286 saprotrophs (e.g. *Geastrum* sp., *Lepista sordida, Clitopilus* sp., etc.), and given the
287 fluctuating environmental conditions, we hypothesize that they are highly plastic
288 with genetic adaptations that resist drought, high temperatures and nutrient fluctua-
289 tion. These species had low sensitivity to disturbance because they are highly
290 adapted to the ecosystem, and they influenced in particular processes (Allison &
291 Martiny, 2008), such as decomposition.

292 Several 'new' species appeared in soil after hurricane. With all the vegetation
293 damage could be that endophytes that turn to saprotrophs (Promputtha et al.,
294 2007) become abundant at soil. Also, water, wind, and animals, could be responsi-
295 ble of the increase of richness after hurricane, they can transport spores through
296 long distances (e.g. Jumpponen 2003; Behzad et al., 2018; Correia et al., 2019).
297 Thus, hurricanes also can be agents of import fungal species as it happens with
298 plants (Bhattari & Cronin, 2014). After the peak of diversity brought by the hurri-
299 cane, fungal diversity declined in each of the posterior samplings. Ecophysiological
300 characteristics of exotic species are tested when they arrive to a new environment
301 (Svoboda & Henry, 1987), and interspecific interactions, such as competition could
302 inhibit in the establishment of these (Koide et al., 2011).

303 Our results supported the hypothesis that predicted Basidiomycota saprotrophs
304 would increase after hurricane. After hurricane, deposition of 17.8 Mg ha^{-1} litterfall
305 (Parker et al., 2018) induced organic matter increment and C:N ratio reduction.
306 Basidiomycota saprotrophs –such as *Lepista sordida* or *Geastrum* sp.– abundance
307 increased after Patricia. Litterfall physico-chemical properties change through de-
308 composition, and so fungal communities: Basidiomycota prevails in the latest stage
309 (Purahong et al., 2016) because they high enzymatic capacity to decompose ligno-
310 cellulosic compounds (Voříšková & Baldrian, 2013).

Nutrient increment affects directly mycorrhizal establishment (Verlinden et al., 2018). Phosphorus input was notably higher after Patricia, and after a year decreased to be lesser than before hurricane. Nitrogen remained higher than before Patricia. Plants dispense with mycorrhizal interaction when available nutrients are high (Verlinden et al., 2018). Nutrient stress-gradient reinforce mycorrhizal symbiosis but hurricane nutrient-disturbance shaped mycorrhizal communities differentially. However, after hurricane, arbuscular mycorrhizal (AM) and ectomycorrhizal fungi (ECM) increased their abundance on soil (e.g. *Membranomyces* sp. increased its abundance after Patricia). After hurricane –when ratio C:P increased– AM remained abundant. AM are more specialized on phosphorus acquisition while ECM rather obtain nitrogen (van der Heijden et al., 2015). ECM abundance increased immediately after Patricia and decreased in posterior samplings.

On the other hand, plant pathogens and parasites increased its diversity immediately after the hurricane, probably due to damaged suffered by plants. A successful infection of a plant pathogen depends on a susceptible host and an ideal environment (Garrett et al., 2009). Our monitoring of soil fungal diversity was done on a hilltop, where Patricia predominantly removed the canopy (Parker et al., 2018) damaging strongly the vegetation. Many plant pathogens produce billions of mitospores that travel aerially (Tedersoo et al., 2014) and they could find an establishment opportunity in damaged vegetation. One year after Patricia and thereafter, pathogens diversity decreased, and their abundance became lesser than before hurricane.

Dry and rainy season maintained the same fungal diversity; however, forest seasonality can be responsible of the slow recovery. In tropical dry forest rains less than 1800 mm per year for 6-8 months (DRYFLOR 2016). Decomposition rate increases with water availability in this ecosystem, and stops during dry season (Anaya et al., 2012). Fungi require water to break lignin and cellulose complex molecules. Fungal spores can linger dry conditions waiting for humid conditions, especially those who have cellular melanin wall (Fernandez et al., 2016). Soil fungal spores may be inactive with basal metabolism when water is no available. We

could have same diversity in any season because our sequence technique did not differentiate active and inactive fungi.

Hurricanes will increase in frequency and severity while ocean water gets warmer (Knutson et al., 2015), causing disturbance in tropical and subtropical ecosystems around the globe. Climatic change scenarios predict desertification of the tropical forests (Salazar et al., 2007). Fungal species with high plasticity and strategies to survive droughts will continue as part of the soil community. While the fungal community continue high diverse, the ecological redundancy will be also higher and will drive the ecosystem to resilience. Same as other organisms (e.g. Ameca y Juárez et al., 2013; Hogan et al., 2017; Lloyd et al., 2019; Paz et al., 2018; Temeles & Bishop, 2019), fungi can vary between damage till beneficial impact. Hurricanes disturbance, drought, land-use change, etc. jeopardize soil diversity that could generate 'defungation', i.e. loss of fungal diversity. Proper soil management can cause survival of the soil diversity; in the face of such a threat is a light of hope in the face of the predicted environmental catastrophe. Understanding how communities are affected by disturbance gives us the opportunity to make good decisions about the management of resources.

Conclusions

Basidiomycota saprotrophs were the main fungal guild after hurricane due the increase of soil organic matter, same as mycorrhizal fungi. Plant pathogens increased on soil after Patricia probably due vegetation damage. After two years the pattern of high dominance tended to recover, showing resilience in more than two years. Some fungal species form a resistant community to disturbance, showing plasticity to harsh environment. The response of each community depends on the magnitude and severity of the hurricane and the previous state of the site.

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Supplementary information

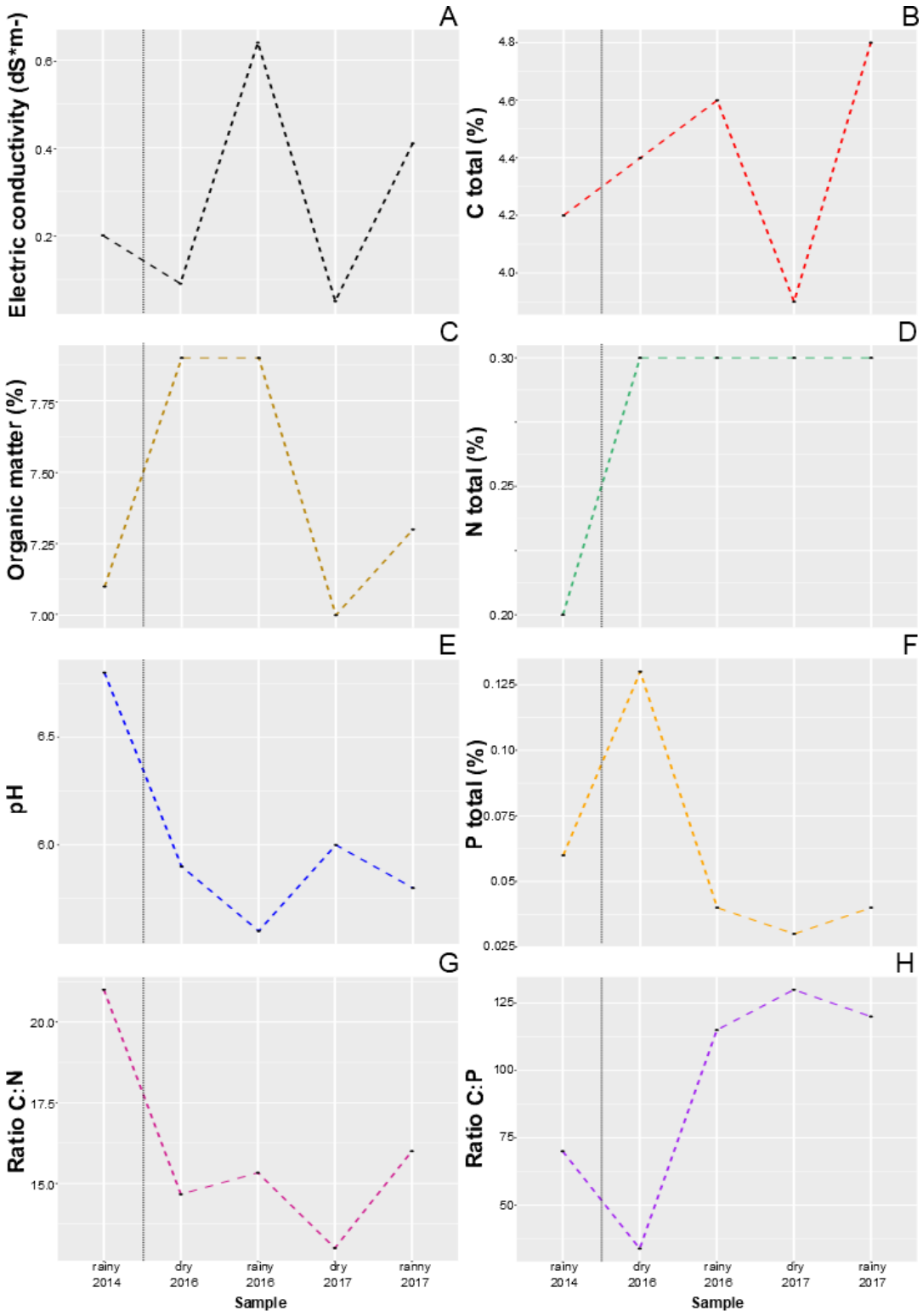


Figure S1. Soil nutrients per sampling, rainny season 2014 correspond to the sampling before the Patricia hurricane. The black vertical line indicates Patricia hurricane landfall.

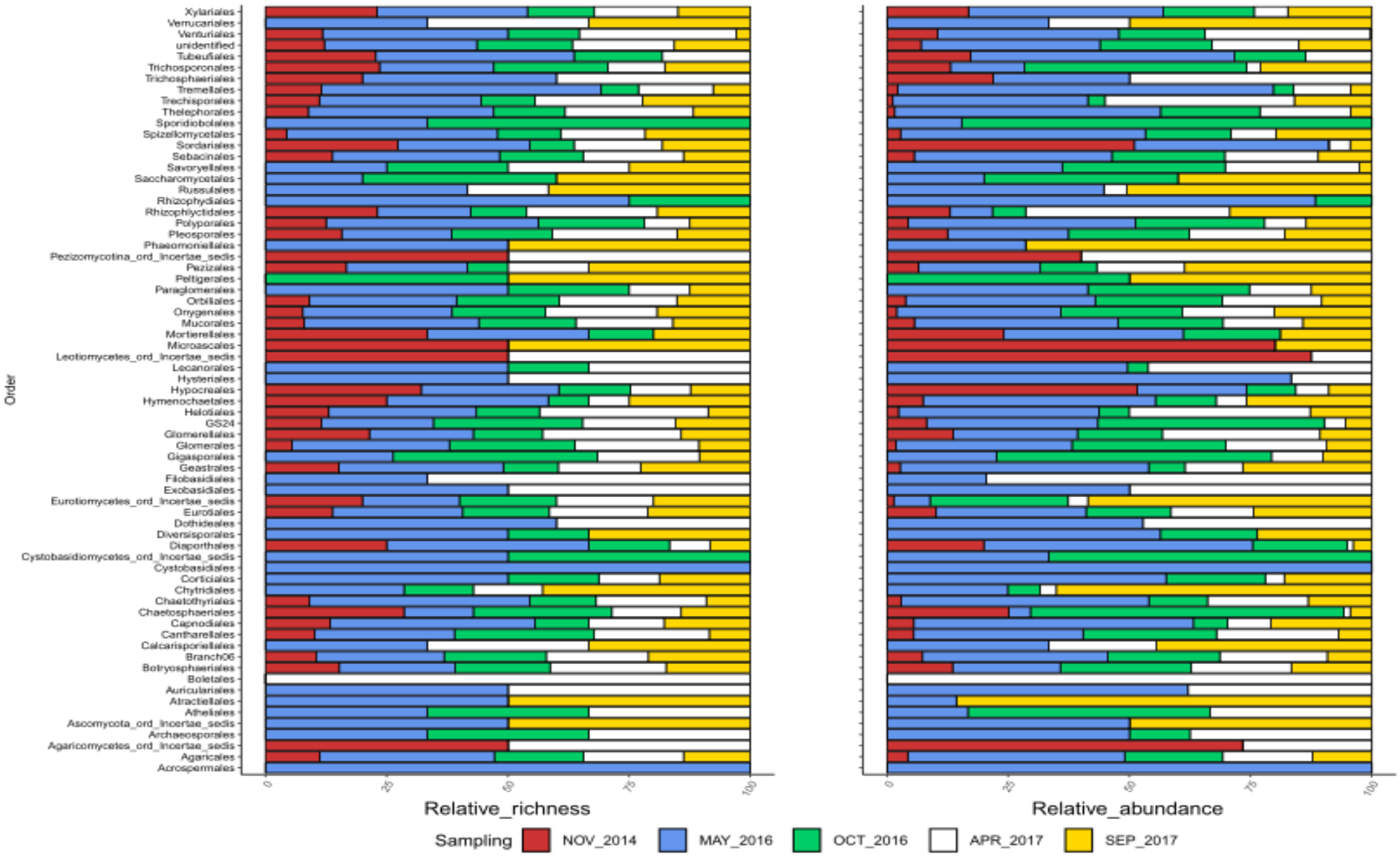


Figure S2. Relative richness (left) and relative abundance (right) of Order in each sample.

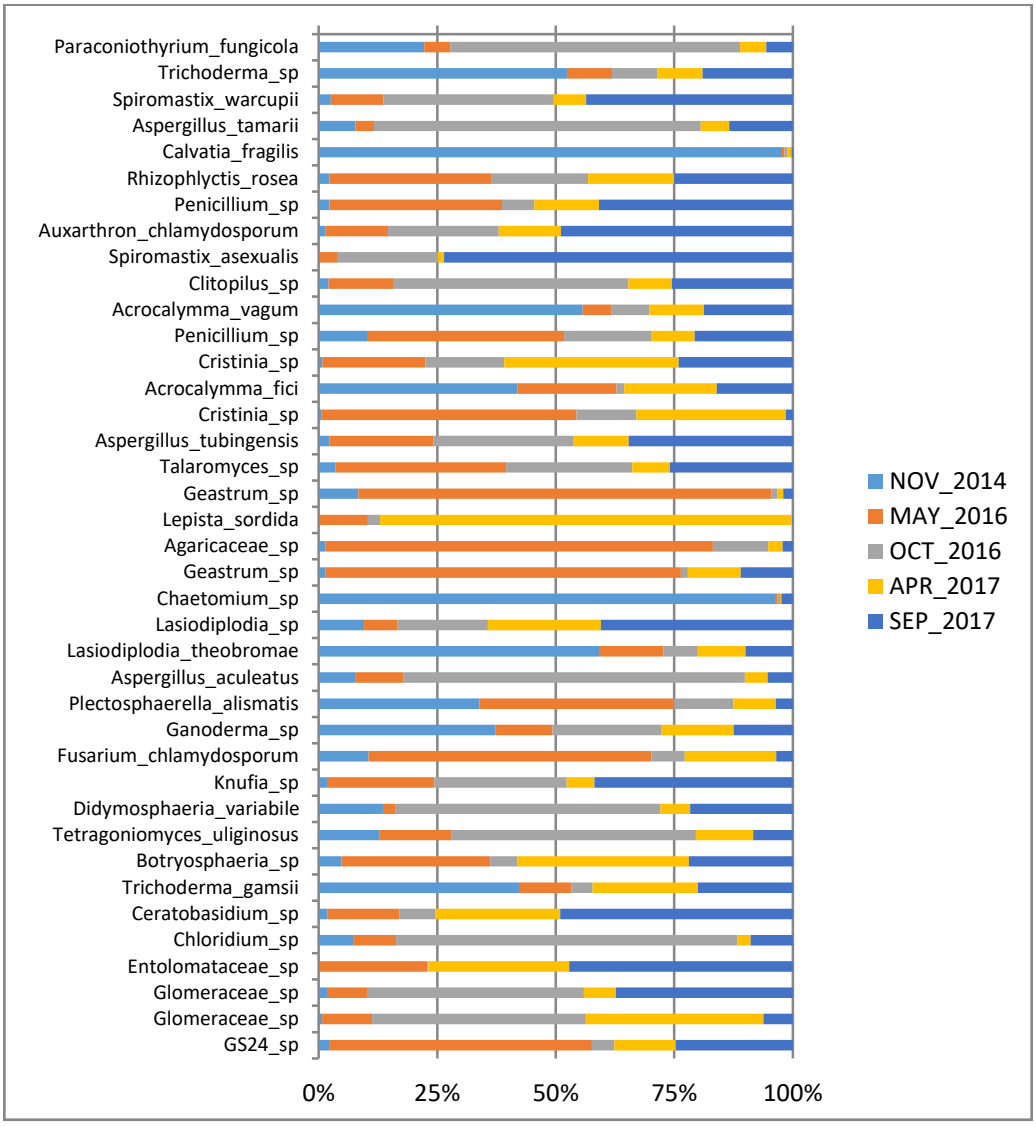
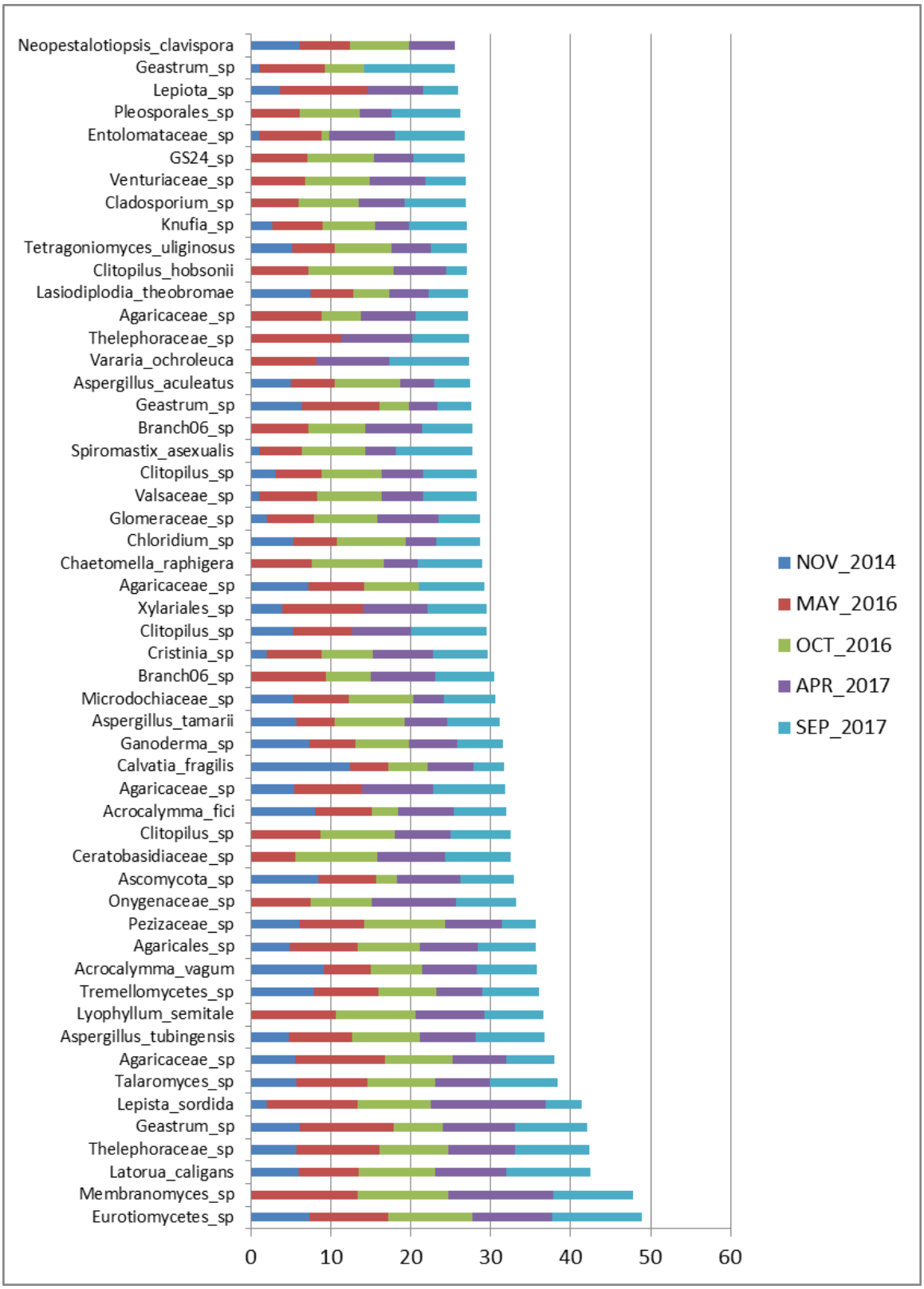


Figure S3. Abundance of fungi belonging to the persistent community. This graph contains just 39 taxa with taxonomical assignment from 105 species that shapes the resistant community.



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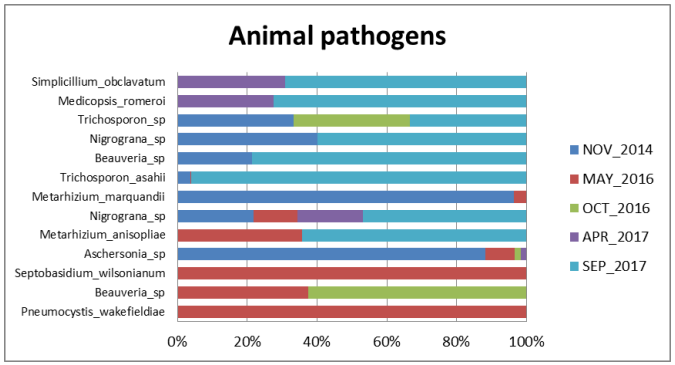
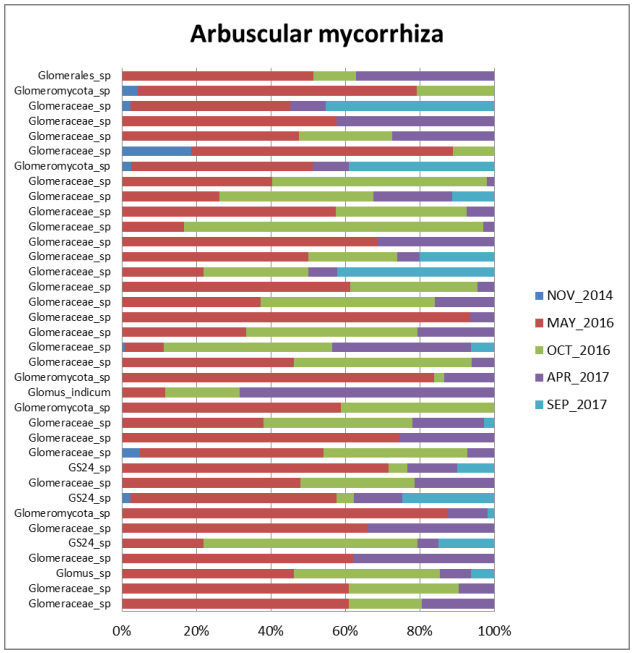
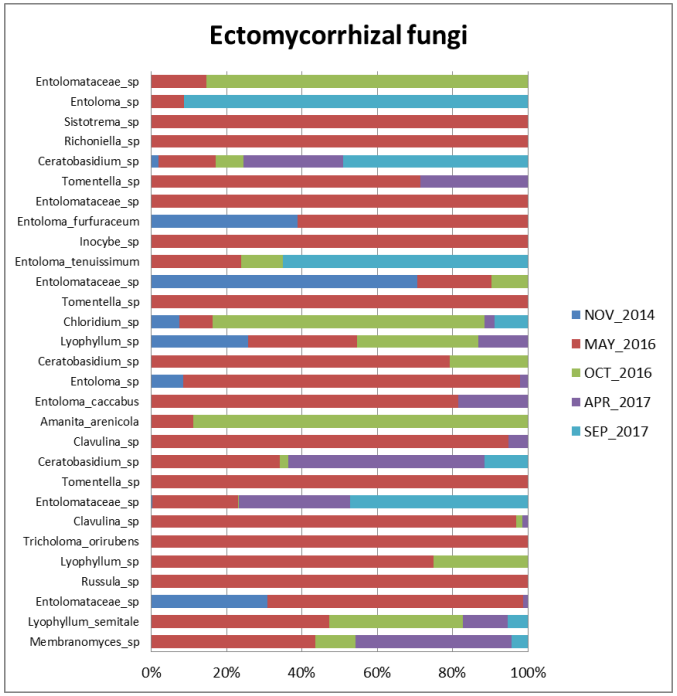
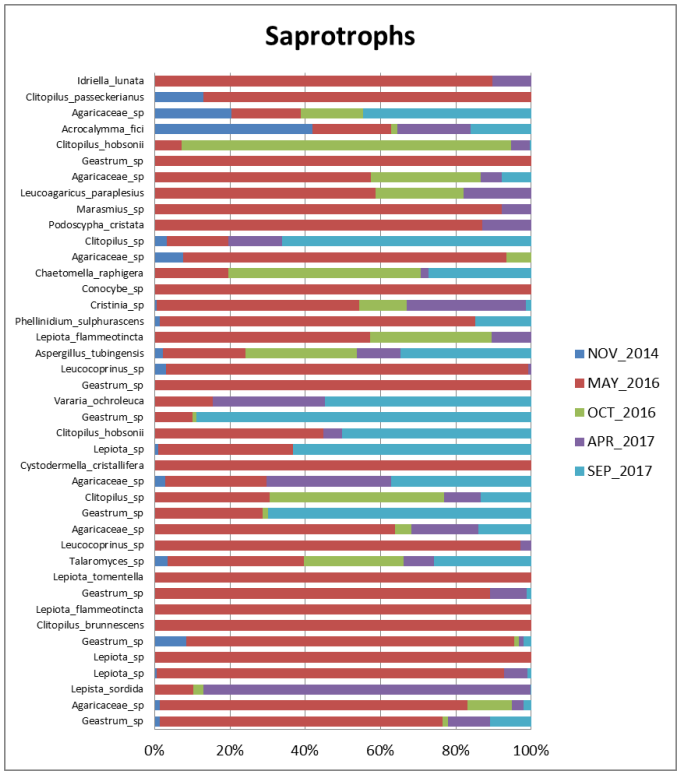
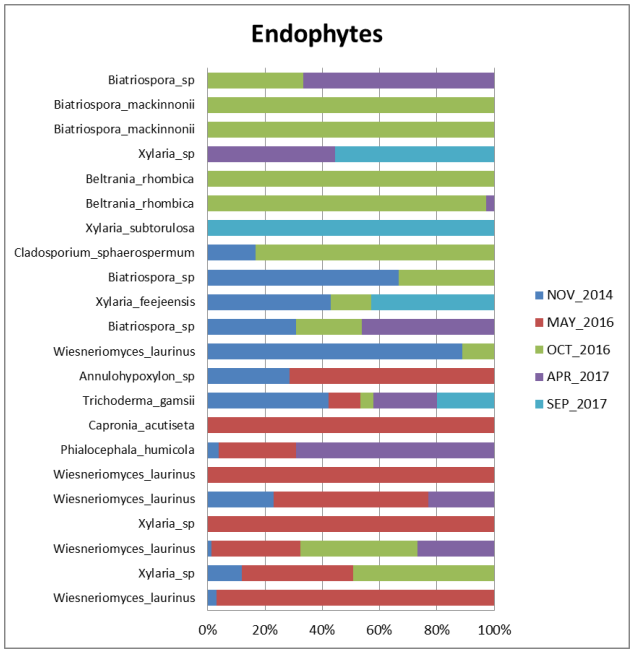
592 Figure S4. Abundance fluctuation through time (plot includes just the 53 more abundant
593 fungi).











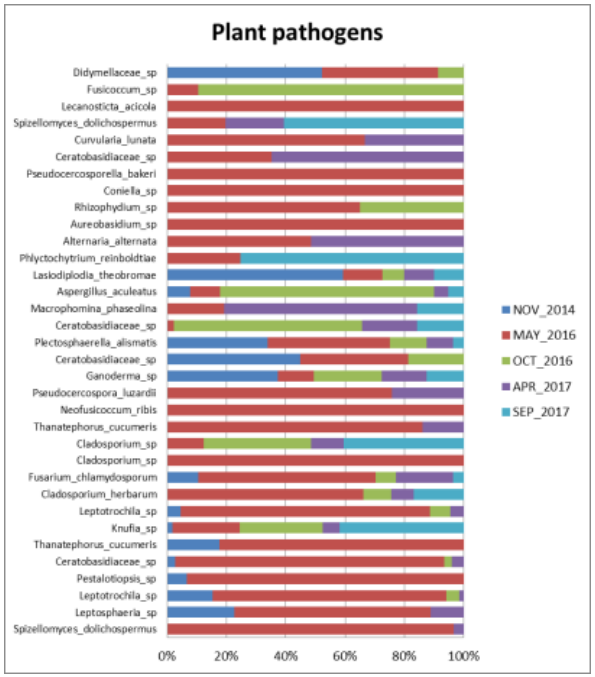


Figure S5. Abundance of the persistent community in each fungal guild.

CAPÍTULO 3. THE MYCORRHIZAL NETWORKS AND RHIZOSPHERIC FUNGAL COMMUNITIES IN A NEOTROPICAL DRY FOREST ARE RESILIENT

Running title: Hurricane affects mycorrhizal networks

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Resumen

Los ecosistemas forestales están cada vez más sujetos a eventos climáticos extremos asociados al cambio climático, sin embargo, las consecuencias para la diversidad subterránea y sus interacciones bióticas siguen siendo poco exploradas. En este trabajo se examinó el efecto del huracán en las redes micorrízicas y las comunidades fúngicas de la rizósfera. Estudiamos los efectos del huracán Patricia (categoría 4) que azotó en el 2015 el bosque tropical caducifolio de la costa del Pacífico. Patricia dañó sustancialmente la vegetación y aumentó el mantillo, y por ende los nutrientes del suelo. Usamos la secuenciación Illumina MiSeq para caracterizar comunidades fúngicas rizosféricas de plantas con colonización micorrízica dual. Se recolectaron raíces de nueve parcelas en 2016 y 2017, después de huracán. Se usaron matrices de presencia-abundancia para calcular las propiedades de las redes micorrícicas –anidamiento, modularidad, especialización– y la concurrencia de especies fúngicas. Inmediatamente después de Patricia, la pérdida de conectividad de la red micorrízica produjo una alta modularidad y recuperó las conexiones en 2017. Cuando las conexiones se recuperaron, solo una parcela tenía anidamiento, pero la mayoría

de las redes eran modulares. La red micorrícica arbuscular fue la más dañada en contraste con la red ectomicorrízica. Los gremios de hongos cambiaron sus interacciones interespecíficas entre años: todos los gremios se excluían mutuamente el primer año de muestreo, y al segundo año, los patógenos de plantas, saprótrofos y endófitos tuvieron una mayor co-ocurrencia. Encontramos una correlación negativa significativa entre la cobertura del dosel (es decir, falta de luz), así como la temperatura del suelo con diversidad fúngica. La identidad del huésped y la perturbación determinan la comunidad fúngica. La comunidad fúngica de la rizosfera fue menos diversa el año siguiente al huracán, pero aumentó en el año siguiente. En comparación con los grupos taxonómicos, la composición de los gremios funcionales respondió con mayor fuerza a la perturbación: los saprótrofos fueron los gremios de hongos más abundantes en los sitios de alta perturbación. El cambio global puede aumentar la frecuencia e intensidad de los huracanes; Nuestros resultados sugieren que las comunidades fúngicas y sus interacciones son vulnerables a los huracanes pero resilientes.

Abstract

Forest ecosystems are increasingly subject to climate change associated extreme climatic events, yet the resulting consequences for belowground diversity and its biotic interactions remain little explored. Here we aimed to examine the effect of hurricane disturbance in mycorrhizal networks and rhizosphere fungal communities. We studied the effects of Patricia hurricane (category 4) landfall in a tropical dry forest of Pacific coast in 2015. Patricia substantially damaged vegetation and increased litterfall and thus soil nutrients. We used Illumina MiSeq sequencing to characterize rhizospheric fungal communities of dual-mycorrhizal plants. Their roots were collected from nine plots in 2016 and 2017. Presence-abundance matrixes were used to calculate properties of mycorrhizal networks –nestedness, modularity, specialization– and co-occurrence of fungal species. Immediately after Patricia the mycorrhizal network lost connectivity producing high modularity and it recovered connections in 2017. When connections were recovered, just one plot was relatively nestedness but mostly networks were modular. Arbuscular mycorrhizal network was the most damaged in contrast with ectomycorrhizal network. Fungal guilds changed their interspecific interactions between years. The first year of sampling we found all fungal guilds had

mutual exclusion; in second-year, plant pathogens, saprotrophs and endophytes switch to co-occurr. We found a significant negative correlation between canopy coverage (i.e. lack of light), as well as soil temperature with fungal diversity. Host identity and disturbance category determined fungal community. Rhizosphere fungal community was less diverse the year following hurricane but increased in the subsequent year. Compared to taxonomic groups, the composition of functional guilds responded more strongly to disturbance: saprotrophs were the more abundant fungal guild in the high disturbance sites. Global change may increase frequency and intensity of hurricanes; our results suggest that fungal communities and their interactions are vulnerable to hurricanes but resilient.

Key words

Arbuscular mycorrhiza, cyclone, ectomycorrhiza, extreme events, fungi, interspecific interactions, Pacific coast, Patricia hurricane

Introduction

Fungi are a major component of topsoil microbial communities, with essential roles for soil functioning as decomposers and plant mutualists. Recent advances in high-throughput-sequencing (HTS) have facilitated studying biogeographic patterns and factors that affect fungal communities in natural preserve systems (Tedersoo et al., 2014; Peay et al., 2016; Bahram et al., 2018). Rapid advances in the field also allow to classify HTS-based identification into functional guilds such as saprotrophic, mycorrhizal, parasitic/pathogen, endophytic, etc. (e.g. Tedersoo et al., 2014; Nguyen et al., 2016; Nilsson et al., 2019). These methods allow the inference of biotic interactions between fungal species, including different guilds (Chen et al., 2019) as well as those occurring inter-kingdom (Bahram et al., 2018). However, our knowledge about how fungal communities change due extreme climatic events, and whether their inter-kingdom or interspecific interactions modified by the effect of them is little.

Global change is causing the disturbance to become increasingly common in ecosystems. Commonly, anthropogenic disturbance combines with natural disturbance such as floods, drought and hurricanes (Banks et al., 2013). High temperature on the oceanic surface has a direct effect on tropical storms and hurricane formation (Henderson-Sellers et al., 1998). Hurricanes will be more frequent and stronger in the second

half of 21 century (Knudtson et al., 2015). As a result, there is a growing interest in the effect of hurricanes on vegetation and their outcome in other organisms such as birds, insects, mammals, etc. (e.g. Ameca et al., 2018; Bhattarai & Cronin, 2014; Jiménez-Rodríguez et al., 2018; Lloyd et al., 2019; Novais et al., 2018), with few studies on fungi (Cantrell et al., 2014; Vargas et al., 2010).

Soil fungal communities, same as above-ground communities, can be affected by disturbance (Banerjee et al., 2019) partly of a cascade effect. Further, environmental changes can modify species interactions (Kennedy 2010; Mahmood 2003). Mycorrhizal fungi have mutualist interactions forming complex networks with plants (Bingham & Simard, 2011; Toju et al., 2014). Arbuscular mycorrhiza is formed by 71% of terrestrial plants, and ectomycorrhizal is formed by 2% of plant (Brundrett & Tedersoo, 2018). Ectomycorrhizal fungi commonly habits in 30-60° latitudes (Steidinger et al., 2019) and some species in tropics (Corrales et al., 2018). Mycorrhizal fungi are affected differentially depending on the agent and intensity of disturbance (García de León et al., 2018).

Network ecology can help to evaluate ecosystem resilience and stability (Ramirez et al., 2018) or even interspecific interactions in microbial communities (Barberán et al., 2012). In general, mutualistic networks are nested, i.e. arranged in a cohesive nucleus (Bascompte et al., 2009). For example, in plant-animal interactions, generalist plants interact more with generalist animals; this result in functional redundancy on the ecosystem (Bascompte et al., 2009). In contrast, modularity is the compartmentalization of closely interacting species (Toju et al., 2014); in disturbed systems, high modularity is proposed to retain the impact of the cascading effect to the neighbor modules (Gilarranz et al., 2017), however still is a debatable topic.

Plant-fungal networks are more modular than expected by chance (Toju et al., 2014), same as ectomycorrhizal networks in different ecosystems (Bahram et al., 2014). Mycorrhizal networks found that orchid and ericoid mycorrhizal networks were more modular than ectomycorrhizal, and arbuscular mycorrhizal were intermediate (Põlme et al., 2018). The same properties previously mentioned could be used to study the effect of disturbance.

In October 2015 Patricia hurricane category 4 was the strongest record (winds of 345 km/h) that made landfall in the Pacific Mexican coast. Our aim was to determine the

effect of disturbance caused by Patricia hurricane landfall on mycorrhizal networks properties, on fungal rhizosphere communities and its interspecific interactions. Given that Patricia hurricane modified drastically vegetation composition and structure (Jiménez-Rodríguez et al., 2018; Parker et al., 2018), that the input of literfall resulted in increased litter C, N, N:P and C:P ratio on soil (Gavito et al. 2018), and that there was a high degree of short-term soil biogeochemical resilience (Jaramillo et al., 2018); we hypothesized that: 1) mycorrhizal networks will be highly modular because a high disturbance, 2) increase of soil nutrients caused by hurricane Patricia's disturbance has increased rhizosphere fungal diversity, 3) interspecific interactions will be modified boosting competition between guilds.

Materials and methods

Sampling

The study site was the biological station of Chamela, Jalisco, Mexico where Patricia hurricane made landfall in October 23rd, 2015. For sampling we established nine plots of 20 x 20 m in October 2016, were randomly selected on same soil type (coordinates Table S4). For each plot, we identified, counted and measured diameter of breast height (DBH) of all living trees and shrubs exceeding 3 cm of DBH (Table S1). Light and temperature were measured on the forest floor with HOBO Pendant UA-002-08, and humidity with Kestrel three times per plot. We also included in our analysis the slope to calculate erosion (Stone & Hilborn 2000; table S2). All ectomycorrhizal hosts were identified and marked (Alvarez-Manjarrez et al., 2018; Figure S1), and three root systems of 10 cm length were sampled per plant and pooled per host for further analyses. In 2017, we re-sampled roots from the same host tree individuals as in 2016. Additionally, we collected three soil cores (5 x 5 cm), they were pooled in a same soil sample from each plot. Samples were stored upon collection at 4°C until further processing. Ectomycorrhizal root-tips were extracted under stereo microscope and preserved in 96% ethanol for further analyses. Soil samples were analyzed by the "Laboratorio de Fertilidad de Suelos y Química Ambiental" from Colegio de Posgraduados, Mexico. Total N and P were obtained by Kjedahl method and quantified colorimetrically of molybdate yellow. Total C was determined by Warkley and Black method. Electric conductivity and pH were analyzed by a conductivity bridge and

158 pHmeter, respectively. PO_4 was extracted by blue molibdenum colorimetry, NO_3 and
159 NO_4 were obtained my steam distillation (Figure S2; Table S2).
160 DNA extraction from rhizosphere and soil was performed using PowerMax Soil DNA
161 isolation kit (MoBio; USA). ITS2 rDNA was amplified with five forward primers and
162 one reverse using NextEra adapters at 2.5 µM (Table S3): ITS3NGS1-ITS3NGS5
163 and ITS4NG (Tedersoo et al. 2014). We followed the Taq Platinum Multiplex PCR
164 Master Mix protocol (Life technologies; USA) to make three multiplex PCR replicates
165 per each sample. PCR replicates were pooled to be normalized, purified and se-
166 quenced by Illumina Miseq in “Instituto de Medicina Genómica” (INMEGEN), Mexico.

167 **Bioinformatics**

168 Reads were quality filtered using vsearch software with the default parameters (mi-
169 novlen=15; maxdiffs=99; minlength=150; maxee=1; truncqual=0; maxns=0). Se-
170 quences were demultiplexed with MOTHUR (Schloss et al. 2009) with default param-
171 eters (bdiffs=0). Chimera filtering was done *de novo*, with UNITE ITS2 v7.1 as a ref-
172 erence base filtering, cutting primers, and removing primer artefacts. After, fungal
173 ITS2 was extracted with ITSx (Bengtsson-Palme et al., 2013). To generate the OTU
174 abundance table, resulting ITS regions were clustered using CD-HIT with parame-
175 ters: threshold=0.97, min length=50, memory=400, min size=2, length cutoff=0,
176 threads=1, storing=0, algorithm=0. Taxonomy of the most abundance read per clus-
177 ter was assigned using BLASTn comparing with UNITE ver. 7.1 (Kõljalg et al. 2013);
178 singleton, i.e. reads with one sequence, were avoided. All this tools were performed
179 in PipeCraft v1.0 toolkit (Anslan et al., 2017). Sequence counts found in controls
180 were subtracted per sample from the OTU table (Nguyen et al., 2014). Fungal guild
181 of each OTU was determined by FUNGuild software (Nguyen et al., 2016).

182 **Network analysis**

183 To analyze nestedness and modularity of mycorrhizal networks we used a co-
184 occurrence matrix of plant-fungi taking into account all mycorrhizal fungal species
185 (i.e. AM, ECM, ericoid and orchid) to compare the variation of the network between
186 years. Separate calculations for AM and ECM networks were performed per each
187 year, per plot and per disturbance classification of plots. Nestedness index was cal-
188 culated with NODF function in bipartite R package (Dormann et al., 2008) and its sig-

nificance was tested based on comparing observed and 999 randomized matrices using quantitative swap and shuffle methods 'swsh_both' in vegan R package. In addition, modularity index and specialization (*H2'*; Blüthgen et al. 2006) were calculated using netcarto in rnectarto R package (Doulcier & Stouffer, 2015) and bipartite R package, respectively. Specialization measures the interaction strength or interaction frequency between two organisms, making distinction between strong or occasional interactions (Blüthgen et al., 2006). Nonparametric comparisons between network properties were performed with gao function in nparcomp R package (Gao et al., 2008) using zero value instead missing data to run the test; missing data were common in samples from 2016 due many mycorrhizal species were not colonized. Centrality was calculated with igraph in R to make the network plots and were visualized using Kamada-Kawai algorithm with ggnetwork in ggplot2 R package (Wickham, 2016), coloring by fungal guilds. Bipartite network was plotted using function plotweb in igraph R package (Csardi & Nepusz, 2006).

The co-occurrence network analysis was done in CoNet app of Cytoscape, using data from rhizosphere and soil separated by years. The matrices contained only fungal OTUs with known guilds, excluding lichenized and fungal parasite lichens because they are not consider as common rhizosperic fungi. The parameters used were minimum row sum of 20, with Log standardization, using Pearson and Spearman correlation with Bray-Curtis dissimilarity distance. The analysis was performed using 100 bootstrap iterations with Benajmin-Hochberg test correction for the P-value threshold 0.05. The graph was generated using the mean of multi-graph, using union as network merge, adding the guilds as attributes to compare co-occurrence between them.

Statistical analysis

Sequences abundances bigger than median were rarefied with rrarefy in vegan package of R (Oksanen et al., 2019). The rarefied matrix was used to calculate β diversity turnover Simpson index, nestedness resultant from dissimilarity matrix Sorensen and β diversity with Sorensen index with betapart in R package.

To compare the effect of disturbance on plot vegetation, soil and environmental characteristics, a cluster analysis was used based on Ward distance with hclust in R package (Figure S3).

The data were visualized in a NMDS ordination plot using Bray-Curtis dissimilarity matrix (Bahram et al. 2018). Prior to that, data were normalized using Hellinger transformation. To determine the significance of the effect from abiotic characteristics a permutational analysis of variance (PERMANOVA) was performed with adonis in vegan package of R (Oksanen et al., 2019). We calculate Shannon diversity index of every sample and calculate a linear regression with lm in stats package of R. We used a Student-*t* test to compare Shannon diversity index between 2016 and 2017.

Results

Characteristics of plots

Plant richness in plots varied between 28 to 59 species. The most abundant ectomycorrhizal hosts were *Achatocarpus gracilis, Apoplanesia paniculata,* and *Guapira petenensis* (Figure S1; Table S1); we also found *Coccoloba liebmanii, Lonchocarpus eriocarinalis,* and *Lonchocarpus* spp. Cluster analysis grouped the samples according to the level of disturbance: 1) plots T2800 and A500 with low light at ground level, lowest density of trees, tendency to be eroded, high content of PO_4, and low number of stand-up trees alive; 2) plots T450 and T1000 with high tree density, high number of fallen trees alive, lowest slope and erosion, and high organic matter and total; 3) the rest of plots with fewer dead trees, moderate slope, and lower NH_4 (Figure S2; Table S2). Hereafter, these groups are referred to as “high disturbance”, “low disturbance, and “recovery”, respectively (Figure S3).

Mycorrhizal network analysis

Mycorrhizal network properties did not show any difference according to level of disturbance. The comparison of mycorrhizal networks of all plots between one and two years after the hurricane exhibited both anti-nestedness and low modularity: in 2016 the network had 78 fungal OTUs, NODF= 9.019 (z-value= -2.77, 2.5% CI=9.44, 97.5% CI=11.51, P=0.011, WNODF=10.093) and 0.41 modularity; and in 2017 the network had 146 fungal OTUs, NODF= 5.496 (z-value= -3.257, 2.5% CI=5.82, 97.5% CI=6.745, P=0.003, WNODF= 5.71) and 0.38 of modularity.

In 2016 mycorrhizal richness and abundance was low and increased in 2017 (Table 1). The first year after hurricane we found few mycorrhizal species shared between hosts. Also, most of the shared fungal species were similar between same plant spe-

cies. *Tomentella* sp. (SH006884.07FU) and *Clavulina* sp. (SH629574.07FU) were the most generalist fungal species, meanwhile *Guapira* and *Achatocarpus* were the hosts with more centrality. The second year after hurricane more and different fungal species connected the plants such as *Russula* sp. (SH526877.07FU), *Clavulina* spp. (SH629574.07FU, SH220229.07FU), *Ceratobasidium ramicola* (SH218661.07FU), *Tomentella* spp. (SH006884.07FU, SH489022.07FU), *Inocybe* sp. (SH493665.07FU), *Helvella* sp. (SH492769.07FU), *Chloridium* sp. (KY88725), and some Glomeraceae, sp. (SH001065.07FU). The plants with more centrality were *Guapira petenensis*, *Apoplanesia paniculata,* and *Achatocarpus gracilis* (Figure 1). In both years, Thelephoraceae species were common and abundant on host roots (Figure 1a, d).

Analyzed rhizospheres harbored both arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM). Throughout both years following the hurricane AM networks showed tendency for nested structure, while ECM communities exhibited anti-nested patterns; none of the observations were statistically significant (P= 0.06 in 2016; P=0.05 in 2017; Table 1). Modularity was always highest in AM networks. The specialization of networks (*H2*') increased during following years after the hurricane (Table 1). According to nonparametric multiple comparison there were no significant differences in mycorrhizal network properties between years (wNODF: $F_{18,\ 15.68}$=0.63, P-value=0.53; Modularity: $F_{18,\ 14.42}$=1.63, P-value=0.12; Specialization: $F_{18,\ 15.75}$=-0.63, P-value=0.53).

Table 1. Properties of mycorrhizal networks pooling all plots by years.

Year	Myconet*	No. OTUs	OTUs abun*	NODF*	z-value	2.5% CI	97.5% CI	P value	wNODF*	Mod*	H2'*
2016	AM	31	172	7.889	0.509	5.759	9.085	0.627	8.185	0.504	0.758
	ECM	46	25833	10.78	-1.74	10.712	13.431	0.063	12.039	0.358	0.791
2017	AM	51	1468	7.905	0.31	6.592	8.707	0.793	4.89	0.372	0.827
	ECM	91	41373	7.088	-2.01	7.081	8.654	0.053	8.794	0.33	0.899

*Myconet=mycorrhizal network, AM= arbuscular mycorrhizal, ECM= ectomycorrhizal, OTUs abun= OTUs abundance, Mod=modularity, NODF= nestedness, wNODF= weigthed nestedness, H2'= specialization

When the same analyses were performed separately for ECM and AM communities, the first year just two plots had at least one mycobiont shared between plants species, restoring mainly ectomycorrhizal fungi co-occurrence in 2017 (Table S5). One year after hurricane it was impossible to calculate nestedness or modularity in most of the plots because they were few mycorrhizal species shared by hosts (Table 2).

Table 2. Comparison of mycorrhizal network properties pooling all mycorrhizal fungi in two different years in each plot

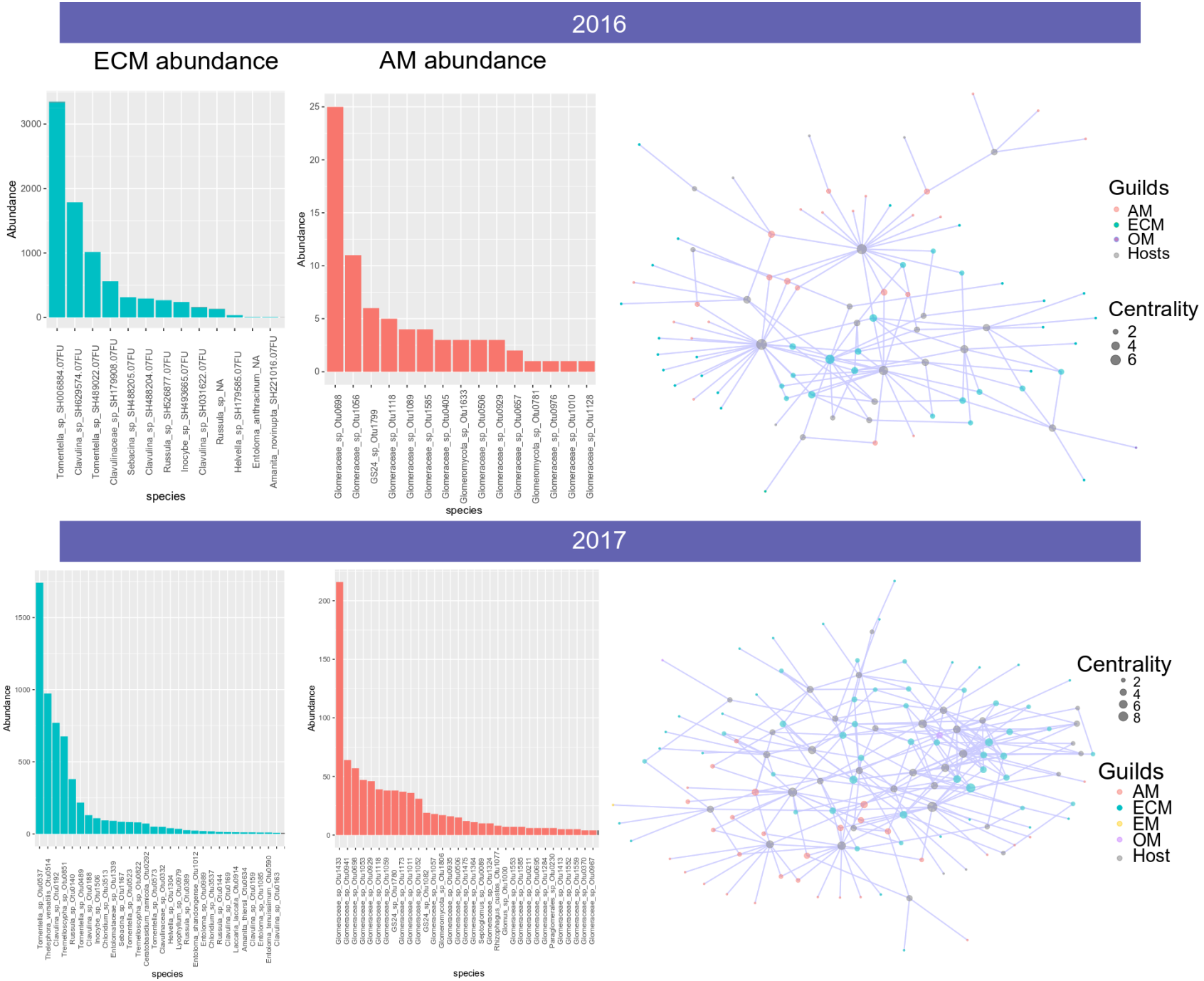
Year	Plot	No. OTUs	OTUs abun*	NODF	z-value	2.5% CI	97.5% CI	P value	wNODF	Mod*	H2'*
2016	A250	30	11425	6.316	0	6.31	6.316	1	6.24	NA	0.899
	A500	5	11	0	0	0	0	1	0	NA	1
	B200	14	303	0	0	0	0	1	0	NA	1
	EC650	19	1284	14.91	-0.255	11.6	17.956	0.711	13.352	0.48	0.62
	T450	27	7526	6.818	0	6.81	6.818	1	0.852	NA	0.993
	T700	8	35	0	0	0	0	1	0	NA	1
	T1000	5	16	0	0	0	0	1	0	NA	1
	T2650	6	77	0	-2.621	0	16.667	0.185	5.55	0.625	0.789
	T2800	13	5329	0	0	0	0	1	0	NA	1
2017	A250	59	26725	**1.692**	**-3.012**	**1.99**	**4.132**	**0.011**	4.307	NA	0.985
	A500	42	1211	6.265	1.151	3.03	6.372	0.087	3.344	0.437	0.941
	B200	20	213	13.6	-0.22	9.35	16.78	0.69	9.75	0.494	0.745
	EC650	42	11648	**5.717**	**-2.12**	**5.67**	**8.361**	**0.05**	8.432	0.619	0.949
	T450	25	218	3.921	-1.718	3.41	7.23	0.119	4.35	0.701	0.856
	T700	9	28	0	0	0	0	1	0	NA	1
	T1000	41	774	3.38	-2.02	3.17	6.159	0.069	5.34	0.553	0.916
	T2650	15	128	5.66	0	5.66	5.66	1	0	NA	0.746
	T2800	13	1924	0	0	0	0	1	0	NA	1

*OTUs abun= OTUs abundance, Mod=modularity, H2'= specialization, wNODF= weigthed nesteness.
NA= missing value.

Interspecific interactions of rhizospheric fungal community

Interactions between the rhizospheric fungal guilds changed in each year. During 2016, ECM fungi had negative occurrence interactions among saprotrophs, plant pathogens, animal pathogens, endophytes, and other ECM species. Most of the abundant Glomeraceae species co-occurred with ECM, saprotrophs, between other

293 arbuscular mycorrhizal fungi, and excluded plant pathogens (Figure S4a). In general,
294 plant pathogens co-occurred with saprotrophs and some endophytes species (Figure
295 2a, S4a).


2016
ECM abundance
AM abundance
Abundance
species
Guilds
AM
ECM
OM
Hosts
Centrality
2
4
6
2017
Abundance
species
Centrality
2
4
6
8
Guilds
AM
ECM
EM
OM
Host

296

⇦Figure 1.Mycorrhizal fungal species abundance in 2016 and 2017, and the mycorrhizal network, plotted by Kamada-Kawai algorithm.

In 2017, richness increased generating more significant interactions in a more complex network. Ectomycorrhizal fungi contained more OTUs but with lower abundance compared to other guilds, showing mainly intra-guild and inter-guild negative co-occurrence, especially with saprotrophs. Arbuscular mycorrhizal species showed low number of negative co-occurrences with saprotrophs and endophytes. Plant pathogens had relations of positive correlations with most of the saprotrophs and arbuscular mycorrhiza. Endophytes were co-present with arbuscular mycorrhiza, plant pathogens, saprotrophs, however there were some species that excluded saprotrophs (e.g. *Xylaria* can be classified also as saprotroph, exclude another saprotrophs) and ectomycorrhizal fungi (figure 2b).

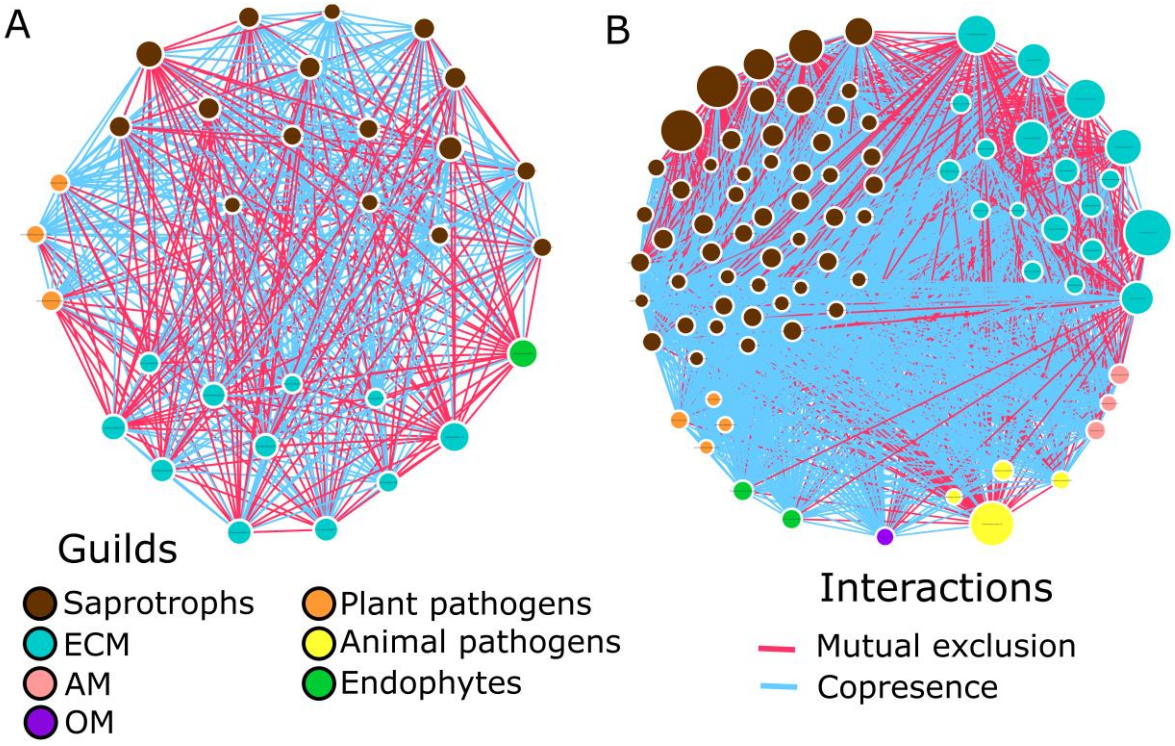


Figure 2. Interspecific interactions between more abundant taxa of the rhizospheric guilds one year (A) and two years (B) after hurricane Patricia. A) Build with the 31 OTUs with more than 100 sequences; B) Build with the 85 OTUs with more than 200 sequences. Size of the node is the frequency of negative interactions (mutual exclusion). Abbreviations: AM= Arbuscular mycorrhizal, ECM= ectomycorrhizal, OM= orchid mycorrhizal.

Hurricane effect on rhizosphere fungal communities

PERMANOVA analysis revealed that significant predictors of rhizosphere community were soil temperature ($F_{1, 59}$= 2.858, R^2= 0.04, P= 0.001), year ($F_{1, 59}$=2.851, R^2=0.051, P=0.001), hosts ($F_{9, 59}$=1.689, R^2=0.214, P=0.001), disturbance in plots ($F_{2, 59}$=1.4, R^2=0.039, P=0.018), and light at ground level ($F_{1, 59}$=1.338, R^2=0.018, P=0.042) (Figure S2). Rhizospheric fungal community had a drastic replacement one year after Patricia hurricane and recovered changed again two years after (Figures S5-8). Ectomycorrhizal community 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), soil ammonium concentration ($F_{1, 53}$=2.637, R^2=0.036, P=0.028), soil temperature ($F_{1,53}$= 3.15, R^2=0.043, P=0.014), and plant richness ($F_{1,53}$= 2.483, R^2=0.034, P=0.037) (Figure S9).

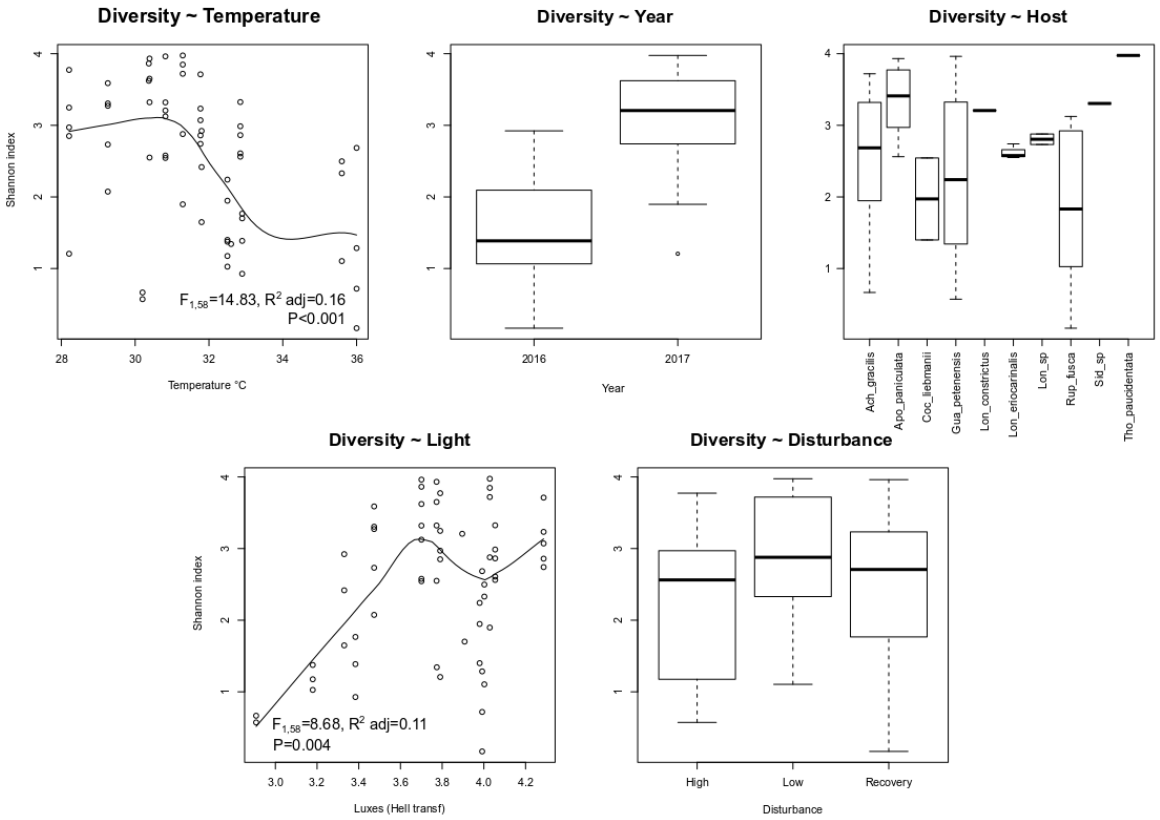


Figure 3. The significative predictors of the rhizosphere fungal community: A) Soil temperature, B) year of sampling, C) plant species, D) light at ground level, E) plot disturbance. Bold horizontal lines from boxplots represents mean values, and box margins are variance.

Discussion

Hurricane Patricia affected mycorrhizal networks, interspecific interactions between guilds and the structure of rhizospheric fungal communities. We provide the first analysis from dual mycorrhizal networks in a tropical forest. Mycorrhizal networks lost connectivity and specialization one year after hurricane and it recovered connections in most of the plots in 2017. Fungal diversity was lower in 2016 than 2017; thus, in 2017 the increased diversity produced more complex networks and changed the interactions between species. Higher soil temperature was correlated negatively with rhizospheric fungal diversity. Also we found an effect depending on year, host identity, disturbance level and light at level ground.

Arbuscular mycorrhizal network was lost one year after hurricane; most of the mycorrhizal species were restricted to colonize just one plant species. AM colonization can increase after hurricane (Varga et al., 2010), but colonization loses the sight of connections between plants. We hypothesize that vegetation damage would produce a bottom-up effect on rhizosphere communities in general, and mycorrhizal species could be the most harmed due their need of photosynthetic carbon.

Results of ECM and AM networks showed no-nestedness and modularity in both mycorrhizal interactions, with higher modularity in ECM network. Additionally, we found more specialization in 2017 in both interactions. Mycorrhizal species specificity to their host could explain the high modularity (Bahram et al., 2014). Specificity together with modularity, can change with disturbance, e.g. plant-herbivore network comparison between before and after hurricane, found a decrease in specificity and number of compartments (Luviano et al., 2018). Our data agree with the idea that more specialized species are more common in seasons with high availability of resources (low stressful abiotic conditions) and generalists prevail in any conditions (López-Carretero et al., 2014). Also, high modularity of mycorrhizal fungi could give resilience to the disturbance (Gilarranz et al., 2017).

Mycorrhizal communities showed host preference (Figure S7). The same pattern had observed in tropical forests (Peay et al., 2013; Tedersoo et al., 2008; 2010). Before and after hurricane, hosts associated with few common fungal species (Alvarez-Manjarrez et al., 2018), however successional changes occurred in the community. The generalist species before hurricane were not resistant one year after hurricane

but were resilient two years after: *Tremelloscypha* sp. (SH016792.07FU), *Membranomyces* sp. (SH1143177.08FU), *Sebacina* sp. (SH488205.07FU), *Thelephora versatilis* (SH490448.07FU) and *Tomentella* sp. (SH495677.07FU) connected plants species before hurricane (Alvarez-Manjarrez et al., 2018). In 2016, these fungi were replaced by *Tomentella* sp. OTU 537 (SH006884.07FU), *Clavulina* sp. OTU 169 (SH629574.07FU), *Inocybe* sp. OTU 1506 (SH493665.07FU), *Tomentella* sp. OTU 489 (SH489022.07FU) and Clavulinaceae, sp. OTU 332 (SH179908.07FU). Two years after Patricia (2017), dominant species before hurricane replaced those that appeared in 2016.

Besides abiotic factors, biotic interactions structure relationships between fungal species. Co-occurrence network analysis demonstrated significant correlations in presence-absence patterns of fungal species. Abundance and rarity could be interpreted as competition between fungi (Kennedy 2010). In 2016, ectomycorrhizal fungi excluded arbuscular mycorrhizae, saprotrophic, pathogenic and other ECM species, and same interactions were found in AM. Meanwhile, in 2017 when diversity increased, arbuscular mycorrhizal were more abundant than ECM, and co-occur more with pathogens. ECM species can inhibit pathogens' establishment (Mohan et al., 2015), mainly inhibit saprotrophs ('Gadgil effect'; Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2015), and AM establishment (Chen et al., 2000). When hurricanes landfall, the C allocation from plants to fungi change ebbs at root system, so competition strengthened for the same resource. AM can exclude or improve establishment other fungal species. AM species compete for root-resources, but also some AM species promote the mycelial growth of other fungi (Bennett & Bever, 2009). Arbuscular colonization can be diminished by endophytes, while AM had not impact on endophytes (Mack & Rudgers, 2008). In general, we found antagonistic relationships are unbalanced (Mack & Rudgers, 2008) and tend to change with environmental alterations (Kennedy 2010).

There is growing evidence that a regime of environmental disturbance has different effects on plant communities depending on frequency, intensity, spatial and temporal scale of the disturbance event. The main disturbance effect of a hurricane is the mortality and loss of vegetal biomass (e.g. Zimmerman *et al*., 1994; Parker et al., 2018), which has cascading effects on the rest of the biotic communities. Our comparison

between years suggest that similarly to plants, rhizospheric fungal communities show great changes following hurricane, pointing to their possible role in establishing the recruitment of plants.

We refute our hypothesis about the soil nutrients having an effect on rhizosphere fungal diversity, as it was demonstrated in different studies (Lilleskov et al., 2012; Truong et al., 2019). Interestingly, diversity increased together with the light at level ground, probably because the secondary succession of the forest. In 2016, light at forest floor scarce on plots with few survival trees, because creeping pioneer herbs (*Mimosa pudica* and others) covered completely the ground. Next year, lianas disappeared, and new plant community grew up, they were herbs and recruits that allowed more light on forest floor.

The fungal community composition did not differ between our three categorical disturbance levels, i.e. “low”, “recovery”, “high” disturbance (except when accounting for fungal guilds). Fungal diversity was higher in plots categorized as ‘recovery’, though we had more sampled plots in that category (five plots in comparison with two in other categories). Diversity could be explained by the ‘intermediate disturbance hypothesis’, where disturbance produce variations in spatial-temporal resources developing different coexistence mechanisms of species (Roxburgh et al., 2004).

Extreme climatic events, such as hurricanes, disturb more frequently, and will increase even more caused by global warming (Walsh et al., 2016); both, anthropogenic and extreme climatic events create disturbance and these in turn shape secondary successional forests (Lewis et al., 2015; Salazar et al., 2015). Disturbance complexity creates not a unidirectional effect on fungal communities, e.g. arbuscular mycorrhizal communities (García de León et al., 2018). Hurricane Patricia harmed rhizospheric communities and their interaction networks (i.e. mycorrhizal networks and interspecific symbioses), however high fungal diversity contributed to their resilience. Whether human activities preserve high fungal diversity, the future will be promising in the face of global change.

Conclusions

This study was the first to examine the effect of hurricane on root associated fungal communities and its interactions. It is important to consider that each hurricane event vary the environmental conditions depending on its strength, vegetal community as-

sembly and local conditions. Overall, our results indicate arbuscular mycorrhizal network is more sensible to disturbance than ectomycorrhizal network, and in general rhizospheric fungal community are vulnerable to hurricane disturbance and able to recover. Given the growing number of climate change associated disturbance, further studies are needed to determine the functional implications of such changes.

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Additional files

Characteristics of plots

The most common species were *Achatocarpus gracilis* (Achatocarpaceae), *Apoplanesia paniculata* (Fabaceae subfam. Papilionoideae), *Bonelia macrocarpa* subsp. *pungens* (Primulaceae), *Caesalpinia eryostachis* (Fabaceae subfam. Caesalpinioideae), *Cordia alliodora* (Boraginaceae), *Guapira petenensis* (Nyctaginaceae), *Heliocarpus pallidus* (Tiliaceae), *Piptadenia obliqua* (Fabaceae), and *Thouinia paucidentata* (Sapindaceae).

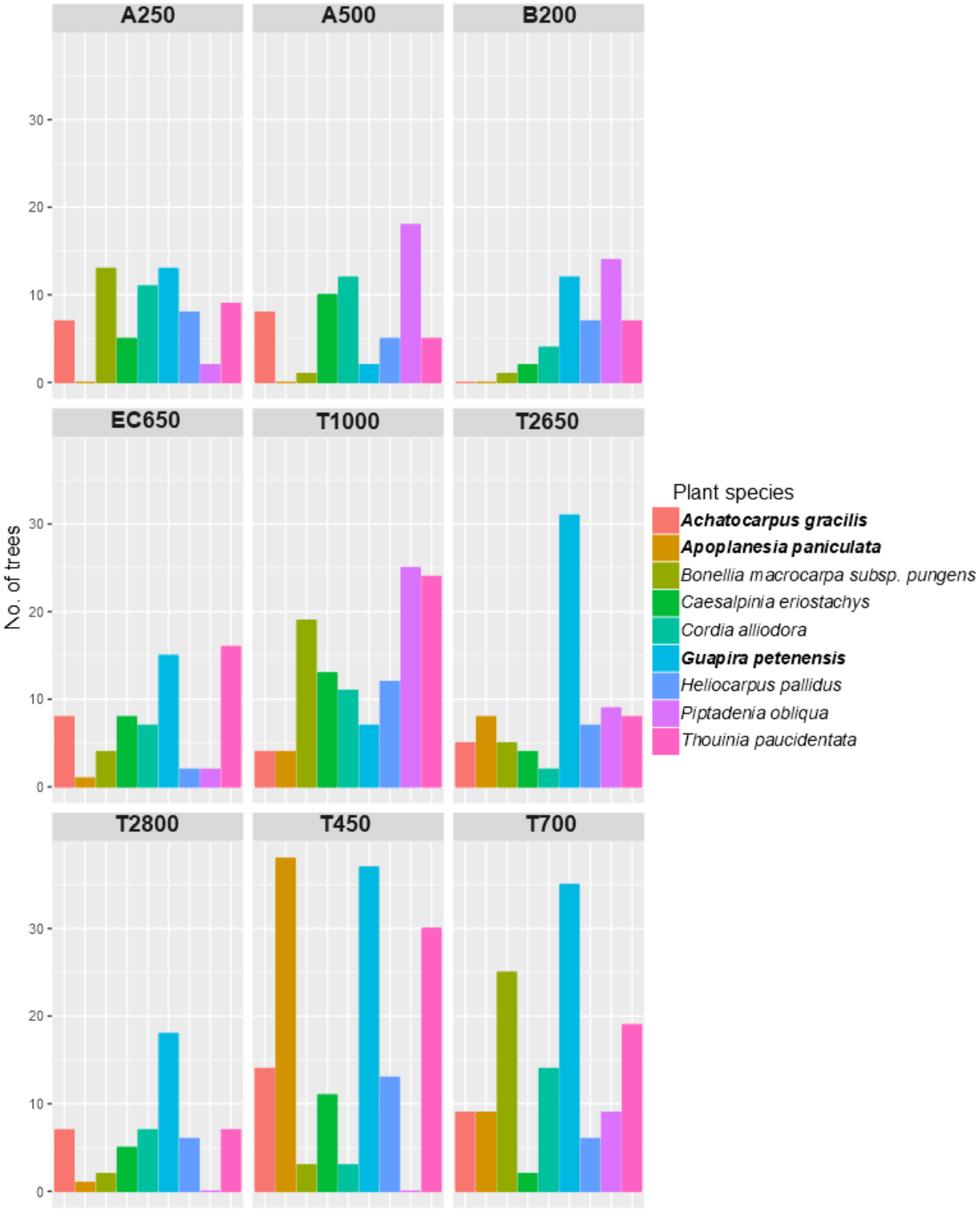
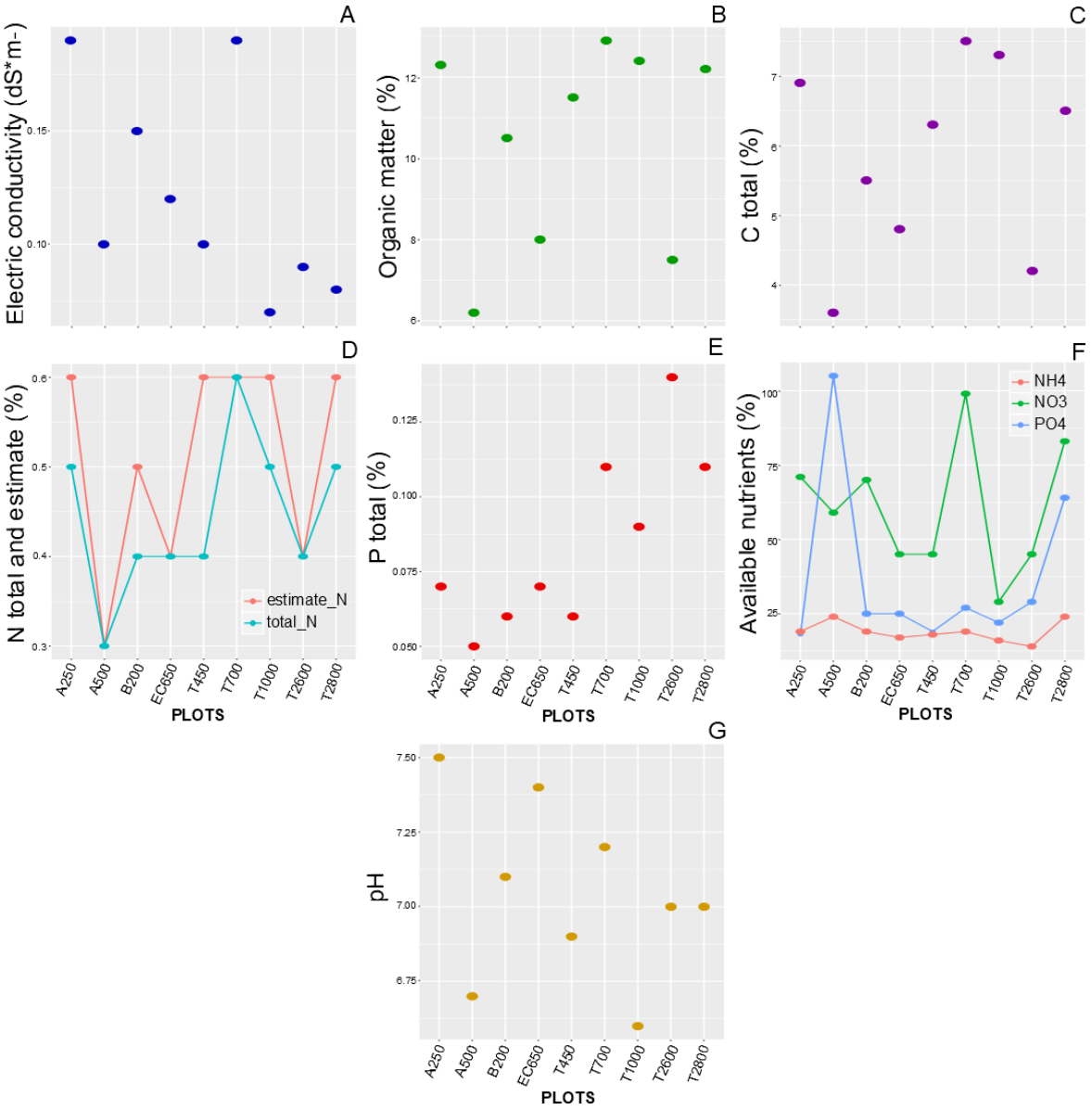


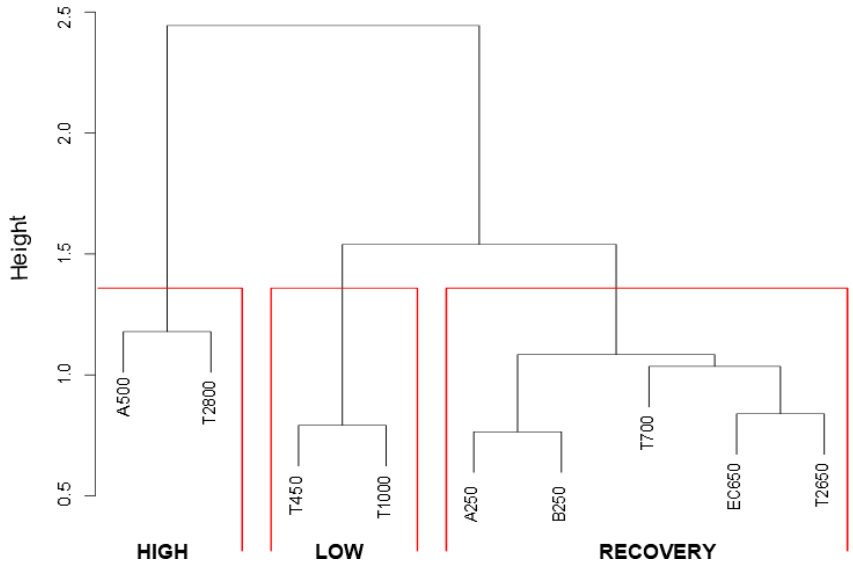
Figure S1. Abundance from the most common plant species in each plot. Ectomycorrhizal (ECM) hosts are indicated in bold.



713

714 Figure S2. Soil characteristics in each plot. A) Electric conductivity (EC); B) Percent-
715 age of organic matter (OM); C) Percentage of total carbon; D) Percentage of total
716 and estimated nitrogen; E) Percentage of total phosphorus; F) Percentage of mineral
717 nutrients: NH_4, NO_3, PO_4; G) Potential of hydrogen (pH).

718



719

720 Figure S3. Cluster analysis by Ward distance from soil, environmental and vegetation

721 characteristics of plots. Rectangles separate plots in three main groups.

722

723 Table S1. Trees and shrubs alive from each plot

SPECIES	A250	A500	B250	EC650	T450	T700	T1000	T2600	T2800	Total
Guapira petenensis	13	2	12	15	37	35	7	31	18	170
Thouinia paucidentata	9	5	7	16	30	19	24	8	7	125
Piptadenia obliqua	2	18	14	2	0	9	25	9	0	79
Bonellia macrocarpa subsp. *pungens*	13	1	1	4	3	25	19	5	2	73
Cordia alliodora	11	12	4	7	3	14	11	2	7	71
Heliocarpus pallidus	8	5	7	2	13	6	12	7	6	66
Achatocarpus gracilis	7	8	0	8	14	9	4	5	7	62
Apoplanesia paniculata	0	0	0	1	38	9	4	8	1	61
Caesalpinia eriostachys	5	10	2	8	11	2	13	4	5	60
Lonchocarpus mutans	6	8	7	2	5	5	9	11	0	53
Croton niveus	0	2	6	7	12	0	3	1	3	34
Caesalpinia pulcherrima	0	5	18	2	0	0	0	7	0	32
Casearia tremula	1	1	6	8	7	2	5	1	0	31

SPECIES	A250	A500	B250	EC650	T450	T700	T1000	T2600	T2800	Total
Lonchocarpus eriocarinalis	3	2	6	6	0	5	7	2	0	31
Ruprechtia fusca	2	2	9	4	1	6	2	2	0	28
Caesalpinia platyloba	13	1	10	0	2	0	0	1	0	27
Croton pseudoniveus	0	1	0	8	6	0	12	0	0	27
Lonchocarpus minor	0	0	0	1	11	7	8	0	0	27
Lysiloma microphylla	1	2	1	0	11	4	0	2	6	27
Maclura tinctoria	2	2	0	7	1	13	0	0	2	27
Cordia elaeagnoides	1	0	1	0	2	1	11	9	1	26
Trichilia trifolia	1	0	1	8	0	0	5	4	3	22
Caesalpinia sclerocarpa	1	1	0	2	1	2	11	0	2	20
Spondias purpurea	0	6	2	1	0	0	4	0	2	15
Lonchocarpus magallanesii	0	0	0	0	0	5	9	0	0	14
Recchia mexicana	0	0	0	2	0	7	2	0	3	14
Urera caracasana	0	1	6	0	4	0	3	0	0	14
Bursera simaruba	0	1	0	1	4	1	1	3	2	13
Chloroleucon mangense	0	2	4	0	1	2	1	3	0	13
Ipomoea wolcottiana	0	3	2	0	1	2	5	0	0	13
Unknown1	0	0	0	9	0	0	0	0	0	9
Guettarda elliptica	0	0	0	0	1	1	7	0	0	9
Mimosa albida	0	2	1	0	0	0	0	6	0	9
Vitex hemsleyi	0	0	0	0	3	1	5	0	0	9
Cochlospermum vitifolium	0	0	4	0	0	0	3	0	1	8
Leucaena lanceolata	3	0	1	0	2	0	1	0	1	8
Brosimum alicastrum	0	0	0	0	3	2	2	0	0	7
Celosia monosperma	1	0	0	2	0	4	0	0	0	7
Lonchocarpus sp1	0	4	0	0	0	3	0	0	0	7

SPECIES	A250	A500	B250	EC650	T450	T700	T1000	T2600	T2800	Total
Cordia alba	0	0	0	0	1	2	3	0	0	6
Cordia sp.	0	6	0	0	0	0	0	0	0	6
Jatropha sympetala	1	0	0	1	0	0	0	2	2	6
Lonchocarpus sp.2	0	0	0	0	0	6	0	0	0	6
Vitex mollis	0	0	0	0	0	6	0	0	0	6
Unknown2	0	0	0	0	2	0	3	0	0	5
Unknown3	0	0	0	0	0	0	5	0	0	5
Unknown4	5	0	0	0	0	0	0	0	0	5
Caesalpinia coriaria	0	0	0	0	3	0	1	1	0	5
Erythrina lanata	0	0	1	0	2	2	0	0	0	5
Lonchocarpus sp.3	0	4	0	0	0	1	0	0	0	5
Psidium sartorianum	0	0	0	1	4	0	0	0	0	5
Sinclairia caducifolia	1	1	1	0	2	0	0	0	0	5
Tabebuia rosea	0	0	0	3	0	0	2	0	0	5
Astronium graveolens	0	0	0	0	2	0	0	1	1	4
Bursera instabilis	0	0	1	0	2	1	0	0	0	4
Bursera sp.	0	0	4	0	0	0	0	0	0	4
Coccoloba liebmannii	0	0	1	2	0	0	1	0	0	4
Styphnolobium protantherum	0	0	0	0	2	1	0	0	1	4
Unknown5	1	0	0	0	0	0	0	0	2	3
Unknown6	0	0	3	0	0	0	0	0	0	3
Amphipterygium adstringens	0	0	3	0	0	0	0	0	0	3
Bursera heteresthes	0	0	0	0	3	0	0	0	0	3
Capparisdastrum frondosum	0	0	0	0	1	0	2	0	0	3
Cascabela ovata	2	0	0	0	0	0	0	1	0	3
Colubrina heteroneura	0	0	1	0	2	0	0	0	0	3
Colubrina triflora	0	0	0	0	0	2	0	1	0	3

SPECIES	A250	A500	B250	EC650	T450	T700	T1000	T2600	T2800	Total
Croton suberosus	0	0	0	0	3	0	0	0	0	3
Forchhammeria pallida	0	0	0	0	1	0	2	0	0	3
Guazuma ulmifolia	0	0	0	1	1	0	1	0	0	3
Jatropha malacophylla	0	0	1	0	2	0	0	0	0	3
Randia aculeata	0	0	0	0	3	0	0	0	0	3
Bursera excelsa	0	0	2	0	0	0	0	0	0	2
Casearia nitida	0	0	1	0	0	0	0	1	0	2
Ceiba aesculifolia	0	0	0	1	0	0	0	1	0	2
Coccoloba barbadensis	0	0	0	2	0	0	0	0	0	2
Coccoloba sp.	0	0	0	1	1	0	0	0	0	2
Comocladia macrophylla	0	0	0	0	2	0	0	0	0	2
Unknown 7	0	0	0	0	0	2	0	0	0	2
Jacaratia mexicana	0	0	0	0	0	0	2	0	0	2
Lagrezia monosperma	0	0	0	0	0	0	2	0	0	2
Lonchocarpus constrictus	0	0	0	2	0	0	0	0	0	2
Lonchocarpus sp.3	0	0	0	0	0	0	0	0	2	2
Lonchocarpus sp.4	0	0	0	0	0	0	0	0	2	2
Machaonia acuminata	0	0	0	0	1	1	0	0	0	2
Piranhea mexicana	0	1	0	0	0	0	0	0	1	2
Sideroxylon stenospermum	2	0	0	0	0	0	0	0	0	2
Unknown8	0	0	0	0	0	0	0	0	1	1
Unknown9	0	0	1	0	0	0	0	0	0	1
Unknown10	0	1	0	0	0	0	0	0	0	1
Unknown11	0	0	1	0	0	0	0	0	0	1
Unknown12	0	0	0	1	0	0	0	0	0	1
Unknown13	0	0	1	0	0	0	0	0	0	1
Unknown14	0	0	1	0	0	0	0	0	0	1

SPECIES	A250	A500	B250	EC650	T450	T700	T1000	T2600	T2800	Total
Unknown15	0	0	0	1	0	0	0	0	0	1
Unknown16	0	0	0	0	1	0	0	0	0	1
Aralia excelsa	0	0	0	1	0	0	0	0	0	1
Bourreria sp	0	0	0	0	0	0	1	0	0	1
Unknown 17	0	1	0	0	0	0	0	0	0	1
Brongniartia sp.	1	0	0	0	0	0	0	0	0	1
Capparis sp.	0	0	0	1	0	0	0	0	0	1
Capsicum annuum	0	1	0	0	0	0	0	0	0	1
Croton sp.	0	1	0	0	0	0	0	0	0	1
Euphorbia tan-quahuete	1	0	0	0	0	0	0	0	0	1
Ficus cotinifolia	0	0	0	0	0	0	0	0	1	1
Heliocarpus sp.	0	0	0	0	0	0	0	1	0	1
Jatropha chame-lensis	0	0	1	0	0	0	0	0	0	1
Lonchocarpus sp.5	0	0	0	0	0	1	0	0	0	1
Opuntia excelsa	0	0	1	0	0	0	0	0	0	1
Pachycereus pec-ten-alboriginum	0	0	0	1	0	0	0	0	0	1
Pterocarpus orbi-culatus	0	0	0	0	0	0	1	0	0	1
Roseodendron donell-smithii	0	0	0	0	0	1	0	0	0	1
Senna atomaria	0	0	0	0	0	0	0	1	0	1
Tabernaemontana donnell-smithii	1	0	0	0	0	0	0	0	0	1
Unknown18	0	0	0	0	0	0	0	0	0	0
Cordia gerascant-hus	0	0	0	0	0	0	0	0	0	0

724

725 Table S2. Biotic and abiotic variables taken in each plot

Variable	A250	A500	B200	EC650	T450	T700	T1000	T2600	T2800
Dead trees	13	20	13	13	19	24	31	12	16
Fall alive trees	17	21	26	31	30	27	47	20	11

Variable	A250	A500	B200	EC650	T450	T700	T1000	T2600	T2800
Stand up alive trees	102	114	142	120	275	246	217	121	81
T (°C)	31.8	30.2	32.6	32.5	35.6	36	33.6	32.9	32.5
Humidity	88.4	87.4	70.43	71	65.4	66.5	66.6	80.9	85.2
Light (lux)	2139.23	808.44	5947.60	9546.31	10052.72	9814.43	8085.28	2420.87	1511.18
Litter (cm)	7.5	6	11.25	4	7.5	3.85	6.5	4	3.5
Total plant richness	52	36	43	43	59	47	45	33	28
ECM host richness	4	4	4	8	5	5	6	5	3
ECM host abundance	25	14	28	39	91	64	25	48	26
Slope (°)	26	32	32	28	18	35	17	24	45
Tree den-sity	0.29	0.33	0.42	0.37	0.76	0.68	0.66	0.35	0.23
Erosion (Kg*ha-)	3.44	4.97	3.55	2.80	1.31	4.18	1.19	3.95	12.25
pH	7.5	6.7	7.1	7.4	6.9	7.2	6.6	7	7
CE (dS*m-)	0.19	0.1	0.15	0.12	0.1	0.19	0.07	0.09	0.08
OM (%)	12.3	6.2	10.5	8	11.5	12.9	12.4	7.5	12.2
Nt (%)	0.5	0.3	0.4	0.4	0.4	0.6	0.5	0.4	0.5
PO_4 (ppm)	18	105	25	25	19	27	22	29	64
Pt (%)	0.07	0.05	0.06	0.07	0.06	0.11	0.P09	0.14	0.11
NO_3 (ppm)	71	59	70	45	45	99	29	45	83
NH_4 (ppm)	19	24	19	17	18	19	16	14	24
Ct (%)	6.9	3.6	5.5	4.8	6.3	7.5	7.3	4.2	6.5

726 Abbreviations: Ct= total carbon; EC=electric conductivity; ECM=ectomycorrhizal; Nt=
727 total nitrogen; OM=organic matter; Pt=total phosphorus; T=temperature.
728
729 Table S3. NextEra adapters with primers sequences used in the PCR multiplex

Sequence	Name	Target fungal group
tcgtcggcagcgtcagatgtgtataagagacag**catcgatgaagaacgcag**	ITS3NGS1	Universal
tcgtcggcagcgtcagatgtgtataagagacag**caacgatgaagaacgcag**	ITS3NGS2	Phylum Chytridiomycota
cgtcggcagcgtcagatgtgtataagagacag**caccgatgaagaacgcag**	ITS3NGS3	Order Sebacinales
tcgtcggcagcgtcagatgtgtataagagacag**catcgatgaagaacgtag**	ITS3NGS4	Subphylum Glomeromycotina
tcgtcggcagcgtcagatgtgtataagagacag**catcgatgaagaacgtgg**	ITS3NGS5	Order Sordariales
gtctcgtgggctcggagatgtgtataagagacag**tcctscgcttattgatatgc**	ITS4NG	Reverse

730 Primers sequences are bold, the rest correspond to NextEra sequences.

731

732 Table S4. Coordinates of the plots

Latitude	Longitude
19.504935° N	-105.03988° W
19.505019° N	-105.040835° W
19.498762° N	-105.041002° W
19.502078° N	-105.040591° W
19.501029° N	-105.044208° W
19.503951° N	-105.044596° W
19.504644° N	-105.047465° W
19.50953° N	-105.040987° W
19.509748° N	-105.039097° W

733

734

735 Table S5. Characteristics of the arbuscular and ectomycorrhizal networks in same plots from two years (2016 and 2017).

		2016						2017					
		Nestedness					Modularity	Nestedness					Modularity
Plot	Net	NODF	Z-value	Mean	P-value	WNODF		NODF	Z-value	Mean	P-value	WNODF	
A250	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
A500	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	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
T1000	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	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
EC650	ECM	12.87	0.273	12.501	1	17.82	0.401	10.484	0.419	10.03	0.79	15.46	0.374
	AM	20	0.261	20	1	0	NA	NA	NA	NA	NA	NA	NA
T2800	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
T2650	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	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

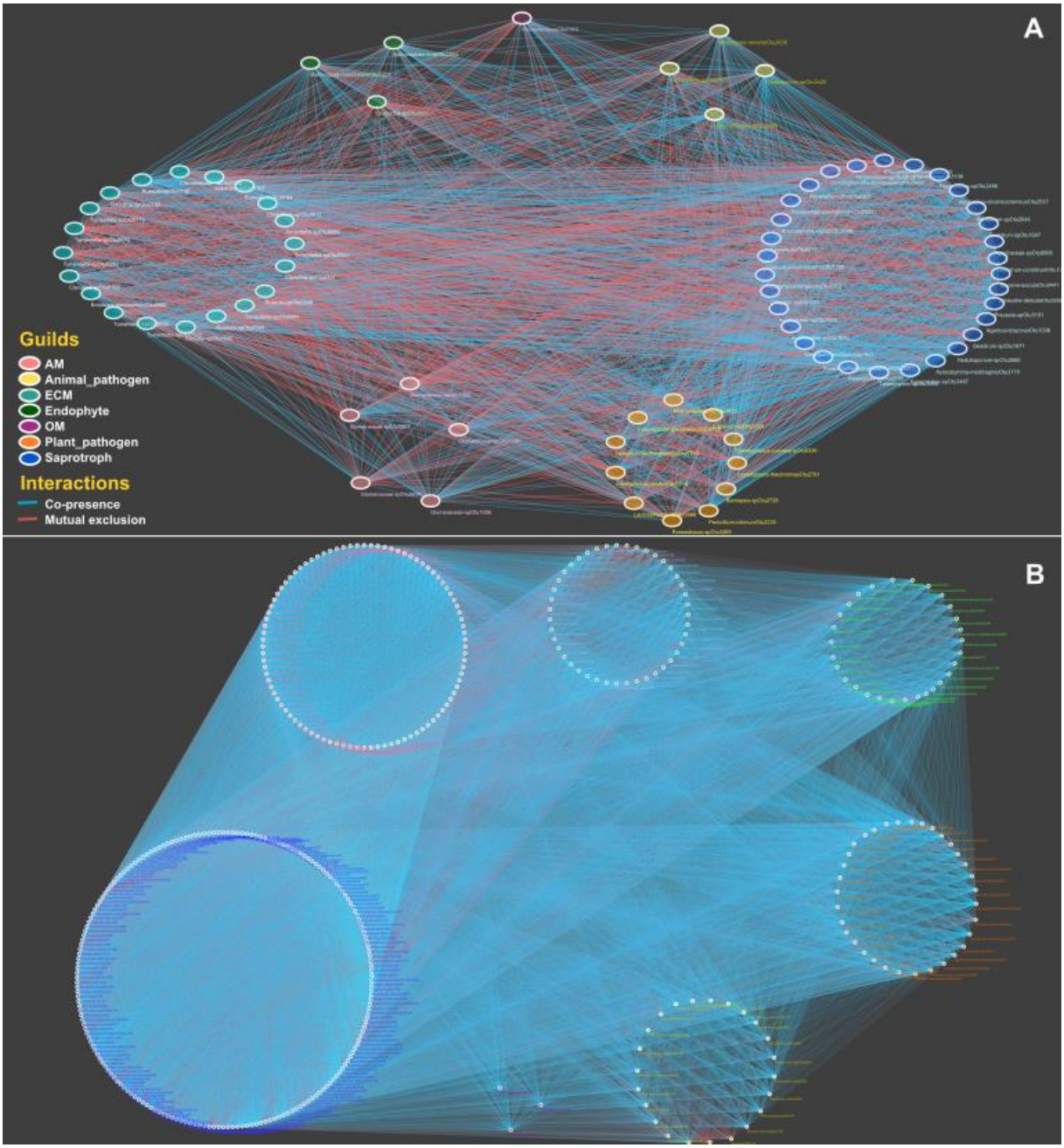


Figure S4. Co-occurrrence network with of all known fungal guilds with minimum abundance of 20 sequences using Pearson and Spearman correlation, 100 bootstrap iterations with Benajmin-Hochberg test correction for the P-value threshold 0.05. A) in 2016, N=284 OTUs. B) in 2017, N=1029 OTUs.

Hurricane effect on fungal community

We obtained 2,003,944 (9.82%) quality-filtered sequences from initial 20,402,884 reads; after chimeras filtering 1,268,036 sequences were left that clustered in to 3763 OTUs; after the subtraction from control sequences, we obtained 3625 OTUs. Eight

samples contained less than 200 sequences (i.e. 28-193 sequences), four of them belong to *Ruprechtia fusca* rhizospheres, and the rest were from 2016, following the hurricane. From 3625 OTUs, 996 belonged to Ascomycota, 704 to Basidiomycota, 251 to Glomeromycota, 69 to Chytridiomycota, 34 to Mucoromycota, and 16 to Mortierellomycota. They belong to 36 class, 91 orders, 224 families, and 424 genera. The first three OTU richest classes were Agaricomycetes (626 OTUs), Dothideomycetes (345), and Eurotiomycetes (262); the OTU richest orders were Agaricales (350), Glomerales (182), and Pleosporales (164); the richest families were Glomeraceae (175), Aspergillaceae (124), and Agaricaceae (121); the richest genera were *Aspergillus* (72), *Geastrum* (46), and *Penicillium* (45).

High disturbance plots were dominated by Ascomycota. Glomeromycota were dominant in recovery disturbance plots followed by low plots but remained rare in high disturbance plots (Figure S5). Agaricomycetes was the most OTU rich class across all plots; Dothideomycetes, Eurotiomycetes, and Sordariomycetes were common in sites with high disturbance and with less richness in low disturbance; Glomeromycetes were absent in plots with high disturbance in both years, and were absent in low disturbance in 2016, recovering diversity in 2017 (Figure S6). Agaricales, Botryosphaeriales, Cantharellales, Eurotiales, Hypocreales, and Pleosporales were the common orders in all plots and years; Thelephorales was abundant in low and high disturbance but not in recovery, in constrast with Glomerales that was found in low and recovery plots (Figure S7). The most common fungal guild in the high disturbance sites were saprotrophs, whereas AM was absent in plots with high disturbance. Ectomycorrhizal fungi had more richness in plots with low and high disturbance, but not in recovery plots (Figure S5). We found significant abundance differences in guilds between plots and years (chi-squared= 38, P= 3.7e-7, df=5). Ordination analysis showed communities are arranged by year and with some hosts (Figure S10).

In both years, Ascomycota was the Phylum with more species, and in 2016 Basidiomycota had more abundance (Figure S8).

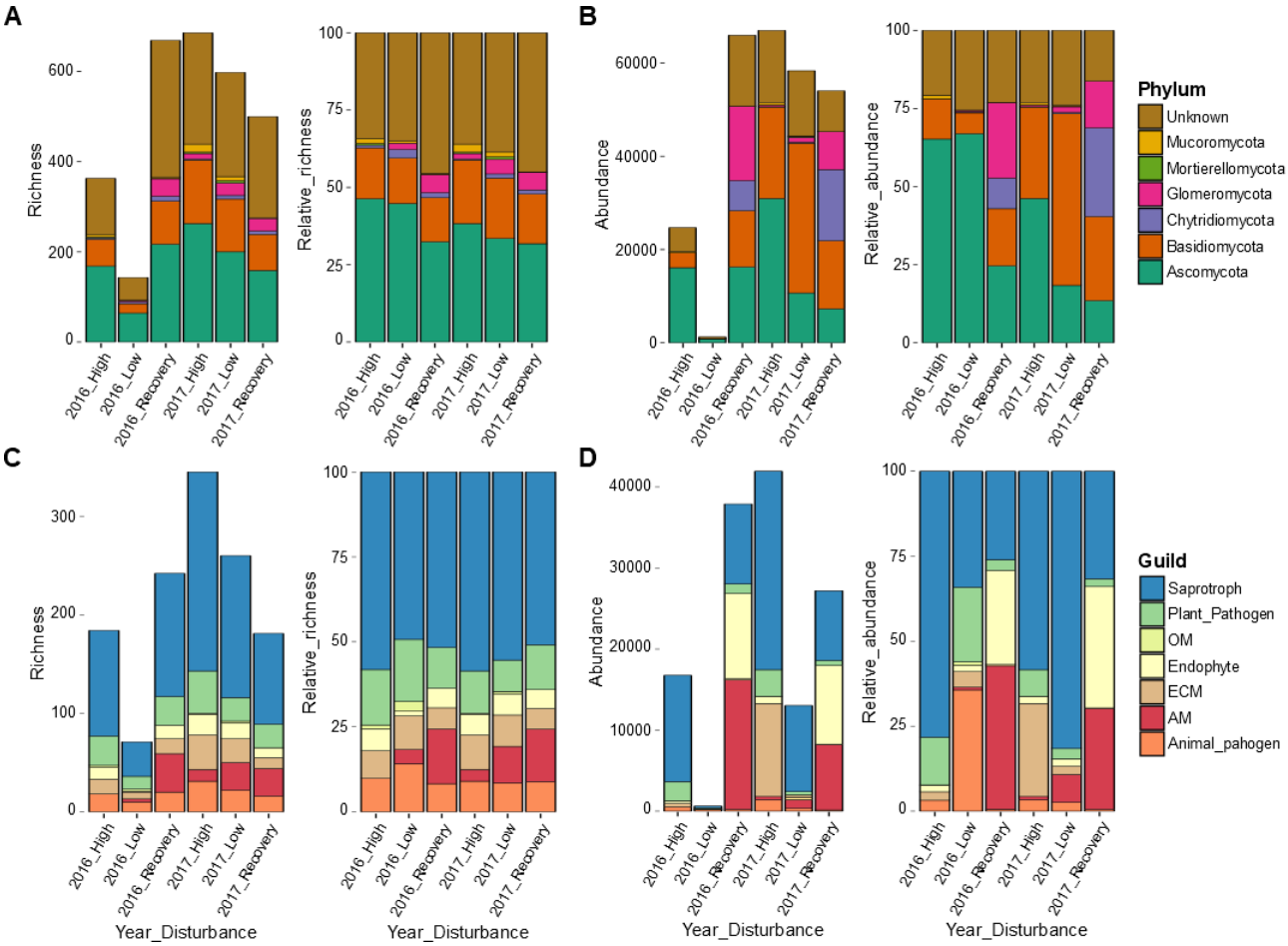


Figure S5. Fungal community in different disturbance level in 2016 and 2017. A) Richness and relative richness of each phylum, B) Abundance and relative abundance of each phylum, C) Richness and relative richness of each guild, D) Abundance and relative abundance of each guild.

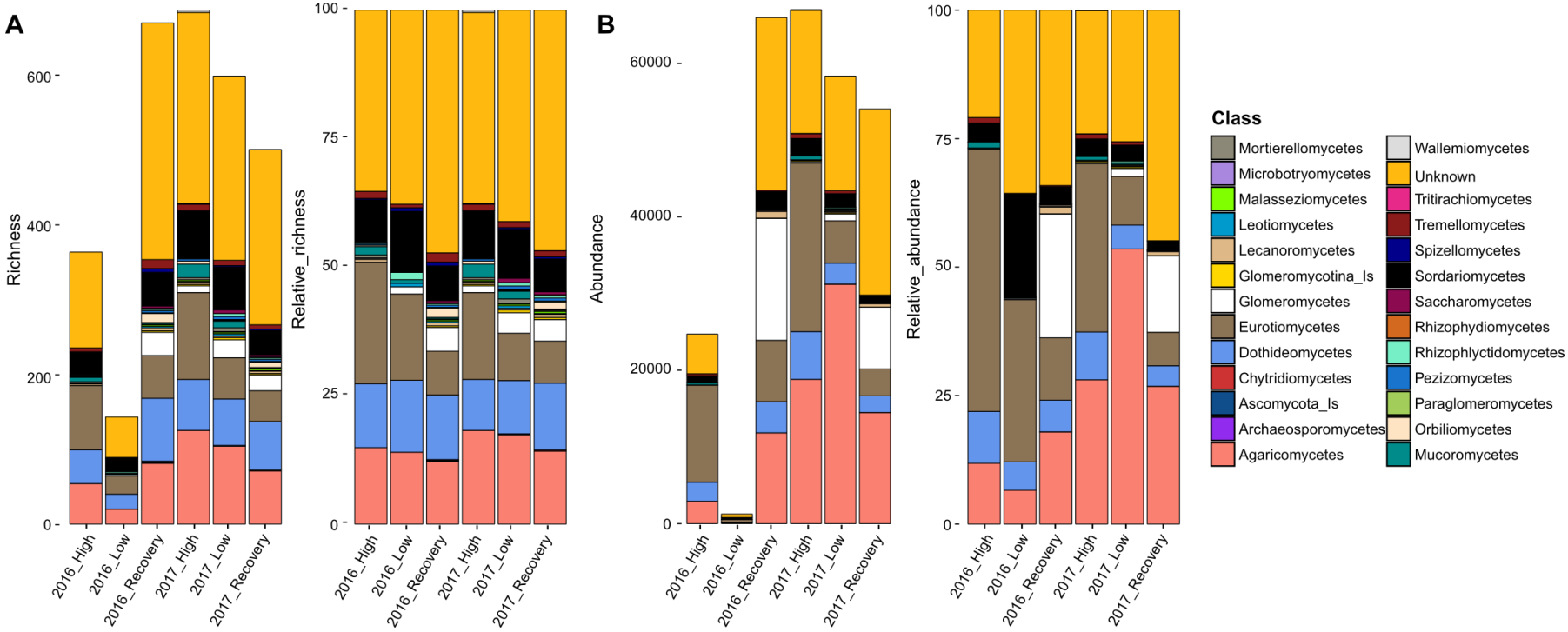


Figure S6. A) Class richness and relative richness in each year and disturbance plots, B) Class abundance and relative abundance in each year and disturbance plots

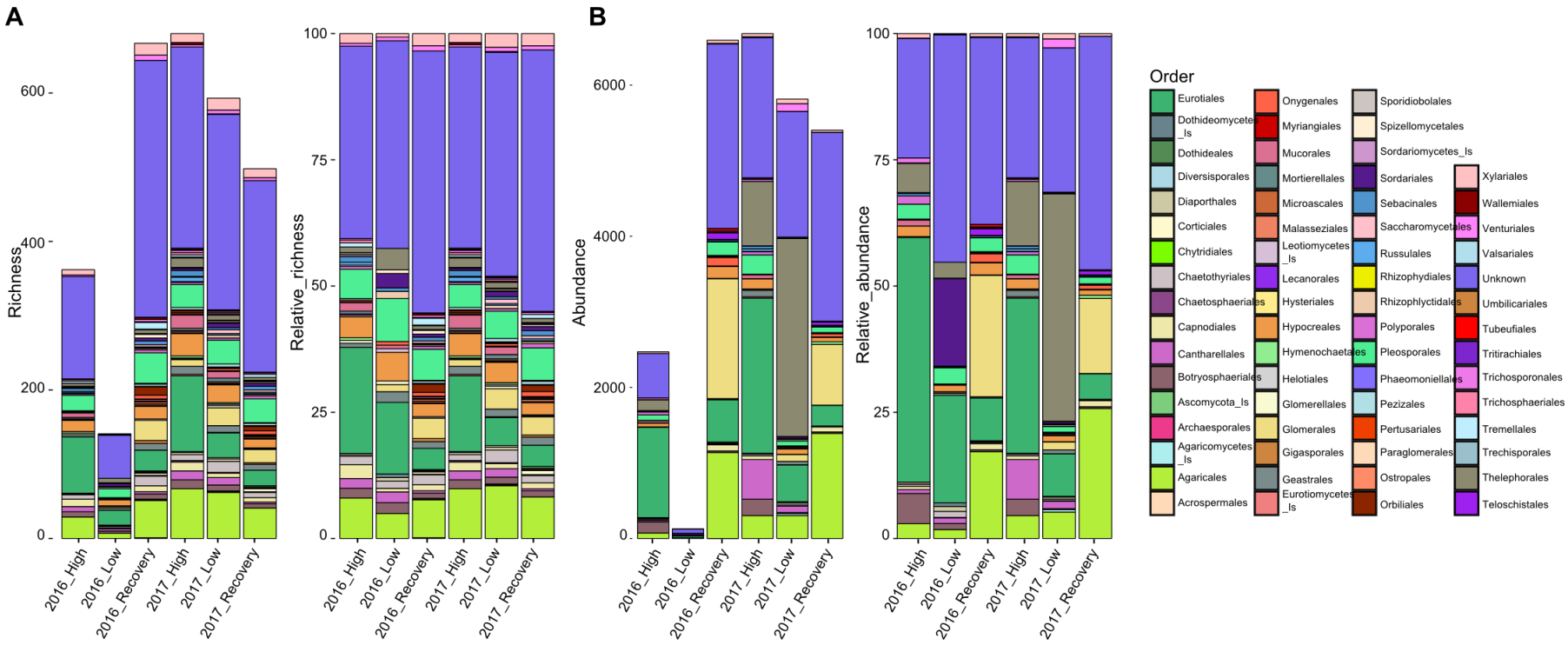


Figure S7. A) Order richness and relative richness in each year and disturbance plots, B) Order abundance and relative abundance in each year and disturbance plots

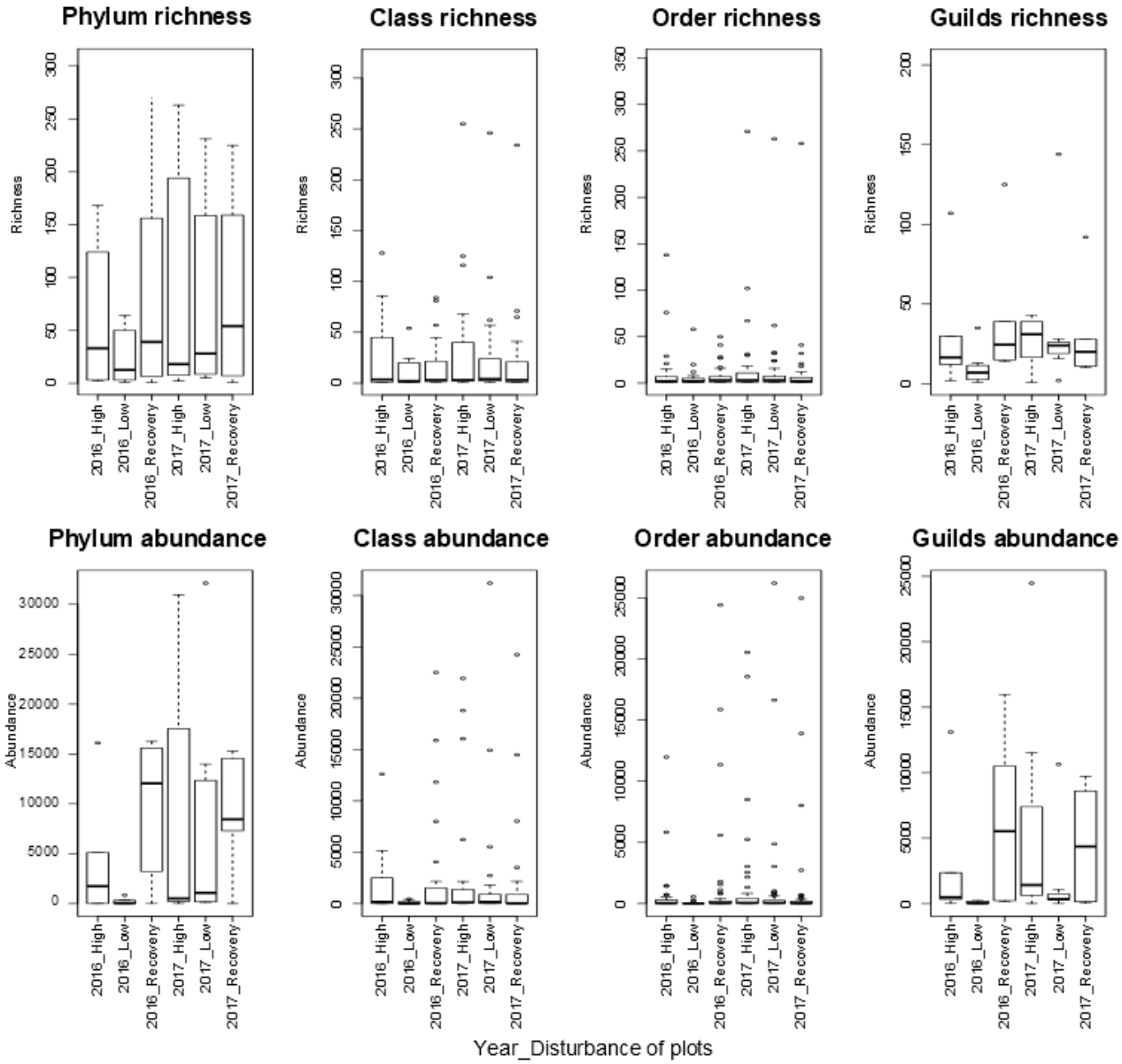


Figure S8. Boxplot showed no differences in richness and abundance in different classification level depending on disturbance degree and year.

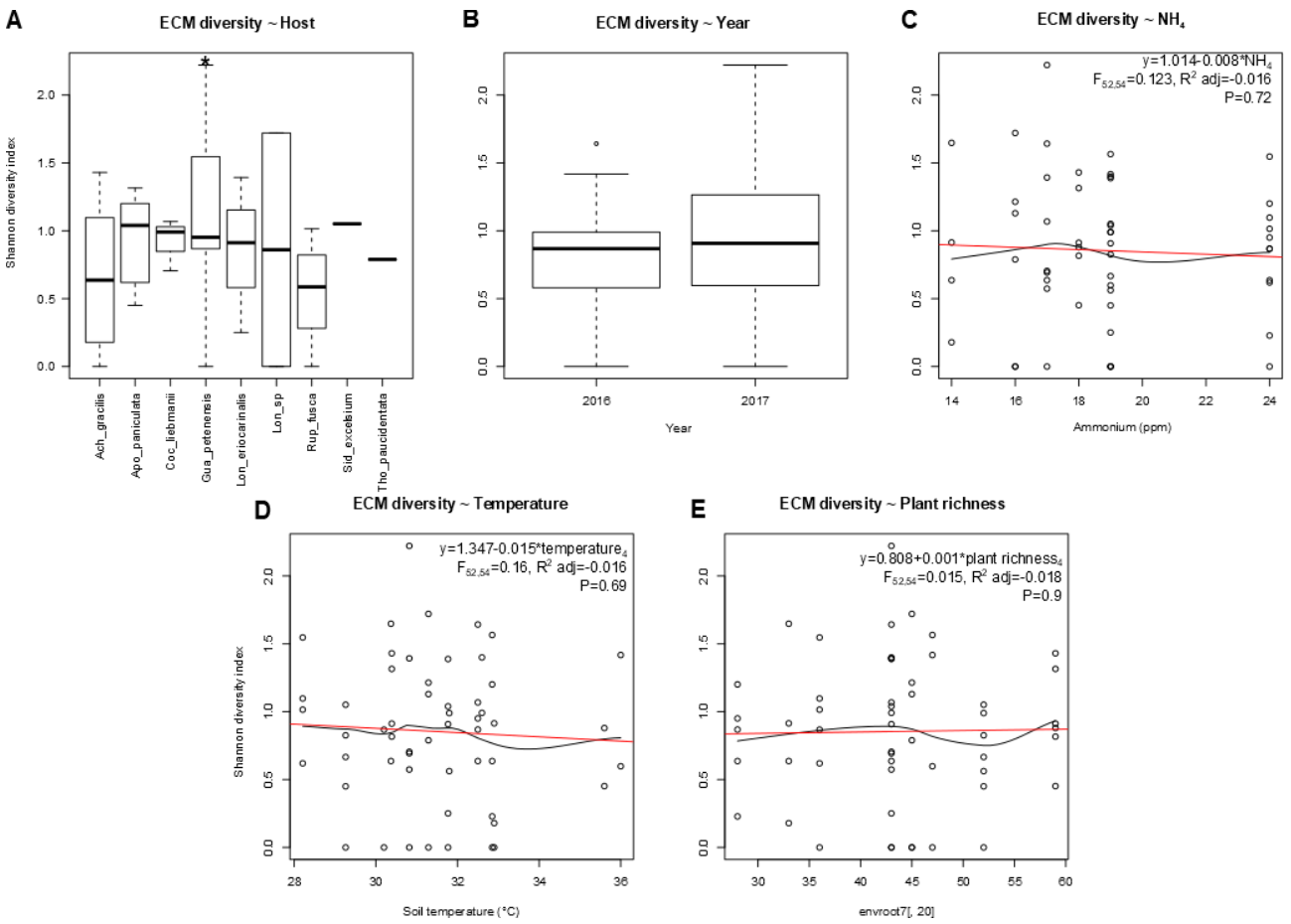


Figure S9. Ectomycorrhizal fungal diversity with the significative predictors: A) plant species, B) year of sampling, C) soil ammonium, D) soil temperature, and E) plant richness. Abbreviations: Ach_gracilis= Achatocarpus gracilis, Apo_paniculata= Apoplanesia paniculate, Coc_liebmanii= Coccoloba liebmanii, Gua_petenensis= Guapira petenensis, Lon_eriocarinalis= Lonchocarpus eriocarinalis, Lon_sp= Lonchocarpus sp, Rup_fusca= Ruprechtia fusca, Sid_excelsium= Syderoxylon excelsium, Tho_paucidentata= Thouinia paucidentata.

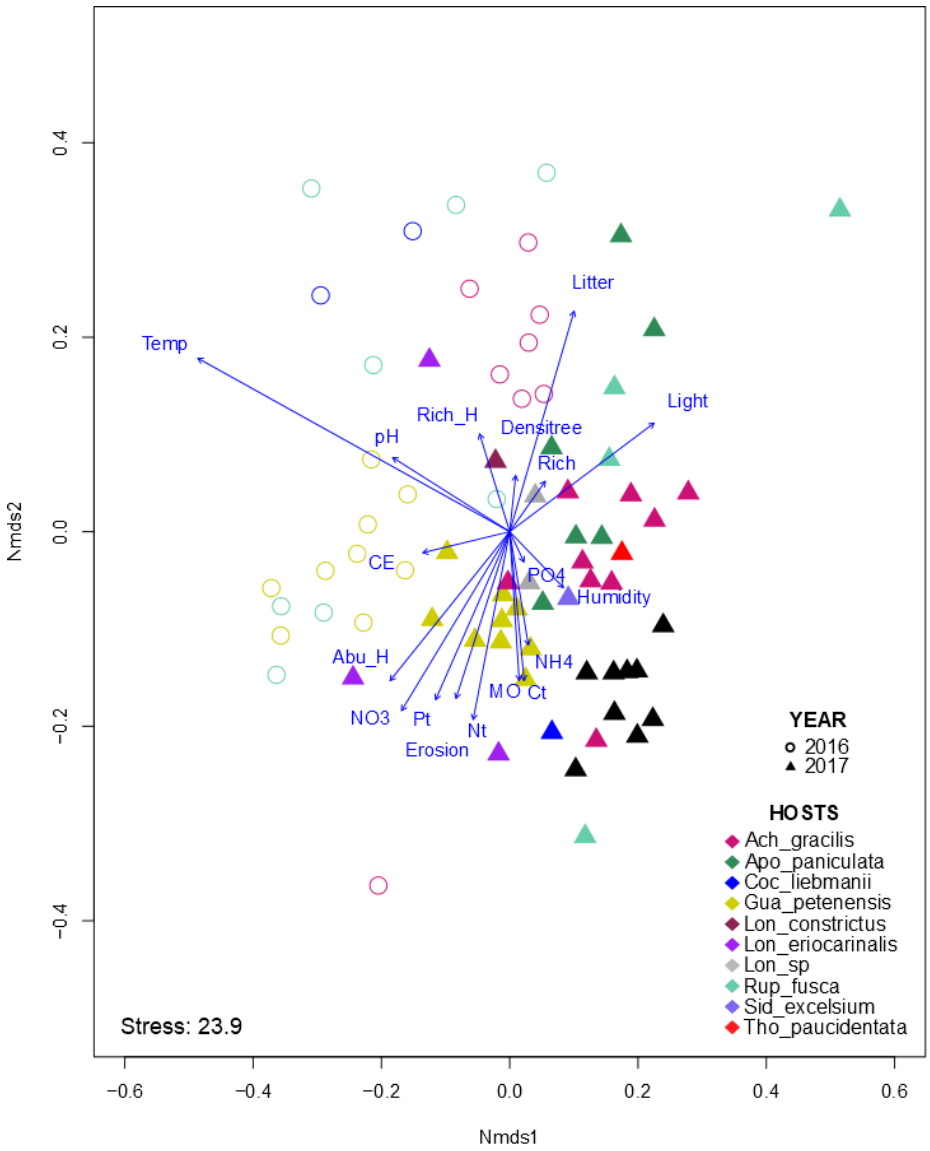
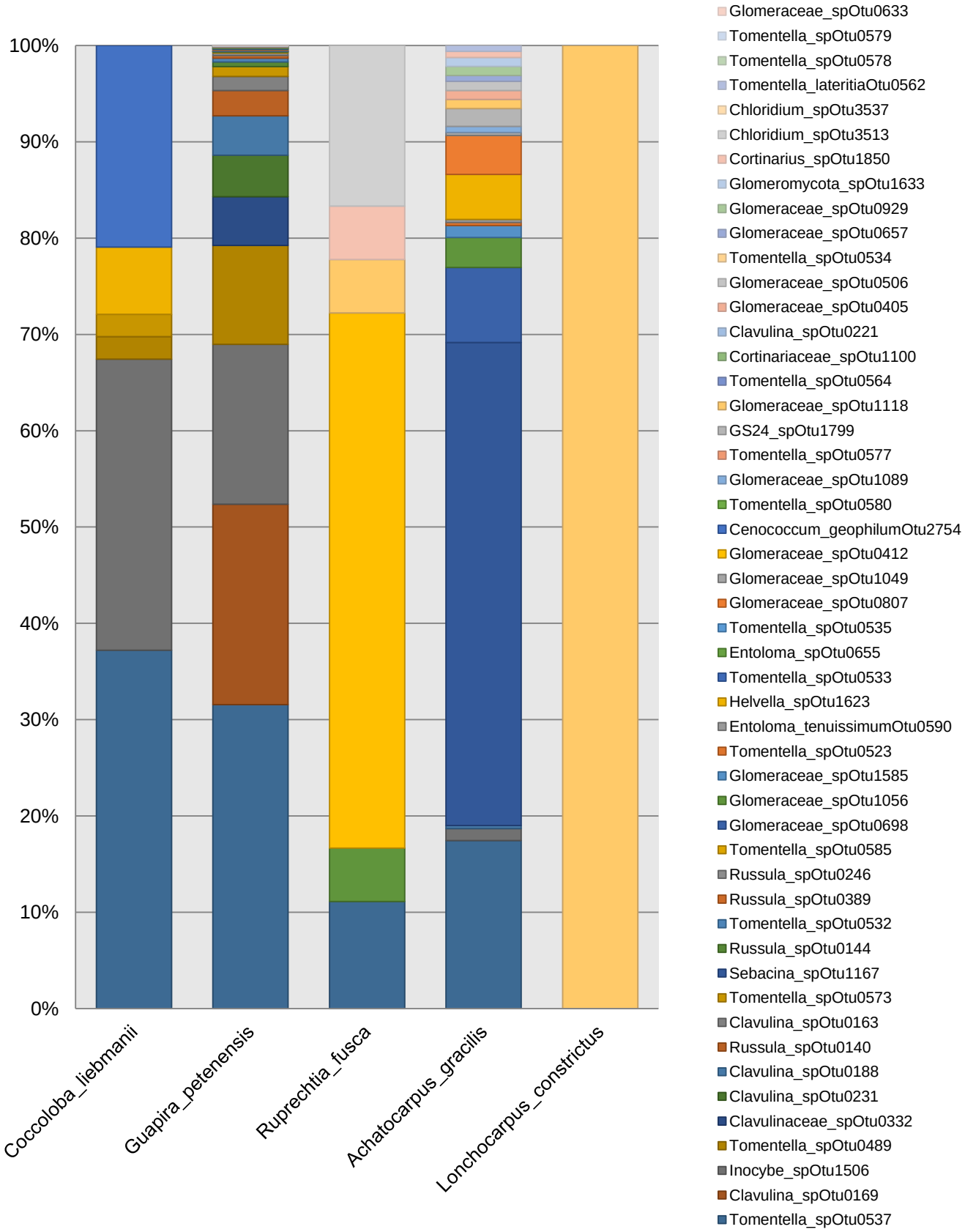


Figure S10. NMDS ordination plot of the fungal communities. Open figures correspond to samples of 2016 and solid figures belong to 2017. Each figure belongs to the three plot groups and colors represent host species. Black figures were soil samples. Abbreviations: Abu_H=abundance of ectomycorrhizal hosts, CE=electric conductivity, Ct= total Carbon, Densitree= tree density, MO=organic matter, Nt= total Nitrogen, Pt= total Phosphorus, Rich= plant richness, Rich_H=richness of ectomycorrhizal hosts, Temp= temperature. Ach_gracilis=*Achatocarpus gracilis*, Apo_paniculata=*Apoplanesia paniculata*, Coc_liebmanii=*Cocoloba liebmanii*, Gua_petenensis=*Guapira petenensis,* Lon_constrictus=*Lonchocarpus constrictus*, Lon_eriocarinalis=*L. eriocarinalis,* Lon_sp= *Lonchocarpus* spp. Rup_fusca=*Ruprechtia fusca,* Sid_excelsium= *Sideroxylon excelsium*, Tho_paucidentata=*Thouinia paucidentata.*

A

Mycorrhizal community in each host (2016)



B

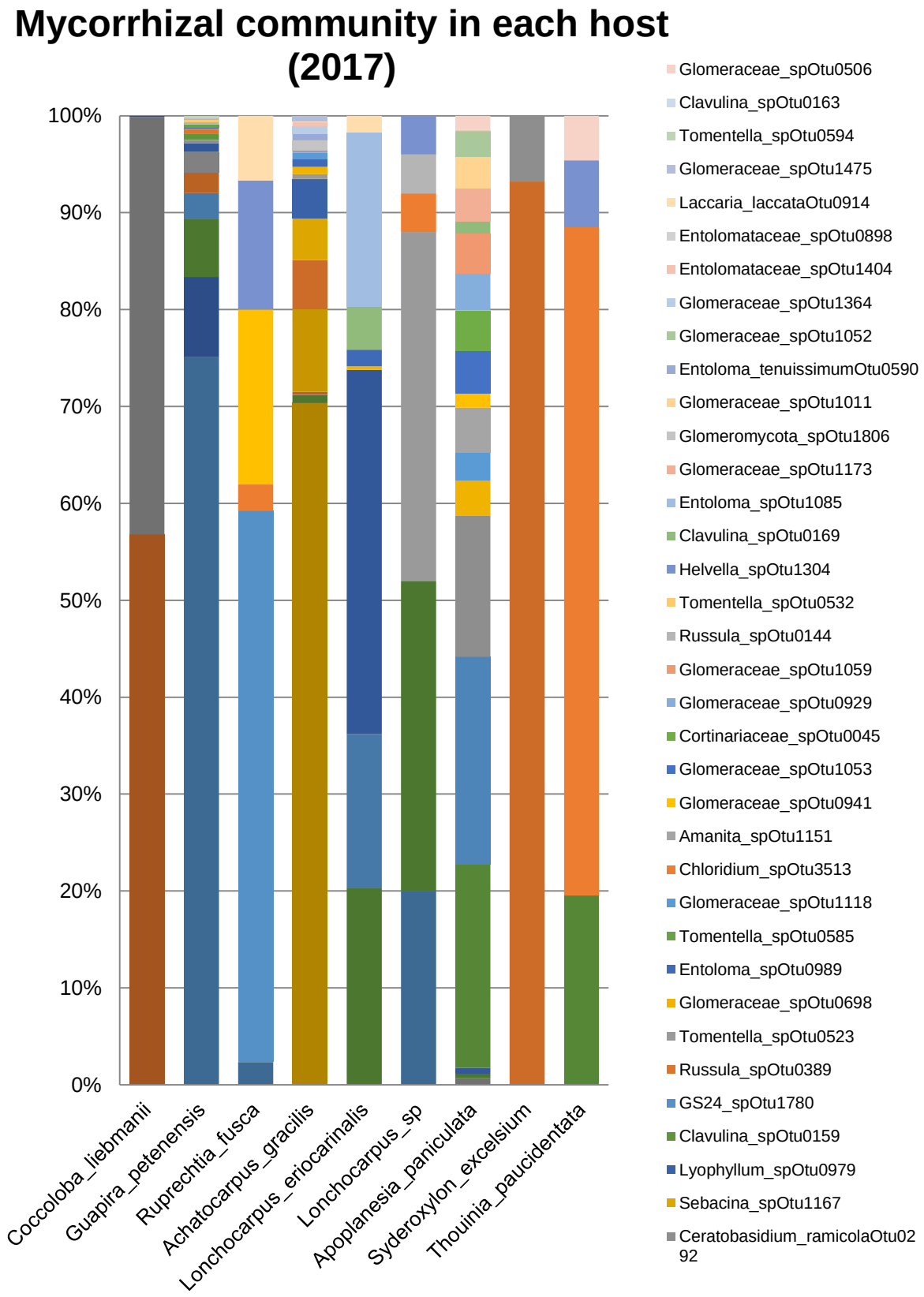


Figure S11. A) Mycorrhizal community in each host in 2016 and B) 2017.

DISCUSIÓN

La presente tesis es la primera aportación para conocer a los hongos ectomicorrízicos junto con sus hospederos del bosque tropical caducifolio (BTC); además de entender el efecto de los huracanes sobre las comunidades de hongos del suelo y sobre la red micorrízica en el BTC. Nuestros resultados indican que el huracán Patricia no sólo afectó a la vegetación generando un considerable aporte de materia orgánica y nutrimentos al suelo, sino también a las comunidades fúngicas. En el primer capítulo, se publicó qué plantas del orden Caryophyllales son los principales hospederos ectomicorrízicos en el bosque tropical cafucifolio; estos son datos previos al huracán. En el segundo capítulo se analizó la sucesión, resiliencia y resistencia de las comunidades de hongos en el suelo tras el paso del huracán. Mientras que, en el tercer capítulo encontramos que la diversidad de los hongos en la rizósfera se vio reducida por el paso del huracán Patricia. Dos años después del evento climático, la diversidad rizosférica, así como la conectividad de la red micorrízica fueron altamente resilientes.

Los capítulos 1 y 2 presentan datos previos al huracán: en el primero se descifró la simbiosis ectomicorrízica del BTC y en el segundo se compararon las comunidades del suelo a través del tiempo. En el capítulo 1 se muestreó del 2012 al 2015 bajo el supuesto de que las plantas de la familia Fabaceae –familia que presenta la mayor diversidad en el BTC– serían las principales hospederas ectomicorrízicas tal como ha sido evidenciado en otros ecosistemas tropicales (Henkel et al., 2002; 2012; Smith et al., 2011). Los resultados rechazaron esta hipótesis puesto que los principales hospederos ectomicorrízicos del BTC pertenecieron al orden Caryophyllales: Achatocarpaceae, Nyctaginaceae y Polygonaceae. *Achatocarpus gracilis* es la primera especie de Achatocarpaceae que se conoce como asociada a hongos ectomicorrízicos. En general, estas plantas tienen baja abundancia en el bosque, con excepción de *Guapira petenensis*, por lo que los hospederos ectomicorrízicos se encuentran inmersos en una matriz de plantas con interacción micorrízica arbuscular. Esto genera que los hongos ectomicorrízicos para encontrar sus hospederos dispersos, 1) deben tener esporas de larga vida, dis-

persión por viento o vegetativa, para sobrevivir en un nicho tan restringido; 2) además tienen que ser altamente competitivos con hongos saprotrofos, patógenos y otros ectomicorrízicos; y 3) deben ampliar su nicho mutualista desarrollando nuevas simbiosis oportunistas o especializarse en un solo linaje de plantas (Alvarez-Manjarrez et al., 2018).

En general, los hongos ectomicorrízicos presentan una correlación negativa a la distancia al ecuador (Bahram et al., 2013), donde la mayoría de los organismos tienen mayor diversidad. No obstante, existen bosques tropicales donde hay una alta diversidad de hongos ectomicorrízicos (e.g. Smith et al., 2011; Peay et al., 2015). La baja dominancia de los hospederos ectomicorrízicos en los bosques tropicales caducifolios explica la baja diversidad de hongos ectomicorrízicos. En otros bosques tropicales donde también se presenta baja dominancia de hospederos, han llegado a la misma conclusión (Tedersoo et al., 2010; Roy et al. 2016). Esto podría deberse en parte a una alta especificidad hacia su hospedero, por lo que su nicho se ve reducido al haber baja densidad de hospederos.

Además, se identificaron 19 especies de hongos que se encuentran formando ectomicorrizas con 19 especies vegetales. La mayoría de estos hongos no habían sido secuenciados previamente por lo que la similitud deposistadas en GenBank y UNITE era menor al 90% en casi todas las especies –aspecto que pone en evidencia lo novedoso del trabajo, y en particular, la diversidad del ecosistema–. Esta tesis tiene la hipótesis de que el bosque tropical caducifolio es un sitio de alta diversidad fúngica, donde un gran número de especies no han sido descritas. Para la descripción de las nuevas especies realizamos muestreo de esporomas durante del 2012 al 2017 en la época de lluvias.

Los esporomas recolectados nos llevaron a describir al hongo ectomicorrízico *Tomentella brunneoincrustata* M. Villegas & Contreras-Pachecho 2016. Ésta es la primera especie descrita para el clado encontrado en el caribe y la costa del Pacífico mexicano asociado a Nyctaginaceae subfamilia Pisonieae (Anexo 1; Alvarez-Manjarrez et al., 2016). El color de esta *Tomentella* es más oscuro que el resto de los miembros del género y forma ectomicorrizas con *Pisonia* y otros

miembros de la misma subfamilia. De igual forma, durante el muestreo se recolectaron esporomas de *Scytinopogon*, los datos morfológicos y filogenéticos nos indicaron que se trata de una especie nueva, a la cual se nombró como *Scytinopogon minisporus* J. Alvarez-Manjarrez, M. Villegas & R. Garibay-Orijel 2019. Adicionalmente los análisis filogenéticos indican que, tanto *Scytinopogon* como su grupo hermano *Trechispora,* son parafiléticos y se encuentran mal clasificados en Clavariaceae, cuando deberían ser reacomodados en Hydnodontaceae (Trechisporales; Desjardin & Perry 2015). *Tomentella* y *Scytinopogon* son géneros que necesitan una corrección taxonómica, ya que ambos son grupos parafiléticos: *Tomentella* quien es grupo hermano de *Thelephora*, debería ser unificado en *Thelephora* pues los caracteres morfológicos –*Tomentella* es resupinado y *Thelephora* es teleforoide o clavarioide– no se sostienen con las filogenias. Este es el mismo caso para *Scytinpogon* (clavarioide) y *Trechispora* (resupinado), que tendrían que ser sinonimizados en *Trechispora*. El carácter resupinado es un carácter ancestral en los Agaricomycetes (Varga et al., 2019), por lo que es altamente probable que en otros clados también haya este mismo problema taxonómico.

También se describieron dos especies del género *Thelephora: T. versatilis* Ramírez-López & M. Villegas 2015 y *T. pseudoversatilis* Ramírez-López & M. Villegas 2015 (Ramírez-López et al., 2015), del cual se determinó que *Guapira petenensis* es hospedero de *T. versatilis*. Adicionalmente, las secuencias de las ectomicorrizas coincidieron con esporomas de *Clavulina* muestreados antes del 2012, lo cual determinó que *Achatocarpus gracilis* es el hospedero de la nueva especie *Clavulina subtilis* M. Villegas, Garibay-Orijel & Ramírez-López (Villegas et al., en preparción).

Por otro lado, en el segundo capítulo abordamos la hipótesis que establecía que al aumentar los nutrientes en el suelo, la diversidad de hongos incrementaría. El suelo sí aumentó en C, N y P, inmediatamente después del huracán lo cual generó que la tasa C:N y C:P decreciera; estos datos corresponden con los resultados de Gavito y colaboradores (2018) para el mismo huracán. Para la siguiente temporada de lluvias, donde la tasa C:N había vuelto a aumentar, hubo una dismi-

nución en la diversidad fúngica; y los posteriores muestreos siguieron el mismo patrón. La baja tasa de C:N afecta la mineralización de C, N y P en el suelo (Mooshammer et al., 2012) y la descomposición incrementa (Britton et al., 2018). Además, el cambio en la composición de la comunidad pueden alterar la estequiometría de C:N:P (Heuck et al., 2015). Que la tasa de C:P después del huracán bajara drásticamente (< 37.5) y alcanzara meses después niveles más altos (113-130) que previo al huracán (< 75) puede explicar el decremento de diversidad de hongos que hubo con el tiempo.

Después del huracán Patricia se depositaron 17.8 Mg ha^{-1} de biomasa, cuando de manera natural se aporta de 3.2 - 4.2 Megagramos por hectárea (Mg ha^{-1}; Parker et al., 2018). Durante el 2016 se presentaron lluvias atípicas prolongando la época de lluvias, mientras que en 2017 la precipitación volvió a su temporalidad normal, i.e. 730 mm anuales (valores de estación meteorológica). En los BTC la descomposición de la materia orgánica está mediada por la cantidad de agua disponible (Anaya et al., 2007, 2012). Gavito et al. (2018) encontraron que la tasa de descomposición aumentó durante el huracán Patricia, lo cual coincide con la alta diversidad de hongos.

Durante la descomposición de la materia orgánica se conoce que existe una sucesión de especies. Antes de Patricia nosotros encontramos mayor diversidad del phylum Ascomycota, pero posteriormente encontramos mayor diversidad de Basidiomycota. Al inicio de la descomposición, las especies más abundantes son aquellas que pueden aprovechar las moléculas de baja complejidad, tales como la glucosa y otros carbohidratos. Las especies fúngicas que suelen estar en estas primeras etapas son algunos Ascomycota, mientras que en la descomposición tardía aparecen los Basidiomycota (Purahong et al., 2016). Esto se debe al poder enzimático que tienen estos últimos con capacidad para degradar compuestos difíciles de despolimerizar –como la lignina– (Voříšková & Baldrian, 2013) y que muchos microorganismos no pueden llevar a cabo. Los huracanes promueven materia orgánica rica en nutrientes, ya que las plantas no reabsorben N o P antes del huracán. Esto confiere que la materia orgánica sea un sustrato del cual muchos

organismos se puedan alimentar. Nuestro muestreo demostró no sólo que hubo sucesión de especies durante la descomposición de la materia orgánica, siendo más abundantes los hongos con gran poder enzimático justo después del huracán; sino que también había alta dominancia de tres especies antes del huracán, y con el paso del huracán la dominancia cayó, siendo resiliente en los consecuentes muestreos.

Antes del huracán encontramos 519 OTUs, después del huracán cada muestreo secuenció especies que no se compartieron con los demás muestreos. Esto indicó que hubo sucesión sin recambio de especies; es decir, a pesar de que se encontraron especies que no se detectaron antes de Patricia, los 519 OTUs iniciales seguían siendo parte de la comunidad después del huracán (aunque no estuvieran todas presentes en todos los muestreos). La recuperación del sistema es lenta puesto que según la hipótesis de Svoboda y Henry (1987): la incorporación de nuevas especies no desplazan a la comunidad inicial. Esto predice un sitio inhóspito para el establecimiento, por lo que no hay remplazo ni competencia. Efectivamente nuestro muestreo fue en la cumbre de un lomerío –las cuales Parker y colaboradores (2017) reportan como las zonas con mayor afección por el huracán–. El daño en la vegetación generó que el dosel se perdiera, lo cual involucra mayor temperatura y cantidad de luz en el suelo, además de pérdida de humedad. Estos factores representan un ambiente hostil para el establecimiento de los hongos del suelo.

Por otro lado, se encontraron 105 especies de hongos del suelo que estaban presentes antes del huracán y que fueron capaces de sobrevivir, fluctuando su abundancia, al impacto de Patricia. Se considera que la comunidad es persistente cuando hay sobrevivencia en el tiempo de alguno de los elementos del sistema. En este caso, estas 105 especies se encontraron todo el tiempo en el suelo, demostrando que una parte de la comunidad de hongos es presistente y probablemente resistente a los huracanes.

Los datos del capítulo 3 nos muestran como el huracán Patricia redujo la diversidad de las comunidades de hongos rizosféricos, y generó la desconexión de

la red micorrízica. Al hablar de la rizosfera nos referimos a las inmediaciones de las raíces en el suelo, donde se lleva a cabo la rizodepositación de carbohidratos y proteínas, así como compuestos alelopáticos, que propician el establecimiento de diferentes microorganismos (Hinsinger et al., 2005). La rizodepositación depende en gran medida de la intensidad de la fotosíntesis y factores que la afectan como la concentración de CO_2, contenido de N en el suelo, intensidad de luz y humedad del suelo (Pausch & Kuzyakov, 2018). El huracán Patricia hizo que la fotosíntesis declinara (Parker et al., 2018) y el N mineralizado aumentara, lo cual pudo generar una disminución considerable de la rizodepositación. En parte, la reducción de carbohidratos en la rizósfera, junto con las nuevas condiciones inhóspitas pudieron generar la afección a la comunidad rizosférica.

En contraste con las comunidades del suelo, los hongos rizosféricos se vieron menguados después del huracán y su recuperación fue mayor a dos años. Cabe mencionar que el suelo es el hábitat tanto de hongos de vida libre como de simbiontes obligados, por lo que el suelo es un reservorio de la comunidad potencial que colonizará las raíces. Las comunidades rizosféricas pasan por el filtro del hospedero, por lo que la comunidad es principalmente determinada por la identidad del hospedero (Tedersoo et al., 2010; Koide et al., 2011).

Los resultados muestran que la diversidad rizosférica es explicada por la temperatura, la luz a nivel del suelo y la identidad del hospedero, y no por las características del suelo. La diversidad rizosférica tiene una correlación negativa con la temperatura y una correlación positiva con la luz. Particularmente, la diversidad de los hongos ectomicorrízicos (ECM) fue explicada por la identidad de la planta hospedera (i.e. *Guapira petenensis* presentó la mayor diversidad de todas las plantas); además la diversidad tuvo una correlación negativa al amonio al igual que a la temperatura del suelo y una correlación positiva a la riqueza vegetal. Muchos otros estudios han determinado que el NH_4 en el suelo determina las comunidades ectomicorrízicas (e.g. Corrales et al., 2016, 2017; Truong et al., 2019). Estos resultados coinciden con bosques tropicales monodominantes, donde la po-

ca disponibilidad de N se debe a los hongos ECM y la necesidad de asociarse a ellos para obtener N (Corrales et al., 2016).

Por otro lado, la correlación positiva a la riqueza vegetal nos podría estar indicando la presencia de otros hospederos ectomicorrízicos que todavía se desconocen. Además, probamos que la abundancia de hospederos en cada parcela no explicaba la diversidad de ECM. En otros estudios se ha corroborado que la composición de la comunidad vegetal es un buen predictor de la comunidad fúngica (Leff et al., 2018; van der Linde et al., 2018). Después del huracán revisamos las raíces de todas las plantas reportadas en el capítulo 1 sin embargo, muchas de ellas no presentaban ectomicorrizas en el 2016. En el 2017, por considerar que no volveríamos a encontrar ectomicorrizas, ya no repetimos el muestreo en esas plantas, lo cual podría ser un error metodológico.

Cada hospedero tuvo asociada una diversidad específica con unas pocas especies generalistas. Después del huracán estos generalistas no fueron resistentes al disturbio, lo cual generó la pérdida de conexiones entre diferentes especies. En los muestreos del 2012-2014 encontramos que algunas especies como *Tremelloscypha dichroa, Membranomyces* sp., *Sebacina* sp., *Thelephora versatilis* y *Tomentella* sp. eran los hongos que conectaban a plantas de diferentes especies. Para el muestreo del 2016, prácticamente estos hongos estuvieron ausentes y fueron remplazados por *Tomentella* sp. (OTU 537), *Clavulina* sp. (OTU 169), *Inocybe* sp. (OTU 1506), *Tomentella* sp. (OTU 489) y Clavulinaceae, sp. (OTU 332). Dos años después, la comunidad volvió a tener como hongos frecuentes a *Tomentella* sp. (OTU 537), *Thelephora versatilis* (OTU 514), *Clavulina* sp. (OTU 192), *Tremelloscypha* sp. (OTU 851) y *Tomentella* sp. (OTU 489). El recambio a las especies que se conocían antes del disturbio nos podría hablar de la resiliencia del ecosistema.

Por otro lado, el BTC está dominado por hongos micorrízico arbusculares, siendo los ectomicorrízicos los más focalizados a ciertas plantas. Nuestro muestreo encontró que las plantas que tienen asociación ectomicorrízica también forman micorriza arbuscular (AM). Los hongos ectomicorrízicos fueron los más diver-

sos en las raíces de las plantas muestreadas, lo cual era esperable al ser todos hospederos ectomicorrízicos. Sin embargo, la riqueza de AM fue alta (i.e. 251 OTUs), considerando que su riqueza mundial se estima en ~1500 OTUs, y la riqueza reportada para México es de 235 especies morfológicas (Montaño et al., 2012). El único estudio de AM después de un huracán, cuantificó el porcentaje de colonización después del paso del Wilma (Vargas et al., 2010); ellos reportaron un aumento en la colonización de las plantas. Este estudio no midió colonización de ningún tipo de micorrizas, pero la presencia de DNA en la rizósfera fue suficiente para aceverar la interacción. Según los resultados de esta tesis, el porcentaje de colonización no es una medida que nos ayude a entender del todo la interacción. En todos los muestreos se encontraron AM pero de habernos quedado exclusivamente con esa información, habría pasado por alto que la conexión entre plantas de diferentes especies se perdió.

La predicción del aumento en la modularidad de la red micorrízica en sitios con mayor perturbación fue rechazada. A pesar de la clasificación de las parcelas según el nivel de perturbación, encontramos que el huracán tuvo un efecto devastador en todas; después del paso de un huracán tan intenso como Patricia (vientos de 265 km/h) las conexiones de la red micorrízica se perdieron, i.e. no encontramos especies micorrízicas compartidas entre los diferentes hospederos. Al respecto, nuestro muestreo no corrobora si la red micorrízica se rompió entre individuos de la misma especie vegetal. Para el 2017 la red micorrízica se reestableció encontrando diferentes especies de hongos compartidos entre más de dos especies de plantas.

Las redes calculadas en esta tesis encuentran que no hay anidamiento, pero los valores NODF y wNODF fueron más altos en el 2016 que en 2017, al igual que la modularidad; esto coincide con el menor grado de especialización del 2016 comparado contra el 2017 (no hay diferencias significativas en todos los datos). Nuestros datos encuentran que las especies inmediatamente después de Patricia fueron generalistas formando módulos, y con el paso del tiempo las especies especialistas volvieron a establecerse en las raíces. Corroboramos que las especies

especialistas son las más vulnerables a la perturbación y su recuperación puede ser lenta (Devictor et al., 2008; VanWallendael 2019). Estas propiedades de las redes nos pueden ayudar a entender su reacción hacia la perturbación. Por ejemplo, lo que sugiere que las redes modulares son resilientes al disturbio, ya que los cambios sólo afectan dentro del módulo donde ocurrió el disturbio (Gilarranz et al., 2017). Mientras que el anidamiento, al medir la cantidad de especies generalistas que hay, nos indica de forma indirecta la redundancia ecológica de las redes. Esta propiedad también tiene una respuesta a los disturbios, contribuyendo a que el sistema sea resiliente (Bascompte 2009).

La comparación entre redes micorrízicas arbusculares y ectomicorrízicas muestran que las redes ectomicorrízicas fueron menos afectadas por el huracán, pues sus conexiones siempre se mantuvieron. Ambos gremios son simbiontes obligados con diferencias fisiológicas importantes. Los hongos ECM tienen la capacidad de obtener C tanto de su hospedero como de la descomposición de la materia orgánica por medio de oxidación (Tunlid et al., 2016); tienen micelio septado con mayor capacidad de recuperación, y sólo tienen asociación con el 2% de las plantas terrestres (Brundrett & Tedersoo, 2018). Los hongos AM obtienen C exclusivamente de sus fitobiontes, tienen micelio cenocítico el cual es más vulnerable, y se asocian con el 71% de las plantas terrestres (Brundrett & Tedersoo, 2018). A pesar de que los AM se consideran generalistas encontramos que fueron los hongos más afectados. Nosotros consideramos que la afección a la tasa fotosintética después del huracán, el daño físico a las plantas, y las características biológicas de los hongos AM, pudieron tener mayor efecto en los hongos AM, quienes dependen completamente del C de sus hospederos.

Los huracanes son agentes de disturbio que afectan la sobrevivencia de las comunidades que habitan por encima del suelo –animales y plantas (i.e. las plantas de nuestras parcelas tuvieron 5.8-14.8% de mortalidad, mientras que del 9.0-14.3% fueron tumbados y arrancados de raíz pero rebrotaron)– y a la composición de las comunidades fúngicas. Ya sea que los vientos del huracán exporten especies o los animales también dispersen especies (Jumponnen 2003; Behzad et

al., 2018; Correia et al., 2019), los nuevos hongos deben pasar por todos los filtros que generan la estructura y composición de las comunidades. Los factores bióticos y abióticos representan filtros para el desarrollo exitoso de esas especies recién llegadas. Después de un huracán, el primer filtro por pasar serían las condiciones de alta radiación solar y temperatura en el suelo. Si la fisiología de la especie permite la sobrevivencia en ese ambiente, después debe pasar por las condiciones bióticas. Estas condiciones podrían ser la presencia del hospedero y las interacciones interespecíficas, tales como la competencia, la facilitación o el parasitismo (Svoboda y Henry, 1987; Koide et al., 2011).

Los procesos de ensamble que se conoce para hongos son el '*priority effect*', la hipótesis de la lotería, los '*storage effect*', el '*competition-colonization trade-off*' (Kennedy 2010; Kennedy et al., 2011), partición de nicho (Lindahl et al., 2007; Peay et al., 2008; Mujic et al., 2016), dinámica de parches, mortalidad dependiente de la densidad (Bruns, 1995) donde todos ellos asumen competencia entre todos los hongos. La sucesión de especies sin reemplazamiento en el suelo sugiere que la competencia no es el proceso de ensamble de esta comunidad. Aunque la competencia es el proceso de ensamble más comúnmente estudiado (e.g. Johnson et al., 2013; Kunstler et al., 2016; Mills et al., 2019) se ha dejado de lado la coexistencia por facilitación o comensalismo. Ambos procesos de ensamblaje se han observado en diferentes comunidades (e.g. en comunidades bacerianas, redes de polinización o comunidades vegetales; Mittelbach et al., 2015; Losapio et al., 2017; Montesinos-Navarro et al., 2019) La heterogeneidad del ambiente y el enriquecimiento de nutrientes del suelo pudieron haber generado nichos donde se permitiera la coexistencia de todas las especies sin competir por los mismos recursos, sugiriendo la partición de nicho (Mittelbach et al., 2015) y la dinámica de parches (Bruns 1995) inmediatamente después del huracán.

Para la comunidad de hongos rizosféricos, la historia es distinta puesto que son hongos en asociación obligada u oportunista con la planta huésped. El ensamble de las comunidades puede ser explicado por el '*storage effect*', donde involucra el reclutamiento de especies a través del tiempo y los modelos de lotería,

donde se compite por un recurso limitante (Kennedy 2010). Es decir, las especies eran parte de la comunidad del suelo y con la heterogeneidad del ambiente provocado por el huracán, éstas encontraron las condiciones idóneas para competir por el recurso limitante que eran las raíces vivas. Por lo que las condiciones abióticas, pero también las condiciones bióticas de su hospedero (la pérdida de biomasa que tuvieron las plantas) pudieron afectar la interacción de los simbiontes obligados e.g. los hongos micorrízico arbusculares o ectomicorrízicos.

Las comunidades de hongos micorrízicos se encuentran en constante competencia por el recurso de las raíces y el C que las plantas translocan a ellas. Nuestros análisis de co-ocurrencia nos indican que los hongos ectomicorrízicos compiten con prácticamente el resto de los hongos encontrados en las raíces. Las interacciones de exclusión o co-ocurrencia pueden generalmente no son recíprocas (Mack & Rudgers, 2008). Por ejemplo, los hongos micorrízico arbusculares co-habitan con los ECM, patógenos, endófitos y saprótrofos. Los ECM mostraron el mismo patrón durante los dos años muestreados, sin embargo los AM cambiaron de tener mutua exclusión con varios grupos a co-habitar con ellos. Kennedy (2010) y Mahmood (2003) mencionan que el ambiente puede hacer cambios en la interacción y nuestros resultados sugieren que el ambiente de un año a otro sí modeló el tipo de simbiosis entre especies.

Mientras la temperatura del océano siga incrementando la probabilidad de formación de huracanes sigue aumentando. Los huracanes Jova y Patricia han demostrado que el bosque no es resistente pero sí resiliente a los huracanes (Parker et al., 2017; Gavito et al., 2018; Jaramillo et al., 2018; Martínez-Yrízar et al., 2018; Paz et al., 2018), al igual que sus comunidades fúngicas e interacciones con las plantas. Aunado a esto, el aumento de temperatura en el continente generará la desertificación de las zonas tropicales y pérdida de hospederos micorrízicos (Salazar et al., 2007; Setidinger et al., 2019). A pesar de que las interacciones puedan modificarse por el disturbio, la resiliencia de todo el ecosistema siempre dependerá de la alta diversidad. La conservación de la diversidad del suelo redituará en la resiliencia de los ecosistemas ante los disturbios que se prevén por el

calentamiento global. La conservación de la diversidad del suelo del bosque tropical caducifolio es un seguro de vida ante las perturbaciones.

CONCLUSIONES

Los daños que generó el huracán Patricia incrementaron la cantidad de nutrimentos del suelo. Estos nutrimentos a su vez generaron un cambio en las comunidades de hongos del suelo; mientras que el daño a la vegetación afectó directamente a los simbiontes rizosféricos. Las respuestas entre suelo y rizósfera fueron contrastantes: en el suelo la diversidad incrementó después del huracán y disminuyó dos años después; mientras que en las comunidades rizosféricas justo después del huracán la diversidad disminuyó e incrementó dos años después. El ensamble de las comunidades de hongos del suelo y rizosféricos siguen diferentes procesos; los hongos rizosféricos son simbiontes facultativos u obligados de sus hospederos vegetales, mientras que los hongos del suelo pueden ser organismos de vida libre o cualquier otro estilo de vida.

Las comunidades de hongos del suelo fueron resilientes puesto que la dominancia de especies tendió a aumentar con el tiempo, tal y como estaba antes del huracán. Por otro lado, las comunidades rizosféricas fueron reducidas por la alta temperatura del suelo, lo cual a su vez podría ser explicado por la baja tasa de productividad primaria neta que experimentaron las plantas después del huracán. La red micorrízica recobró conectividad conforme la diversidad rizosférica aumentó. Tanto la comunidad rizosférica, como sus interacciones con las plantas, fueron resilientes después de dos años después del huracán Patricia. Sin embargo, es probable que la resiliencia de las comunidades pueda reducirse conforme se vuelvan más frecuentes e intensos los huracanes.

Las investigaciones por largos periodos de tiempo en el sitio de estudio han demostrado que la variación interanual es alta, al igual que la variación para eventos catastróficos, como lo fueron los huracanes Jova y Patricia. Esta tesis asienta los primeros antecedentes de los efectos que tiene el huracán más fuerte que se

haya registrado en el Pacífico en las comunidades de hongos. Sin embargo, se debe considerar que cada huracán puede generar diferencias importantes en las comunidades, ya sea por el estado de conservación del bosque, así como de la cantidad de materia orgánica aportada al suelo.

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ANEXO 1. *Tomentella brunneoincrustata*, the first described species of the Pisonieae-associated Neotropical *Tomentella* clade, and phylogenetic analysis of the genus in Mexico

Resumen

El linaje /tomentella- thelephora es uno de los clados más dominantes entre las comunidades de hongos ectomicorrízicos en todo el mundo. A pesar de la importancia de estos hongos como simbiontes de raíces, sus esporomas son inconspicuos y raros de encontrar. El conocimiento de la diversidad de *Tomentella* en el Neotrópico es escaso, y está basado en secuencias ambientales. Aquí describios la nueva especie *Tomentella brunneoincrustata,* incluyendo la morfología de los basidiomas, anatomía de las micorrizas y su ecología. Ya que el conocimiento de México sobre *Tomentella* es poco, nosotros realizamos el primer análisis filogenético del género para este país. Nosotros secuenciamos la región nrITS de las muestras fúngicas, y secuencias las regiones rbcL y trnL para identificar a las plantas hospederas. Llos análisis filogenéticos se realizaron con inferencia bayesiana. Los análisis bayesianos mostraron que muchos clados parafiléticos dentro del linaje /tomentella-thelephora están asociados a Pisonieae, presentes a través de áreas tropicales del mundo. Sin embargo, las secuencias de las ectomicorrizas de Puerto Rico, Florida, Dominica y México constituyeron un clado monofilético bien soportado, el cual denominamos el “clado de *Tomentella* Neotropical asociado a Pisonieae”. Dentro de este clado, *T. brunneoincrustata* fue descrita como: basidioma finamente costroso, fuertemente adherido al sustrato; subículo del mismo color, indiferenciado de margen estéril; con dos tipos de hifas en el subículo; y esporas globosas a elipsoides de tamaño pequeño (<8 µm). Esta especie se desarrolla en los bosques tropicales caducifolios, donde se asocia con hospederos de la tribu Pisonieae dentro de Nyctaginaceae. Los otros esporomas de *Tomentella* fueron recolectados en bosques templados de México y pertenecen a los clados de *T. atramentaria, T. pilosa, T. muricata, T. fuscocinerea, T. stuposa, T. punicea, T. artroarenicolor, T. bryophylia* y *T. lateritia*. Cinco basidiomas tuvieron secuencias con clados independientes y previamente desconocidos de *Tomentella.*

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ORIGINAL ARTICLE

Tomentella brunneoincrustata, the first described species of the Pisonieae-associated Neotropical *Tomentella* clade, and phylogenetic analysis of the genus in Mexico

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Abstract The /tomentella-thelephora lineage is one of the most highly dominant clades among ectomycorrhizal communities worldwide. Despite its importance as a root symbiont, its fruit bodies are inconspicuous and rarely found. Knowledge regarding the diversity of *Tomentella* in the Neotropics is scarce, and is based largely on environmental samples. Here, we describe a new species, *Tomentella brunneoincrustata*, including its basidiocarp morphology, mycorrhizal anatomy, and ecology. Because knowledge of *Tomentella* in Mexico is scarce, we provide the first phylogenetic analysis of this genus in the country. We sequenced the nrITS region of the fungal samples, and sequenced the *rbcL* and *trnL* regions to identify the host plant. The phylogenetic analyses were conducted by Bayesian inference. The Bayesian analysis showed that several paraphyletic clades within the lineage /tomentella-thelephora are associated with Pisonieae present across tropical regions of the world. However, the ectomycorrhizae sequences from Puerto Rico, Florida, Dominica, and Mexico constituted a well-supported monophyletic clade that we denote as the "Pisonieae-associated Neotropical *Tomentella* clade". Within this clade, *T. brunneoincrustata* was characterized as follows: a thin crustose, strongly attached to the substrate basidiome; concolorous subiculum, undifferentiated and sterile margin; two types of subiculum hyphae; and small (<8 μm) globose to ellipsoid spores. This species develops in tropical dry forests, where it associates with hosts in the Pisonieae tribe within the Nyctaginaceae. The remaining *Tomentella* fruit body vouchers collected in temperate forests of Mexico belonged to clades related to *T. atramentaria, T. pilosa, T. muricata, T. fuscocinerea, T. stuposa, T. punicea, T. atroarenicolor, T. bryophila, and T. lateritia*. Five fruit body vouchers had unique sequences forming independent and unknown clades of *Tomentella*.

Keywords Ectomycorrhizal · Neotropics · Pisonieae · Phylogeny · *Tomentella* · Tropical dry forest

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Introduction

The Thelephoraceae family comprises the genera *Amaurodon, Thelephora, Pseudotomentella, Tomentella* (Larsson et al. 2004; Agerer 2006), and *Odontia* (Tedersoo et al. 2014). This family presents clavarioid, effused, flabelliform, pileate or resupinate basidiocarps (Agerer 2006). A characteristic apomorphy of the family is the irregular-shaped, non-amyloid,

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ornamented, and often dark basidiospore with a large apiculus (Larsson et al. 2004). *Tomentella* has inconspicuous resupinate fruit bodies formed by several layers of loose hyphae on soil, wood, twigs or rock surfaces (Kõljalg 1996). This genus is paraphyletic, and it comprises species that are divided into two lineages: an ectomycorrhizal (/tomentella-thelephora) and a saprotrophic (*Tomentella* p. parte) lineage. The /tomentella-thelephora lineage has a pan-global distribution and is one of the most species-rich and abundant ectomycorrhizal (ECM) clades associated with all major plant host taxa in a variety of ecosystems (Tedersoo et al. 2010a). The mycorrhizae of *Tomentella* are morphologically diverse (Jakucs et al. 2015), but share more than three of the following features: black-brown to brown mycorrhiza; clamped hyphae; an angular outer mantle layer; mantle cells that are organized in a star-like pattern; a mantle surface network composed of hyphae or angular-triangular, horn-shaped cells; groups of globular cells on the mantle surface; rhizomorphs with bilateral, nodal ramifications and a rind formed by thin, clamped, densely entwined, multi-branched marginal hyphae; and clamped cystidia (Jakucs and Erõs-Honti, 2008).

The /tomentella-thelephora lineage has the following biological and ecological traits. In almost any ECM fungal community (based on mycorrhizal DNA), it is among the three most dominant groups, based on either the number of MOTUs (molecular operational taxonomical units) or the frequency of its DNA sequences (e.g. Dahlberg et al. 1997; Kõljalg et al. 2001; Trowbridge and Jumpponen 2004; Haug et al. 2005; Peay et al. 2007; Smith et al. 2007; Morris et al. 2008; Hynes et al. 2010; Suvi et al. 2010; Tedersoo et al. 2010b; Smith et al. 2011; Bonito et al. 2012; Brown et al. 2013; Wu et al. 2013). Despite its importance as a root symbiont, its fruit bodies are inconspicuous and rarely found (Jakucs and Erõs-Honti, 2008; Bâ et al. 2012). Most of the lineage appears to be ECM (Tedersoo et al. 2010a), while its sister genus *Odontia* has a stable isotope pattern with an intermediate position between ECM fungi and saprotrophs. The ^{13}C pattern of this genus suggests that it does not obtain carbon from its fruiting substratum, although its C source is unknown (Tedersoo et al. 2014). As a consequence of the morphological plasticity of their ectomycorrhizae, the species of /tomentella-thelephora can be distributed either in the mineral soil horizon (Harrington and Mitchell 2005; Baier et al. 2006) developing a "contact exploration type" ECM, or in the organic horizon of broad-leaved forests (Tedersoo et al. 2003), in which they are often attached to plant foliar debris. In the latter case, they develop slightly or highly differentiated rhizomorphs, indicating that these morphotypes belong to the "medium-distance exploration type" (Jakucs and Erõs-Honti, 2008).

While the /tomentella-thelephora is dominant in boreal and temperate forests in the Northern Hemisphere, it has also been identified in the Southern Hemisphere and in tropical and subtropical ecosystems such as those in India (Thind and Rattan 1971), Korea (Jung 1994), and the Canary Islands (Larsen 1994). It was recently found to be dominant in the following tropical areas: subtropical broadleaf mixed forests in China (Gao et al. 2015); *Coccoloba uvifera* coastal forests in the Guadeloupe island in the Lesser Antilles (Séne et al. 2015); African tropical forests containing Caesalpinioideae (Fabaceae), Sarcolaenaceae, Dipterocarpaceae, Asteropeiaceae, Phyllanthaceae, Sapotaceae, Papilionoideae (Fabaceae), Gnetaceae and Proteaceae, distributed in open, gallery and rainforests of the Guineo-Congolian basin; Zambezian Miombo woodlands of East and South-Central Africa; and Sudanian savanna woodlands of the sub-Saharan region (Bâ et al. 2012).

Despite their importance in tropical ecosystems, most *Tomentella* species have been identified in temperate regions (Larsen 1974, Jülich and Stalpers 1980, Stalpers 1993, Kõljalg 1996). Several new tropical species were recently described from Africa (Yorou et al. 2007; Yorou and Agerer 2007; Yorou and Agerer 2008; Yorou et al. 2011; Yorou et al. 2012a; Yorou et al. 2012b) and the Seychelles (Suvi et al. 2010). However, knowledge regarding the diversity of *Tomentella* in the Neotropics is scarce, and based only on environmental samples from Ecuador (Tedersoo et al. 2010b), Dominica, Puerto Rico, and Vieques (Hayward and Horton 2014). Similar to those from other regions worldwide, environmental DNA sequences in the Mexican Neotropics indicate that the /tomentella-thelephora lineage is dominant in the ECM roots of several ecosystems including subtropical pine-oak forests (Garibay-Orijel 2008), cloud oak forests (Morris et al. 2009), alpine conifer forests (Reverchon et al. 2010), and *Alnus* temperate and tropical forests (Kennedy et al. 2011). However, based on basidiocarp collections, only *T. chlorine* (Massee) G. Cunn., *T. ferruginea* (Pers.) Pat., *T. griseoumbrina* Litsch., *T. pilosa* (Burt) Bourdot & Galzin, *T. subsaccicola* M.J. Larsen, and *T. umbrinospora* M.J. Larsen have been detected in Mexico (Welden et al. 1979; Urbizu et al. 2004; Contreras-Pacheco 2008; Contreras-Pacheco et al. 2014).

In our laboratory, we study the diversity, ecology, and associations of ECM fungi residing in Neotropical dry forests along the Pacific coast of Mexico. In this seasonal ecosystem, the /tomentella-thelephora lineage has been shown to be dominant in the ECM community, consisting of species new to science (Ramírez-López et al. 2015). Here, we describe a new species, *Tomentella brunneoincrustata,* including its basidiocarp morphology, mycorrhizal anatomy, ecology, and host associations. Because knowledge regarding *Tomentella* in Mexico is scarce, we also provide the first phylogenetic analysis of the diversity of this genus in this country.

Materials and methods

Study site The study was conducted at the Chamela-Cuixmala Biosphere Reserve (N 19°30', W 105°03') in

Jalisco, Mexico (Fig. 1), where the principal type of vegetation is tropical dry forest, and the tropical sub-deciduous forest is restricted to creeks and streams. During the summer, the weather is sub-humid and warm, whereas it is dry in the winter. The tropical dry forest exhibits water stress for 8 months, and the rainy season usually extends from July to October, which coincides with hurricane season. The average annual precipitation is 784.8 mm (1977–2011), and the average annual temperature is 24.6 °C, with an average maximum and minimum of 30.3 °C and 19.5 °C, respectively. The atmospheric humidity is >65 % during the rainy season (Bullock 1986; García-Oliva et al. 1995).

Sampling The reserve was accessed during the rainy season each year from 2012 through 2014, and opportunistic sporocarp sampling of ectomycorrhizal species was conducted according to O'Dell et al. (2004). Root tips were sampled with soil cores (PVC tubes 30 × 5 cm; ~589 cm^3 of soil) under suspected ectomycorrhizal hosts. The ECM were separated from the roots by carefully washing of the soil with tap water into a sieve. All the ECM were then isolated using a stereomicroscope. The ECM were fixed in 96 % ethanol and stored at 4 °C for a maximum of 2 weeks until further processing. All of the morphotypes were photographed prior to the anatomical analysis. The root tips were mounted in Paraplast (Leica Biosystems, Buffalo Grove, IL, USA); the anatomical slices were performed with a rotation microtome, and then mounted and stained in permanent preparations according to Sandoval-Zapotitla (2005). The ECM morphotypes were described after fixation, based on morphological and anatomical characteristics according to Agerer and Rambold (2004–2015).

Morphological data The macroscopic characteristics of the sporocarps were determined based on fresh material, and the color was determined according to the Munsell soil color charts (Munsell Color Company 1954). The microscopic characteristics of the fruit body vouchers were observed using tissue rehydrated in 2.5 % KOH by Nomarski Interference Contrast with an Olympus BX51 microscope. All of the measurements of basidia ($n = 10$), basidiospores ($n = 30$), and hyphae ($n = 30$) were performed using 1000× KOH preparations. We calculated the length/width ratio (Q), average (Q), average length (L) and average width (W) of the spores. The spore ornamentation was observed using a scanning electron microscope (JEOL JSM-5310LV).

Molecular procedures When sufficient material was collected from a given ECM morphotype, a 1–2 mm section was used to extract DNA with the XNAP kit (Sigma-Aldrich Corp., St. Louis, MO, USA). DNA was extracted from the sporocarps using the same protocol as that used for the ECM. We amplified the nuclear ribosomal internal transcribed spacer (nrITS) region by polymerase chain reaction (PCR) with the ITS1F/ITS4 primer pair (Gardes and Bruns 1993) using RubyTaq PCR Master Mix (Affymetrix, Inc., Santa Clara, CA, USA). DNA extraction and PCR were performed as described by Garibay-Orijel et al. (2013). To identify the host plant from the root tips, we amplified the *rbcL* and *trnL* regions using the *rbcL-a*F/*rbcL-a*R and trnC/trnD primer pairs (Kress and Erickson 2007). All of the PCR products were observed in 1 % agarose gels stained with GelRed (Biotium, Hayward, CA, USA). Amplicons of the appropriate size were cleaned with ExoSAP-IT (Affymetrix, Inc.). DNA sequences were generated in both directions using PCR primers and

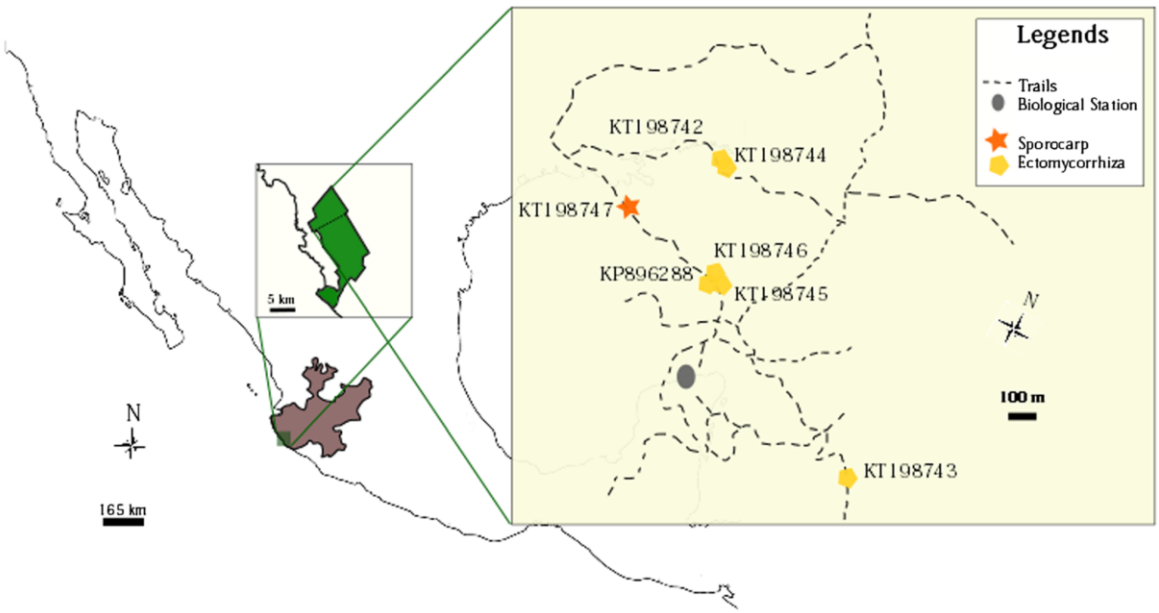

Fig. 1 Location of the Chamela-Cuixmala Biological Reserve, and distribution of the holotype fruit body and ectomycorrhizae of *Tomentella brunneoincrustata*. Samples are indicated by their GenBank accession numbers

BigDye Terminator v3.1 chemistry at the "Laboratorio de Secuenciación Genómica de la Biodiversidad y de la Salud" at the UNAM Biology Institute with an ABI PRISM 3100 genetic analyzer (Applied Biosystems, Foster City, CA, USA).

Bioinformatics The DNA sequences were edited and assembled using Geneious 6.1.4 software (Biomatters Ltd., Auckland, New Zealand). The plant hosts were identified by comparing the DNA sequences with those available in the BOLD Systems genetic barcode database. The identity of the fungal DNA sequences was assessed by phylogenetic analysis. First, we compared the sequences obtained in the present study against those in the GenBank and UNITE databases and downloaded all of the best matches (≥90 % similarity). We included all the tropical /tomentella-thelephora sequences from fruit body vouchers like those from the Seychelles (Suvi et al. 2010) and Benin (Yorou et al. 2011). We also selected environmental samples of /tomentella-thelephora from the Neotropics in GenBank and included *Tomentella* fruit body voucher sequences collected throughout Mexico in recent years by our laboratory (Table S1). The alignment was performed using MAFFT v7 (http://mafft.cbrc.jp/alignment/server/) and revised it manually with Mesquite v2.75. The molecular phylogenetic analyses included a Bayesian analysis that was performed using MrBayes v3.2.2 with 4 MCMC, 5 million generations, and three partitions (ITS1, 5.8S, ITS2). To select the best substitution model for each partition, we performed a reversible-jump Markov chain Monte Carlo computation (Pagel and Meade 2006) with *Thelephora terrestris* as the external group. We generated the consensus tree, adding posterior probabilities on the branches (≥0.75), and the nodes were depicted in decreasing order with FigTree v1.0.4.

Results

The ITS sequences of the six selected root tips and one sporocarp had an overall nucleotide sequence similarity of 98.3 %. The collection sites of these samples were widely distributed across the tropical dry forest of Chamela (Fig. 1). The Bayesian analysis grouped these sequences into a clade together with an ECM sequence from Dominica (JX548248), with high support (BPP = 1). The sequence from Dominica demonstrated an overall nucleotide sequence similarity of 96.8 % with the samples representing *T. brunneoincrustata*, and it contained 12 unique single-nucleotide polymorphisms (SNPs) (Table S2). This clade, together with two clades consisting of environmental samples of ECM from subtropical forests in Florida and tropical dry forests in Puerto Rico, made up the "Pisonieae-associated Neotropical *Tomentella* clade" (Fig. 2). Analysis of the *rbcL* and *trnL* sequences from the ECM revealed that five of the ectomycorrhizae were associated with a member of the Pisonieae tribe in the Nyctaginaceae and that one was associated with *Pisonia* sp. (Table 1). The sister clades from Puerto Rico and Florida were also associated with hosts in the Nyctaginaceae family (Fig. 2). Our samples belong to an undescribed clade with unique morphological and ecological characteristics, which is described here as the new species *Tomentella brunneoincrustata*.

The Bayesian analysis revealed that the *Tomentella* fruit body vouchers collected in temperate forests of Mexico belong to clades with species inhabiting temperate forests worldwide. KC152246 and KT353045 are related to *T. atramentaria* from the USA, Estonia, and Austria; KT353044 and KC152245 are a sister group of *T. pilosa* from Estonia and Sweden; KT353054 and UDB018512 formed a group with *T. muricata* from Estonia and Finland; KT353055 is related to *T. fuscocinerea* from Iran; KT353058 is a sister group of *T. stuposa* from Austria; KC152248 is related to *T. punicea* from China; and KT353052 is similar to *T. atroarenicolor* from Russia. We also found that KT353049, KT353048, and KT353047 are sister groups of *T. bryophila* from Scotland and Canada; however, this species is paraphyletic. The same case was found for KT353051, which is related to *T. lateritia* from Italy. Five fruit body vouchers had unique sequences (i.e. KC152247, KT353046, KT353056, KT353057, and KT353050) that formed independent and unknown clades of *Tomentella*.

Taxonomy

Tomentella brunneoincrustata M. Villegas & Contreras-Pacheco, sp. nov.

MycoBank: MB814303

Diagnosis Basidiome resupinate, crustose, thin, adherent to the substrate, dark brown, undifferentiated sterile margin, without rhizomorphs. Subicular hyphae dimitic, dark brown or purple brown; basidia subclavate, tetrasporic, clamped at base, rarely with transverse septa. Basidiospores subglobose to ellipsoid, dark brown, (6) 6.0–7.5 (8) × 5.5–6.5 μm; ornamentation echinulate, frequently bi- or trifurcate. Inhabiting soil and dead wood on tropical dry forests, forming ectomycorrhizae with different members of the Nyctaginaceae family. HOLOTYPE: Álvarez-Manjarrez 152b, (MEXU 27661).

Basidiome resupinate, thin, less than 1 mm thick, crustose, mostly continuous, indeterminate edges with patches around, strongly adherent to the substrate; hymenium dark brown (2.5/2–3/7.5 YR Munsell), smooth to the naked eye, densely tomentose and iridescent when seen under a dissection microscope, turns darker in 2.5 % KOH; subiculum concolorous

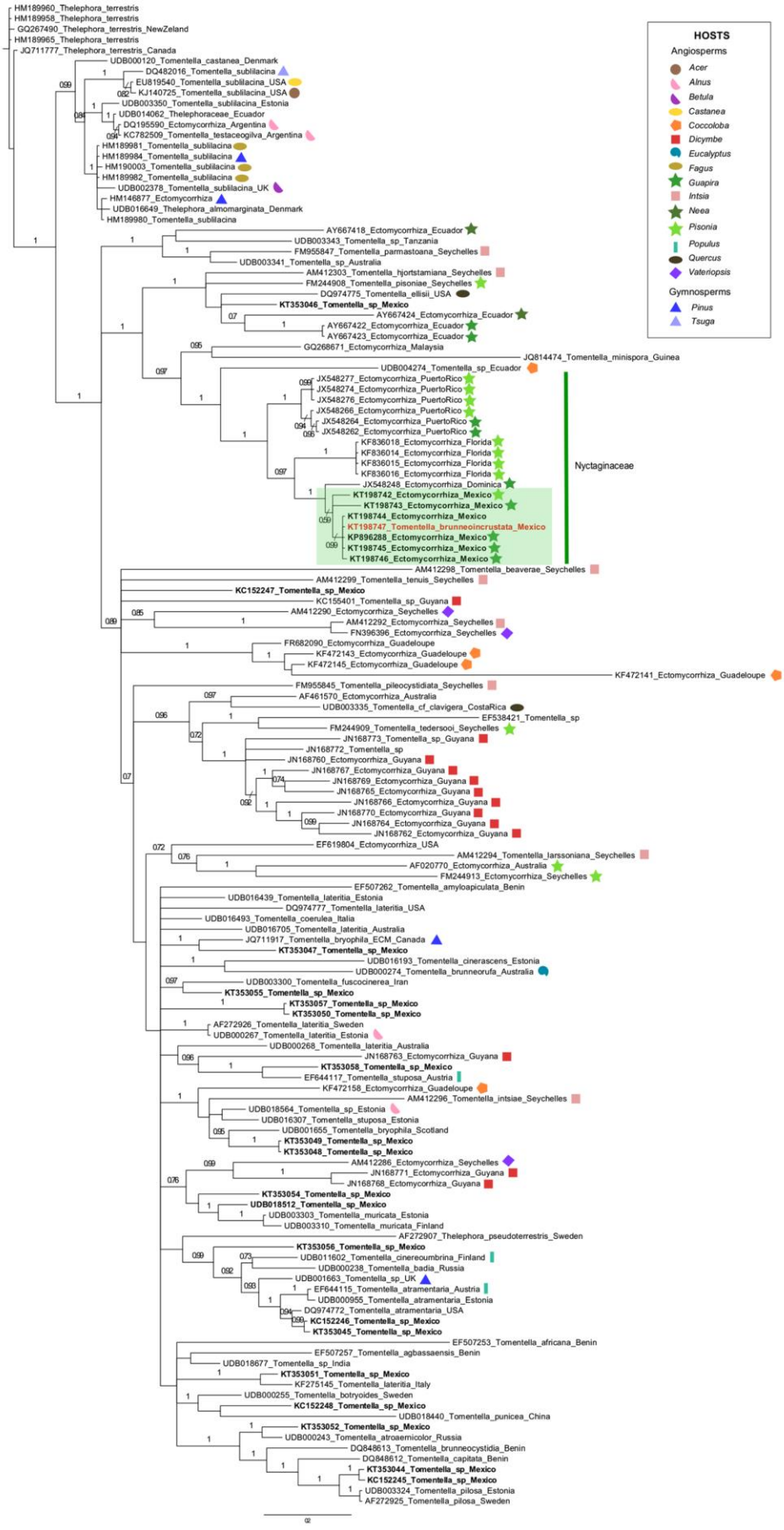

Fig. 2 Phylogenetic Bayesian analysis of vouchers and environmental samples of *Tomentella* and its host preferences. The sequences from *Tomentella brunneoincrustata*, including the ectomycorrhizae and the holotype, are shown in *bold* in a *green square.* The terminals indicate the regions where they were collected; sequences from environmental samples are labeled as "ectomycorrhiza" and sequences of *Tomentella* vouchers are labeled with the species names. The symbols indicate the host family: Aceraceae (*circle*), Betulaceae (*half-round*), Dipterocarpaceae (*diamond*), Fabaceae (*square*), Fagaceae (*oval*), Myrtaceae (*spiral*), Nyctaginaceae (*star*), Pinaceae (*triangle*), Polygonaceae (*pentagon*) and Salicaceae (*bold line*)

Table 1 BLAST identification of the ECM host *rbcL* and *trnL* regions

Sample type	Accession number GenBank	rbcL BLAST results		*trnL* BLAST results		Host
		% Id	Match	% Id	Match	
ECM	KT906429	100	*Pisonia aculeata* (KJ594427)	–	–	Pisonieae sp.
ECM	KT906430		*Neea psychotrioides* (JQ592987)	–	–	
ECM	KT906431		*Guapira standleyana* (GQ981748)	–	–	
ECM	KT906428			–	–	
ECM	KT906427					
ECM	KT906432			95	*Pisonia albida* (JX8444286)	*Pisonia* sp.

with the hymenium, undifferentiated sterile margin, rising slightly from the substrate; rhizomorphs absent (Fig. 3a).

Subicular hyphae consisting of two types: a) very common generative hyphae, dark brown in 2.5 % KOH, 3.2–5.1 (6.3) μm wide, thick-walled (up to 1 μm), clamped, branched mostly at right angles, with irregular swellings of up to 20 μm in some hyphae, anastomoses not observed, hyphae not congophilous, not cyanophilous and not amyloid (Fig. 3b); b) infrequent hyphae with simple septa, purple-brown, thin-walled, sometimes dichotomously branched, 1.8–3.3 μm wide, very ornamented on the surface with fine crystals insoluble in 2.5 % KOH, and not cyanophilous (Fig. 3c).

Subhymenial hyphae consisting of swollen cells with irregular forms, 4.2–11.1 μm wide, thick-walled (up to 1 μm), clamped, dark brown to light brown in 2.5 % KOH, and not congophilous or cyanophilous. Immature basidia dark brown in 2.5 % KOH, clavate, sphaeropedunculate or napiform, clamped and thick-walled; mature basidia 29.1–37.5 × 9.26–15.8 μm, subclavate, four sterigmata (5–7 μm), slightly thickened wall at the base and thin wall at the apex, light brown in 2.5 % KOH, clamped at the base, rarely exhibiting

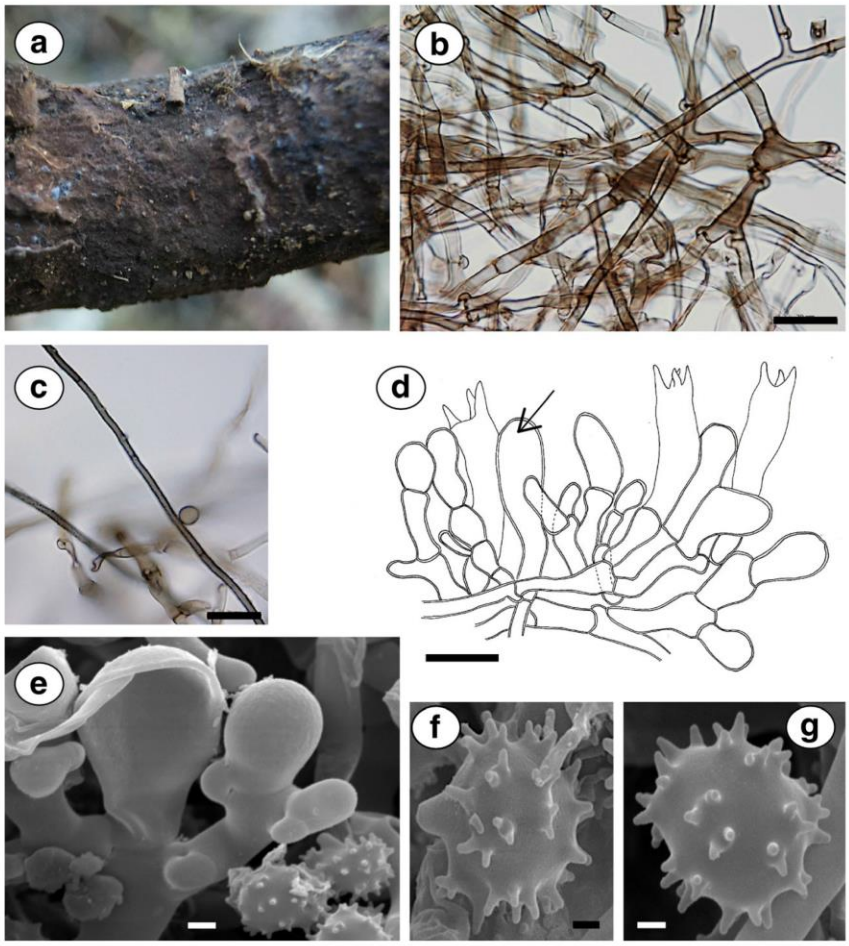

Fig. 3 *Tomentella brunneoincrustata* holotype (Alvarez-Manjarrez 152b). **a** Resupinate basidiome; **b** generative hyphae of subiculum with irregular swellings; **c** ornamented hyphae of subiculum; **d** sub-hymenium hyphae, immature basidia (*arrow*) and tetrasporic basidia; **e** SEM of young basidia with clamp at the base; f, g SEM of basidiospores in lateral and basal view showing obtuse hilar appendix and bi- or trifurcate ornamentation. Scale bars: **b**, **c** = 20 μm; **d** = 15 μm; **e** = 3 μm; **f**, **g** = 1 μm

transverse septa, and most septa collapsed (Fig. 3d, e). **Basidiospores** (6) 6.0–7.5 (8) × 5.5–6.5 μm (Q = 1.1–1.3 μm, Q = 1.1 μm, L = 6.8 μm, W = 6.1), in front view, subglobose to ellipsoid, some slightly lobed, dark brown in 2.5 % KOH, slightly thickened wall and echinulate, not congophilous, not cyanophilous, not amyloid. In SEM, spores showed an obtuse hilar appendix, 1–1.5 × 1.2–1.5 μm; echinulate ornamentation frequently bi- or trifurcate, 1–1.2 × 0.5–1 μm, with rounded or sub-rounded tips (Fig. 3f, g).

Remarks This species is characterized by a thin basidiome that is crustose and strongly attached to the substrate; subiculum concolorous with the hymenium, undifferentiated and sterile margin; two types of subiculum hyphae, of which the ornamented one does not present clamps; and small globose to ellipsoid spores (<8 μm). Among the tropical species described in the literature, this species is similar only to *Tomentella minispora* Yorou et al. (2012a) from Guinea, which also possess basidiomes, strongly attached to the substrate basidiomes, no rhizomorphs, clamps on both hyphae and basidia, ornamentation on the surface of some hyphae, and has a similar spore size. Despite this apparent similarity, *T. minispora* displays important differences, such as the presence of a differentiated sterile margin with clearer pigmentation, hyphae from the subiculum that are thin-walled or slightly thickened, hyphae ornamentation that is present only on the subhymenium, and spore ornaments that are never bi- or trifurcated.

Etymology From the Latin *brunneus* and *incrustata*, in reference to the brown color of the basidiome and extracellular incrustations on the hyphae of the subiculum.

Habit, habitat, and distribution This species develops in tropical dry forests in which it associates with hosts in the Pisonieae tribe within the Nyctaginaceae.

Specimens examined HOLOTYPE: Mexico, Jalisco, La Huerta municipality, Estación de Biología de Chamela, Tejón sidewalk, 19°30' N, 105°39' W, 26 Nov 2014, Álvarez-Manjarrez 152b, (MEXU 27661).

Anatomical description of the ectomycorrhizae

Tomentella brunneoincrustata + *Pisonieae sp.*

Ectomycorrhiza sinuous with monopodial ramifications and rounded tips. Completely black with emanating black and erect hyphae (Fig. 4a, b). **Mantle** thick and partially shiny, with 12–16 hyphal layers consisting of three different conformational structures. **External mantle** black, emanating hyphae septate with clamps, thick walls (>1 μm), and rounded terminations. **Internal mantle** has clearer hyphae in comparison with the remaining mantle, hyphae epidermoid or irregular (4–11 × 4–13 μm). **Hartig net** is prominent, peri-epidermal, enclosing the epidermal and the first cortical cell layer, infrequently lobulated (Fig. 4c, d).

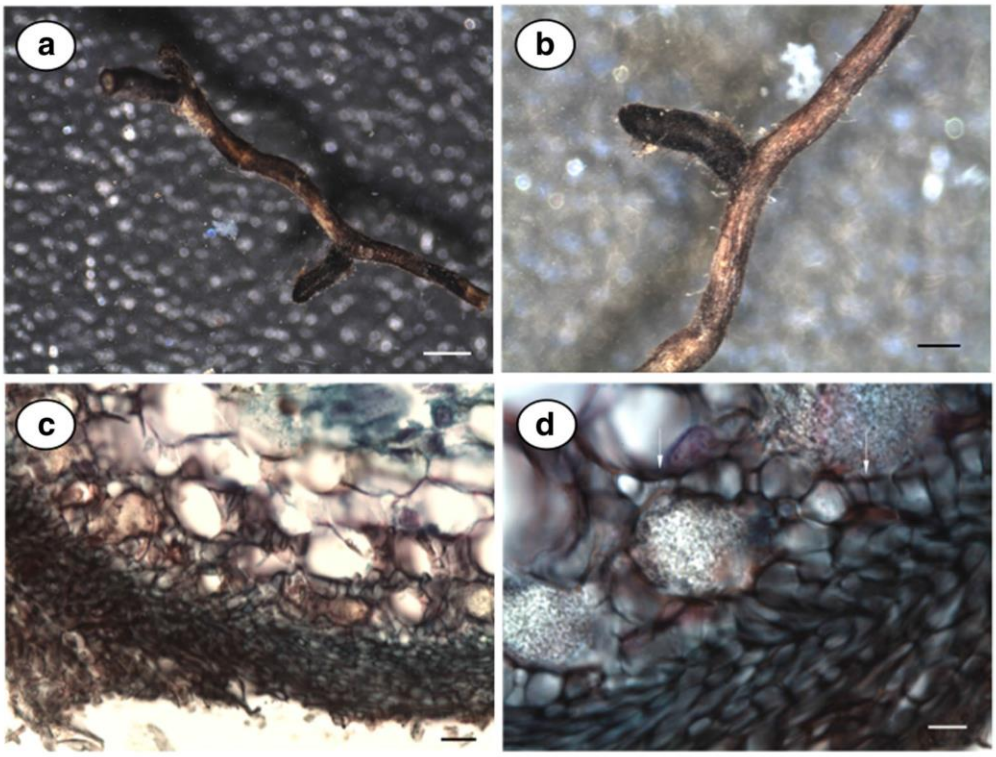

Fig. 4 **a-b** Ectomycorrhiza of *Tomentella brunneoincrustata* associated with Pisonieae sp. **c** Transversal section of an ectomycorrhizal tip showing the hyphal layer of the mantle and the peri-epidermal Hartig net. **d** Detail of the Hartig net, with *arrows* indicating the peri-epidermal hyphae. Scale bars: **a** = 0.5 mm; **b** = 0.25 mm; **c** = 75 μm; **d** = 4.5 μm

Tomentella brunneoincrustata + *Pisonia sp.*

Ectomycorrhiza sinuous with monopodial ramifications and rounded tips. Mantle black and extremely dense, tomentose-granulose surface and emanating hyphae dark in color. Hyphae more abundant and larger at the base of the ECM (Fig. 5a, b). **Mantle** with 10–17 hyphal layers (46–72 μm), resembling divergent lamellar trama. **External mantle** presents cylindrical, emanating straight hyphae (2–4 × 7–19 μm) with dark septa and a wide wall (<1 μm). **Internal mantle** has epidermoid lighter-coloured hyphae (4–8 × 3–7 μm). **Hartig net** hyaline, infrequently lobed, penetrating more than 1 cortical cell (Fig. 5c, d).

Considerations This species forms very similar morphotypes with different Nyctaginaceae hosts, consisting of a black, dense mantle with short exploration type (Agerer 2001) and with monopodial ramifications. The Hartig net is prominent, peri-epidermal, and infrequently lobulated.

Discussion

Tomentella brunneoincrustata produces dark brown fruit bodies that are somewhat similar to those of *T. agbassaensis* Yorou, *T. amyloapiculata* Yorou, *T. guineensis* Yorou, *T. guinkoi* Yorou, *T. minispora* Yorou, *T. afrostuposa* Yorou, and *T. intsiae* Suvi & Kõljalg. Another important characteristic of *Tomentella brunneoincrustata* is its adherence to the substrate and absence of rhizomorphs, both of which are observed in *T. amyloapiculata, T. guineensis, T. guinkoi, T. minispora,* and *T. intsiae*. This new species exhibits greater similarity to *T. minispora* and *T. afrostuposa* due to a common arachnoid subiculum, hymenia exhibiting the same color, and some sub-hymenial hyphae with incrustations. The size of the spores coincides with that of *T. minispora*. Nonetheless, *T. brunneoincrustata* presents unique characteristics: a diffuse concolorous margin, non-cyanescent subiculum hyphae, hyphal ornamentation that is present only on the subiculum, and spore ornaments that are bifurcate or trifurcated.

The fruit body of the holotype was found on the underside of a piece of wood without evident rotting. *Odontia,* the sister genus of *Tomentella*, has been reported to be saprotrophic (Tedersoo et al. 2014). However, *T. brunneoincrustata* forms ECM and belongs to an ectomycorrhizal clade that is associated with the Pisonieae tribe from the Nyctaginaceae. This is the first study to describe a *Tomentella* species from the Neotropics, including its ectomycorrhizae. The ECM of this species displayed a dense, dark brown mantle; the Hartig net was found to be peri-epidermal and very prominent in both morphotypes. This species shares only the dark mantle with the *Tomentella* EMC morphotypes described by Jakucs and Erõs-Honti (2008) and Jakucs et al. (2015). The ECM of this species exhibits greater similarity to the one described for the *Guapira* ECM from Ecuador (Haug et al. 2005), which shares the prominent Hartig net. However, *T. brunneoincrustata* develops a mantle wrapping the root tips completely, with the Hartig net penetrating two cell layers.

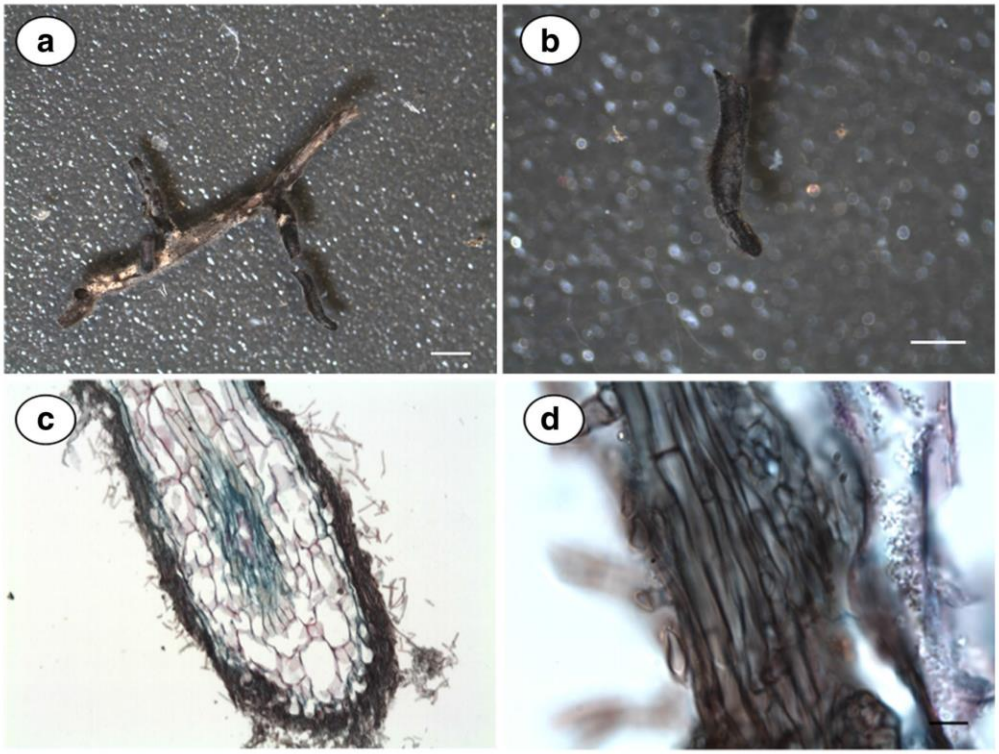

Fig. 5 **a-b** Ectomycorrhiza of *Tomentella brunneoincrustata* associated with *Pisonia* sp. **c** Transversal section of the ectomycorrhizal tip (10×). **d** Detail of the dark mantle. Scale bars: **a** = 1.0 mm; **b** = 0.5 mm; **d** - 4.5 μm

In phylogenetic analysis, the sequence of the ECM from Dominica exhibited the closest similarity to those from *T. brunneoincrustata* (96.3 % similarity). However, according to the 97 % similarity consensus to form MOTUs of ECM fungi (Nilsson et al. 2008; Peay et al. 2008; Setaro et al. 2012) and the UNITE species hypothesis of 98 % (Kõljalg et al. 2013), this sequence is not included with *T. brunneoincrustata*.

Although genetic markers that are recognized as genetic barcodes for plants were used for host identification, we were able to identify only one host to genus level, *Pisonia* sp., according to the list of plants from Chamela (Lott 1993). The reserve contains 13 species from 8 genera of Nyctaginaceae; *Guapira petenensis* is the unique species in this genus, while *Pisonia* has two species, *P. aculeata* and *P. macranthocarpa*.

The association of /tomentella-thelephora with Pisonieae has been reported in several regions throughout the world: Dominica, Ecuador, Florida, Hawaii, Puerto Rico, Rota, the Seychelles, and Vieques (Haug et al. 2005; Hayward and Horton 2012, 2014; Suvi et al. 2010, Tedersoo et al. 2010b). Bayesian analysis showed that several paraphyletic clades within the lineage /tomentella-thelephora are associated with Pisonieae across the tropical regions of the world. However, the ECM sequences from Puerto Rico, Florida, Dominica, and Mexico constitute the "Pisonieae-associated Neotropical *Tomentella* clade", which is monophyletic and inhabits tropical dry and subtropical forests of the Neotropics, especially the Mesoamerican and Caribbean regions. The specificity of this fungal clade to the Pisonieae supports the hypothesis of partner choice phylogenetic trait conservation proposed by Hayward and Horton (2014).

The Pisonieae tribe includes three ectomycorrhizal genera: *Guapira, Neea,* and *Pisonia*. *Neea* and *Guapira* are paraphyletic groups (Hayward and Horton 2014), both of which are exclusive to tropical forests in Mexico, Central America, and South America (Douglas and Manos 2007). There are three *Guapira* species, eight *Neea* species, and five *Pisonia* species in Mexico. These species are distributed in 25 of the 32 Mexican states, among which Chiapas exhibits the greatest diversity, with 13 spp., followed by the Yucatan Peninsula with 11 spp. Given that *T. brunneoincrustata* is associated with two of these genera, there is a high probability that this species, or other undescribed species within the Pisonieae-associated Neotropical clade, has a wider distribution within the Neotropics. More systematic sampling of the entire area is needed to understand the biology, ecology, and diversity of *Tomentella* in the Neotropics.

Given the distribution and ecosystem preferences of the Pisonieae-associated Neotropical *Tomentella* clade, it is likely that this clade is associated with water stress conditions, such as in those present in the Chamela tropical dry forest. The samples from Puerto Rico and Dominica were also obtained from tropical dry forests (Hayward and Horton 2014). In Puerto Rico, the mean temperature is 29.7 °C, with a maximum of 32.4 °C, a minimum of 14.6 °C, and mean annual precipitation of 1687 mm. The distribution of water resources is critical in the Caribbean islands, and similar patterns are observed in different islands (Daly et al. 2003), such as Dominica. Even the samples from Florida inhabited a subtropical region with an average temperature of 23.8 °C and average rainfall of approximately 1524 mm per year, 75 % of which occurred from June through October, coinciding with hurricane season (Multer and Hoffmeister 1968). Thus, all of the members of this clade seem to develop in (sub)tropical areas with high temperatures and heterogeneous rainfall regimes that are unevenly distributed throughout the year.

Six species of *Tomentella* have been reported in Mexico; however, the Bayesian analysis revealed a large diversity of *Tomentella* species, some of which are related to known taxa, and many others which are likely new species. The *Tomentella* fruit body vouchers from temperate forests in Mexico that were included in the analysis showed greater genetic similarity with species from temperate climates than those from tropical climates. These results are consistent with the biology of the species and its host associations. Hayward and Horton (2014) noted that when *Neea buxifolia* and *Pisonia aculeata* were planted in New York soil, in which local thelephoroids were available, the plants failed to form ECM with the local species. The Nearctic and Neotropical biotas coincide in Mexico (Estrada-Contreras et al. 2015), and even if the vegetation types are similar (e.g., the transitions of pine-oak forest, montane cloud forest, tropical dry forest, and sand dunes), temperate and tropical tree species do not intermix, enabling a high diversity of many biological groups.

This is the first study to analyze the diversity of *Tomentella* in Mexico. The phylogenetic analysis presented here will help to guide future investigations designed to identify and describe the *Tomentella* species in this region. However, given the vast diversity and complexity of the genus in this country, a complete knowledge of its diversity and ecology is a long-term task that would require the participation of several research groups.

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ANEXO 2. Fungal diversity notes 1153–1267: taxonomic and phylogenetic contributions to fungal taxa

Resumen

Esta es la onceava contribución en la serie de Notas de Diversidad Fúngica sobre la taxonomía fúngica, donde se recolectaron materiales de muchos países, se examinaron y describieron utilizando los métodos de morfología, anatomía, cultivo de cepas, combinados con análisis de secuencias de DNA. Se describen nuevos taxones, que incluyen seis nuevos géneros, 97 nuevas especies, seis nuevas combinaciones, un sinónimo, un nuevo huésped, una nueva especie secuenciada y tres nuevos registros que se acomodaron en 41 familias y 1 *incertae sedis* en Dothideomycetes. Los nuevos géneros son *Amyloceraceomyces, Catenuliconidia, Hansenopezia, Ionopezia, Magnopulchromyces* y *Pseudothaxteriellopsis*. Las nuevas especies son *Amyloceraceomyces angustisporus, Amylocorticium ellipsosporum, Arthrinium sorghi, Catenuliconidia uniseptata, Clavulina sphaeropedunculata, Colletotrichum mangiferae-indicae, C. parthenocissicola, Coniothyrium triseptais cusp. subsanguineus, C. xiaojinensis, Diaporthe pimpinellae, Dictyosporella guizhouensis, Diplodia torilicola, Fuscoporia marquesiana, F. semiarida, Hansenopezia decora, Helicoarctatus thailandicus, Hirsutella hongheensis, Humidicutis brunneovinacea, L. variabilis, Lycoperdon lahorense, L. pseudocurtisii, Magnopulchromyces scorpiophorus, Moelleriella gracilispora, Neodevriesia manglicola, Neodidymelliopsis salvia, N. urticae, Neoroussoella magnoliae, Neottiella Gigaspora, Nigrograna thailandica, Ophiosphaerella chiangraiensis, Phaeotremella yunnanensis, Podosphaera yulii, Preussia cucurbitae, Pseudothaxteriellopsis obliqus, Rigidoporus juniperinus, Rhodofomitopsis pse udofeei, Russula benghalensis, Scleroramularia pauciseptata, S. sanyaensis, S. vermispora, Scytinopogon minisporus, Sporormurispora paulsenii, Tomentella asiae-orientalis, T. atrobadia, T. atrocastanea, T. aureo-marginata, T. brevis, T. brevis, T. brevis, T. brevis . brunneoflava, T. brunneogrisea, T. capitatocystidiata, T. changbaiensis, T. citrinocystidiata, T. coffeae, T. conclusa, T. cystidiata, T. dimidiata, T. duplexa, T. efibulata, T. efibulis, T . farinosa, T. flavidobadia, T. fuscocrustosa, T. fuscofarinosa, T. fuscogranulosa, T.*

fuscopelliculosa, T. globospora, T. gloeocystidiata, T. griseocastanea, T. griseofusca, T. griseomarginata, T. inconspicua, T. incrustata , T. interrupta, T. liaoningen-sis, T. longiaculeifera, T. longiechinuli, T. megaspora, T. olivacea, T. olivaceobrunnea, T. pallidobrunnea, T. pallidomarginata, T. parvispora, T. pertenuis, T. qingyuanensis , T. segregata, T. separata, T. stipitata, T. storea, Trichoderma ceratophylletum, Tyromyces minu-tulus, Umbelopsis heterosporus y *Xylolentia reniformis.* Las nuevas combinaciones son *Antrodiella descendena, Rhodofomitopsis monomitica, Rh. oleracea, Fuscoporia licnoides, F. scruposa, Ionopezia gerardii.* Se reporta un sinónimo*, Chloridium macrocladum (= Gonytrichum mac-rocladum)*, un nuevo hospedero, *Aplosporella prunicola*, una nueva especie secuenciada *Graphis supracola* y tres nuevos registros*, Paradictyoarthrinium diffractum, Prosthemium betulinum* y *Golovinomyces monardae*.

Fungal diversity notes 1153–1267: taxonomic and phylogenetic contributions to fungal taxa

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Abstract

This is the eleventh contribution in the Fungal Diversity Notes series on the fungal taxonomy, where materials were collected from many countries, examined and described using the methods of morphology, anatomy, strain culture, combined with DNA sequence analyses. Novel taxa are described, including six new genera, 97 new species, six new combinations, one synonym, one new host, one new sequenced species and three new records which accommodated in 41 families and 1 incertae sedis in Dothideomycetes. The new genera are

Amyloceraceomyces, *Catenuliconidia*, *Hansenopezia*, *Ionopezia*, *Magnopulchromyces* and *Pseudothaxteriellopsis*. The new species are *Amyloceraceomyces angustisporus*, *Amylocorticium ellipsosporum*, *Arthrinium sorghi*, *Catenuliconidia uniseptata*, *Clavulina sphaeropedunculata*, *Colletotrichum mangiferae-indicae*, *C. parthenocissicola*, *Coniothyrium triseptatum*, *Cortinarius indorusseus*, *C. paurigarhwalensis*, *C. sinensis*, *C. subsanguineus*, *C. xiaojinensis*, *Diaporthe pimpinellae*, *Dictyosporella guizhouensis*, *Diplodia torilicola*, *Fuscoporia marquesiana*, *F. semiarida*, *Hansenopezia decora*, *Helicoarctatus thailandicus*, *Hirsutella hongheensis*, *Humidicutis brunneovinacea*, *Lentaria gossypina*, *L. variabilis*, *Lycoperdon lahorense*, *L. pseudocurtisii*, *Magnopulchromyces scorpiophorus*, *Moelleriella gracilispora*, *Neodevriesia manglicola*, *Neodidymelliopsis salvia*, *N. urticae*, *Neoroussoella magnoliae*, *Neottiella gigaspora*, *Nigrograna thailandica*, *Ophiosphaerella chiangraiensis*, *Phaeotremella yunnanensis*, *Podosphaera yulii*, *Preussia cucurbitae*, *Pseudothaxteriellopsis obliqus*, *Rigidoporus juniperinus*, *Rhodofomitopsis pseudofeei*, *Russula benghalensis*, *Scleroramularia pauciseptata*, *S. sanyaensis*, *S. vermispora*, *Scytinopogon minisporus*, *Sporormurispora paulsenii*, *Tomentella asiae-orientalis*, *T. atrobadia*, *T. atrocastanea*, *T. aureomarginata*, *T. brevis*, *T. brunneoflava*, *T. brunneogrisea*, *T. capitatocystidiata*, *T. changbaiensis*, *T. citrinocystidiata*, *T. coffeae*, *T. conclusa*, *T. cystidiata*, *T. dimidiata*, *T. duplexa*, *T. efibulata*, *T. efibulis*, *T. farinosa*, *T. flavidobadia*, *T. fuscocrustosa*, *T. fuscofarinosa*, *T. fuscogranulosa*, *T. fuscopelliculosa*, *T. globospora*, *T. gloeocystidiata*, *T. griseocastanea*, *T. griseofusca*, *T. griseomarginata*, *T. inconspicua*, *T. incrustata*, *T. interrupta*, *T. liaoningensis*, *T. longiaculeifera*, *T. longiechinuli*, *T. megaspora*, *T. olivacea*, *T. olivaceobrunnea*, *T. pallidobrunnea*, *T. pallidomarginata*, *T. parvispora*, *T. pertenuis*, *T. qingyuanensis*, *T. segregata*, *T. separata*, *T. stipitata*, *T. storea*, *Trichoderma ceratophylletum*, *Tyromyces minutulus*, *Umbelopsis heterosporus* and *Xylolentia reniformis*. The new combinations are *Antrodiella descendena*, *Rhodofomitopsis monomitica*, *Rh. oleracea*, *Fuscoporia licnoides*, *F. scruposa*, *Ionopezia gerardii*. A synonym, *Chloridium macrocladum* (= *Gonytrichum macrocladum*), a new host, *Aplosporella prunicola*, a new sequenced species *Graphis supracola* and three new records, *Paradictyoarthrinium diffractum*, *Prosthemium betulinum* and *Golovinomyces monardae*, are reported.

Keywords Agaricomycetes · Ascomycota · Basidiomycota · Mucoromycota · New combination · New genus · New species · Phylogeny · Taxonomy

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1251. ***Tomentella liaoningensis*** H.S. Yuan & Y.C. Dai, ***sp. nov.***
1252. ***Tomentella longiaculeifera*** H.S. Yuan & Y.C. Dai, ***sp. nov.***
1253. ***Tomentella longiechinuli*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***
1254. ***Tomentella megaspora*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***
1255. ***Tomentella olivacea*** H.S. Yuan & Y.C. Dai, ***sp. nov.***
1256. ***Tomentella olivaceobrunnea*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***

1257. ***Tomentella pallidobrunnea*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***
1258. ***Tomentella pallidomarginata*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***
1259. ***Tomentella parvispora*** H.S. Yuan & Y.C. Dai, ***sp. nov.***
1260. ***Tomentella pertenuis*** H.S. Yuan & Y.C. Dai, ***sp. nov.***
1261. ***Tomentella qingyuanensis*** H.S. Yuan & Y.C. Dai, ***sp. nov.***
1262. ***Tomentella segregata*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***
1263. ***Tomentella separata*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***
1264. ***Tomentella stipitata*** H.S. Yuan, X. Lu & Y.C. Dai, ***sp. nov.***
1265. ***Tomentella storea*** H.S. Yuan & Y.C. Dai, ***sp. nov.***

Trechisporales K.H. Larsson
Clavariaceae Chevallier, Flore Générale des Environs de Paris: 102 (1826)
1266. ***Scytinopogon minisporus*** J. Alvarez-Manjarrez, M. Villegas-Ríos & R. Garibay-Orijel, ***sp. nov.***

Tremellomycetes

Tremellales Fr.
Phaeotremellaceae A.M. Yurkov & Boekhout, Stud. Mycol. 81: 137 (2015)
1267. ***Phaeotremella yunnanensis*** L.F. Fan, F. Wu & Y.C. Dai, ***sp. nov.***

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Trechisporales K.H. Larsson

Notes: The order *Trechisporales* was proposed by Larsson (2007) and accepted in Agaricomycetes based on phylogenetic analysis (Binder et al. 2005; Larsson et al. 2004; Matheny et al. 2007). It includes stipitate, clavariod and resupinate genera with smooth, hydnoid, grandiniod or poroid hymenia. Hyphae with clamps, forming a monomitic system, and the subicular hyphae with or without ampullate septa. Basidia have four to six sterigmata, and their basidiospores are smooth or ornamented. Some species have cystidia. They grow mostly on wood or soil (Hibbett et al. 2007).

Clavariaceae Chevallier, Flore Générale des Environs de Paris: 102 (1826)

Notes: The family *Clavariaceae* was proposed by Chevallier (1826), and phylogenetic analysis included a variety of fruitbody shapes: species with simple clubs, coralloid, hydnoid, stipitate with lamella and resupinate. The genus type is *Clavaria*, recently discovered as paraphyletic (Birkebak et al. 2013). Other genera included in this family are *Camarophyllopsis*, *Clavulinopsis*, *Clavicorona*, *Hyphodontiella*, *Mucronella*, *Ramariopsis*, *Scytinopogon* and *Setigeroclavula*. However, *Scytinopogon* is related to *Trechispora* which is included in *Hydnodontaceae* (Birkebak et al. 2013; Desjardin & Perry, 2015). Jülich (1981) proposed its own family *Scytinopogonaceae* Jülich, and segregated *Trechispora* and *Hydnodon* to *Hydnodontaceae* Jülich, nonetheless *Scytinopogon* is still considered within *Clavariaceae*.

Scytinopogon Singer, New genera of fungi. Lloydia 8:139-144 (1945)

Notes: The genus *Scytinopogon* was proposed by Singer in 1945, with pallid, cream, alutaceous, tan, tinged pink or purple, or white fruit bodies with flat branches in one plane, dilatating before branching, polychotomous in the first divisions and dichotomous near to the tips, also it can be dichotomous in slim specimens. This genus includes 10 species (www.indexfungorum.org).

Scytinopogon minisporus J. Alvarez-Manjarrez, M. Villegas & R. Garibay-Orijel, ***sp. nov.***

MycoBank number: MB829209; *Facesoffungi number:* FoF 05672; Fig. 258

Etimology: Refers to small-sized basidiospores.

Holotype: MEXU 28300.

Basidiocarps clavarioid 15–40 mm height, branches are 15–17 mm, stipe 5–15 × 1–3 mm, acute to sub-rounded, flat, and whitish or even gray (5A2–5B3), axils rounded. Branching near to the stipe is polytomical and near to the tips can be dichotomical to polytomical. The stipe is cylindrical slightly flat, whitish to pale orange brown (5A2–5A3). The base of the stipe is covered by numerous short hyphae looking plushy. Surface of all the fruit body, except the base of the stipe, looks smooth at naked eye, and dusty under stereoscopic microscope. Consistency is cartilaginous to alutaceous. Flesh of middle portion has the same color as the surface. Odor indistinguishable, taste slightly astringent. *Basidiospores* 4.2–5(–5.6) × 2.1–2.8(–3) µm [x_m = 4.6 ± 0.4 × 2.4 ± 0.3 µm, Q = 1.3–1.6, n = 30], dacryoid with lateral view slightly elliptical, hyaline, thin wall, verrucose where sometimes the warts merge, without conical spines; plage has not ornamentation, and lateral hilar appendix, dimly cyanophylic. Basidia mostly tetrasporic, scarce, (10–)20.3–28 × 4.9–5.6 µm, cylindrical to subcylindrical, hyaline, thick and smooth wall, base with clamp connection. Sterigmata 2.8–4.2 × 1.4 µm, hyaline, straight, acute apex. Cystidia clavate incrusted on the tip, they do not dispel with KOH, very scarce. Subhymenial with monomitic hyphae, generative hyphae of 1.4–3.5 × 50–56 µm, with thickened wall (< 1 µm), septae with clamp connections, and H connections between hyphae. Tramal hyphae strictly parallel, (2.1–)2.8–3.5 µm, thickened wall (<1 µm), septate with clamp connections, and hyphae with H connections. Stipe with generative hyphae, 1.4–2.1 µm width, hyaline, wall slightly thickened, frequent septa with clamp connections, and abundant crystals on their surface forming irregular plates.

Habitat and known distribution: Gregarious or solitary, growing on soil or debris of tropical dry forest from the Pacific coast of Jalisco, Mexico.

Material examined: MEXICO, Jalisco, municipality La Huerta, Estación de Biología de Chamela (EBCH), pathway Camino Antiguo, October 9th 2005, Villegas Ríos M. 2630 (FCME 26014); pathway Chachalaca, August 11th 2006, Villegas Ríos M. 2672 (FCME 26015); pathway Camino Antiguo Sur, August 11th 2006, Aguirre, Bautista and Pulido II-40 (MEXU 26345); October 1st 1977, A. Pérez J. and A. Solís M. (MEXU 11923); pathway Buho, October 10th 2015, Alvarez-Manjarrez AM170 (MEXU 28300, **holotype**) (GenBank ITS: MK328885; LSU: MK328894); pathway Buho, October 18th 2015, collected by Alvarez-Manjarrez AM176 (MEXU 28301, **isotype**) (GenBank ITS: MK328886; LSU: MK328895).

Notes: *Scytinopogon minisporus* differs from other species of *Scytinopogon* in having clavate cystidia with crystals on the tip. Microscopically it is very similar to *S. scaber* (Berk. & M.A. Curtis) D.A. Reid 1962, however *S. minisporus* has verrucose spores, bigger

basidia and encrusted cystidia. *Scytinopogon papillosus* Corner 1970 also coincides in spore size, but has minute papillae in the surface of the fruitbody. Phylogenetic analyses of the combined ITS and LSU dataset reveal *S. minisporus* as an independent branch within *Trechispora* sister of *Trechispora bispora* (Fig. 259). It is important to remark that *Trechispora* and *Scytinopogon*, both are paraphyletic, belonging to the same clade (Birkebak et al. 2013; Desjardin and Perry 2015). The type sequences of both genera are necessary to determine if the resupinate *Trechispora* and coralloid *Scytinopogon* are synonyms (Desjardin and Perry 2015). Based on ITS and LSU phylogenies *Scytinopogon* should be transferred to *Hydnodontaceae* together with *Trechispora* and *Hydnodon*.

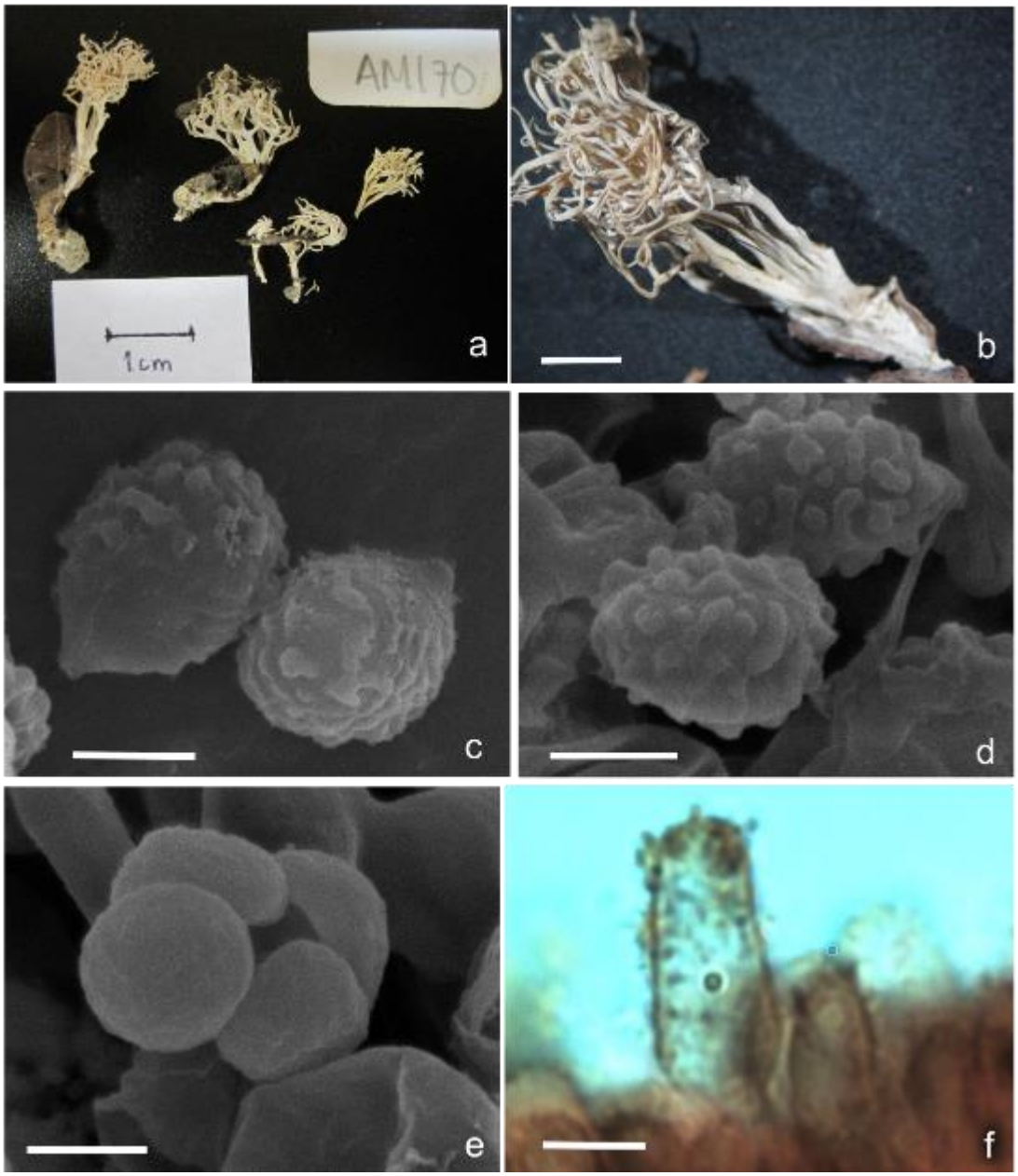

Fig. 258 *Scytinopogon minisporus* (MEXU 28300, **holotype**). **a**–**b** Basidiomes of *Scytinopogon minisporus*. **c** Basidiospores with verrucose ornamentation, showing the plage without ornamentation (spores from the **holotype**). **d** Ornamentation of spores (MEXU 28301,

isotype). **e** Immature basidiospores attached to a tetrasterigmata basidia. **f** Clavate cystidia with crystals on the tip. Scale bars: **b** = 5 mm, **c**–**e** = 1.5 µm, **f** = 4 µm

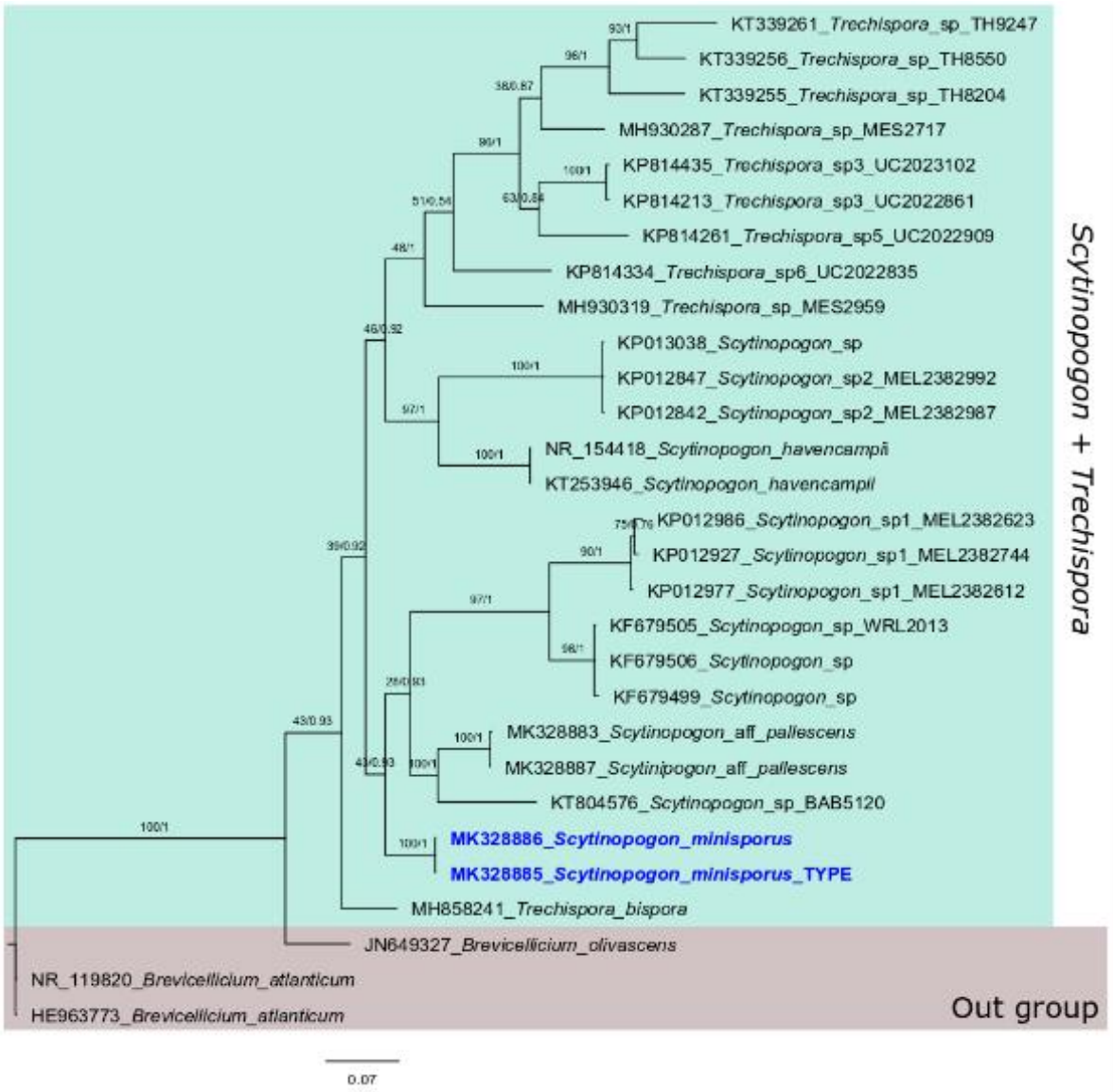

Fig. 259 Bayesian analysis combined dataset of ITS and LSU sequence data of the *Trechispora-Scytinopogon* clade, with bipartitions and mixed substitution model. The node support is indicated as ML/PP. The tree is rooted with *Brevicellicium atlanticum* (NR_119820 and HE963773) and *B. olivascens* (JN649327). The type sequences are indicated in blue bold. Bayesian analysis (Mr. Bayes) of the *Trechispora-Scytinopogon* clade showing the phylogenetic position of *Scytinopogon minisporus* inferred from ITS and LSU sequences. Individual alignments were done in MAFFT (Katoh et al. 2017); concatenated alignment was assembled in Mesquite. The Maximum Likelihood (ML) analysis was performed using the GTR+ gamma substitution model, with 1000 bootstrap replicates. Bayesian analysis applied mix models for two partitions (ITS and LSU) with 5,000,000 iterations. The node support is indicated as ML bootstrap / Bayesian posterior probabilities respectively. New sequences are indicated in blue bold.

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