

Hurricane Disturbance on Soil Fungal Communities in a Tropical Forest

by

EMILY HILL

A THESIS

Presented to the Department of Biology  
and the Division of Graduate Studies of the University of Oregon  
in partial fulfillment of the requirements  
for the degree of  
Master of Science

June 2022

THESIS APPROVAL PAGE

Student: Emily Hill

Title: Hurricane Disturbance on Soil Fungal Communities in a Tropical Forest

This thesis has been accepted and approved in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology by:

Krista McGuire	Chairperson
Bitty Roy	Member
Jeff Diez	Member

and

Krista Chronister	Vice Provost for Graduate Studies
-------------------	-----------------------------------

Original approval signatures are on file with the University of Oregon Division of Graduate Studies.

Degree awarded June 2022

© 2022 Emily Hill

## THESIS ABSTRACT

Emily Hill

Master of Science

Department of Biology

June 2022

Title: Hurricane Disturbance on Soil Fungal Communities in a Tropical Forest

The intensity and frequency of hurricanes are expected to increase Atlantic due to warming temperatures. Hurricanes are the most common natural disturbance on tropical coastal forests. Despite what we know about the tree and soil damage after hurricanes, the effects of hurricanes on soil microbial communities remain poorly known. Soil fungal communities are critical to the health of plant communities through functional guilds like pathogens, decomposers, and mutualists. Here, we use soil samples collected from 2012 and 2018 surveys in the Luquillo LTER plot in Puerto Rico across land use history to investigate the influences of hurricane Maria coupled with land use on fungal communities. Our hypotheses are: H1) Inputs of leaf litter and debris from hurricane-force winds increase saprotrophs and plant pathogens which results in distinct pre and post hurricane composition for both soil and litter communities; H2) Tree defoliation reduces the relative abundance and diversity of arbuscular mycorrhizal fungi due to a lack of photosynthetic carbon; H3) Hurricane disturbance exacerbates land use legacy patterns and further weakens tree microbial signatures.

## CURRICULUM VITAE

NAME OF AUTHOR: Emily Hill

### GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene

### DEGREES AWARDED:

Master of Science, 2022, University of Oregon

Bachelor of Science, Biology, 2020, University of Oregon

### AREAS OF SPECIAL INTEREST:

Fungal Functional Ecology

Mycorrhizal Ecology

Tropical Ecology

### GRANTS, AWARDS, AND HONORS:

O'Day Fellowship, University of Oregon, 2019

GREBES award, University of Oregon, 2019

## ACKNOWLEDGMENTS

I want to express my appreciation to my committee chair and mentor Krista McGuire for fostering positivity and inspiration to pursue microbial research. I also want to thank Kaye Shek for the innumerable knowledge shared during both of my degrees here at the UO. In addition, I want to thank all the undergraduate students who contributed to this project.

## TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION.....	1
II. METHODS.....	5
Site Description and Tree Selection.....	5
Soil and Microbial Analyses.....	6
Sequence Processing and Bioinformatics.....	6
Statistical Analyses.....	7
Network Analyses.....	8
III. RESULTS.....	9
Hurricane Disturbance on Fungal Communities.....	9
Fungal Functional Groups.....	10
Arbuscular Mycorrhizal Composition.....	11
IV. DISCUSSION.....	16
REFERENCES CITED.....	20

## LIST OF FIGURES

Figure	Page
1. Compositional differences of fungal communities across year and substrate ...	9
2. NMDS plots of soil (A) and litter (B) communities with centroids by tree species .....	10
3. Relative abundance of fungal function guilds in soil and litter by year and land use history. ....	11
4. Relative abundances of arbuscular mycorrhizal fungi genera by year and land use .....	12
5. Pairwise PERMANOVAs of AM fungal communities .....	13
6. Modularity matrices of plant-AMF bipartite networks by year and land use....	14-15



# CHAPTER I

## INTRODUCTION

Climate change is expected to increase the frequency and intensity of natural disasters (Balaguru et al., 2018), due to anthropogenic warming of ocean temperatures which contributes to the formation of hurricanes (Lima et al., 2021). Hurricanes are one of the most common naturally occurring disturbances in tropical forests across the Caribbean. Strong winds and heavy precipitation during hurricane events can decrease soil and plant community stability, by causing plant injuries such as defoliation, torn branches, and root exposure. While we can see the impact of these disturbances to above-ground communities, the response of soil communities to hurricanes remains understudied (Alvarez-Manjarrez and Garibay-Orijel, 2021; Vargas et al., 2010).

Soil microbial communities are critical to the structure and function of plant communities due to their roles as decomposers, mutualists, and pathogens which control ecosystem processes such as soil formation and nutrient cycling (Chandler et al., 2011; Van Der Heijden et al., 2008). Past research has shown that the relative influences of abiotic and biotic factors driving major differences in fungal community composition can include soil physicochemical properties (Trivedi et al., 2016; Waldrop et al., 2017), climate (Bennett and Classen, 2020; Classen et al., 2015), land use history (Bachelot et al., 2016; Moora et al., 2014) and properties of plant communities (Van Der Heijden et al., 2008). Plant traits, for instance, are known to influence soil fungal community composition, as different tree species can facilitate assembly of unique communities of fungi surrounding individual trees, also known as microbial signatures (Bais et al., 2006; Prescott and Grayston, 2013). In tropical forests, diverse tree assemblages can thus

maintain microbial signatures through highly diverse fungal communities, making their role in ecosystem functioning and associations with plants particularly useful to study how terrestrial ecosystems will respond to the impacts of climate change.

Arbuscular mycorrhizal fungi (AM fungi) are obligate plant mutualists that form symbioses within roots of more than 80% of all terrestrial plants. AM fungi provide a wide range of benefits to plant hosts such as foraging for limiting nutrients, water retention, and pathogen resistance (Parniske, 2008; Powell & Rillig, 2018; Van der Heijden et al., 2015) The functionality of AM fungi makes them key determinants of plant health and productivity as well as in large global cycles like the carbon cycle. Their obligate association with plants makes them particularly useful to study how terrestrial ecosystems will mitigate climate change.

Fungal community assembly can be influenced by hurricane disturbances in various ways. Hurricanes cause significant defoliation of plants, and the resulting increase of litter inputs to the forest floor can act as a major mode of dispersal from foliar microbes into the soil microbiome. In other forest systems, increased litter inputs after hurricane events have been shown to increase soil organic matter (Gavito et al., 2018; May and Oberbauer, 2021) and nutrient availability while selecting for greater relative abundances of saprotrophs (Alvarez-Manjarrez and Garibay-Orijel, 2021). Defoliation of trees reduces photosynthesis and shifts investment strategies to nutrient storage, which provides less carbon for below ground allocation and limits mycorrhizal survival and colonization (Shi et al., 2020; Wiley et al., 2017). Along with nutrient pulses due to litter inputs and decomposition (Gutiérrez del Arroyo and Silver, 2018; Xu et al., 2004), increased precipitation during hurricane events has been shown to alter the relative

abundances of functional groups of fungi. Differential responses of fungal functional groups to these various consequences of hurricanes can have major implications for forest dynamics under more frequent and intense hurricane events in the tropics.

Over 70% of tropical ecosystems are in some disturbed state with land use being the largest driver of tropical deforestation. While in protected areas many of these practices been halted years ago, there is substantial evidence that historic land use can leave lasting effects on both plant and soil communities, a phenomenon that can persist for up to 200 years after land use (Bachelot et al., 2016; Foster et al., 2003; Uriarte et al., 2009). Prior disturbances compounded with a large single disturbance can exceed ecosystem resilience and create homogenous alternate stable states (Buma and Wessman, 2011; Calderón et al., 2018; Vellend et al., 2007). Above ground response patterns to compounded disturbances have demonstrated these effects (Buma, 2015), yet whether these patterns are reflected below ground remain unclear (Van Der Heyde *et al.*, 2017; Yuan *et al.*, 2021). Fungal community response to natural disasters may be context specific and more complex due to plant host and land use history.

Hurricane María decimated much of the Puerto Rican tropical forests during the fall of 2017. María was the strongest hurricane to make landfall in Puerto Rico since 1928 and had a 2 to 12 fold increase in stem breakage compared to the previous two hurricanes (Uriarte et al., 2019). Here we used soil samples collected before (2012) and after (2018) hurricane María, to study the impacts of hurricane disturbance on fungal community assembly. By comparing the fungal communities our hypotheses were: H1) Inputs of leaf litter and debris from hurricane-force winds increase saprotrophs and plant pathogens which results in distinct pre and post hurricane composition for both soil and

litter communities; H2) Tree defoliation reduces the relative abundance and diversity of arbuscular mycorrhizal fungi due to a lack of photosynthetic carbon; H3) Hurricane disturbance exacerbates land use legacy patterns and further weakens tree microbial signatures.

## CHAPTER II

### METHODS

#### *Site description and tree selection*

Samples were collected in the Luquillo Forest Dynamics Plot (18°20'N, 65°49'W), a 16-ha plot of tropical forest in El Yunque National Forest. Mean temperature is 26C and mean annual rainfall is 3500 mm. This plot was originally selected for its land use gradient as it had previously been used for coffee agriculture, logging, and charcoal production prior to 1934. This same area was hit by hurricane Maria in the fall of 2017 where near full defoliation had been overserved from the forest trees. For 2012 and 2018 sampling, eight tree species were chosen: *Casearia arborea* (Rich.) Urb. (Salicaceae), *Dacryodes excelsa* Vahl (Burseraceae), *Inga laurina* (Sw.) Willd. (Fabaceae), *Manilkara bidentata* (A.DC.) A. Chev. (Sapotaceae), and *Prestoea acuminata* (Willd.) H.E. Moore (Arecaceae), *Guarea Guidonia* (L.) Sleumer (Meliaceae), *Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin (Araliaceae), *Sloanea berteriana* Choisy ex DC (Elaeocarpaceae), *Tabebuia heterophylla* (DC.) Britton (Bignoniaceae). Eight individuals per species were sampled from low and high land use plots totaling to 16 trees per species. Trees were chosen between the 50<sup>th</sup> and 75<sup>th</sup> dbh quantiles for those species on the plot, as smaller individuals may not have had large enough canopy or rooting zones to develop a distinguishable microbial signature. Soil (0 – 20 cm) and litter samples were taken from 0 to 10m, away from the base of the tree. Distinct length samples were taken to investigate distance decay effects of microbial communities from the tree host at 0, 1, 3, 6, and 9 m distances from the base of each tree. The 2012 census data was used to find transect directions for target trees to avoid overlapping tree canopies and rooting zones.

### *Soil and microbial analyses*

Soil cores were first homogenized by using uv-sterilized 2 mm sieves and litter samples homogenized with liquid nitrogen in a uv-sterilized mortar and pestle. Genomic DNA from soil and litter samples was extracted using the MoBio Powersoil isolation kit (MO BIO Laboratories Inc., Carlsbad, CA, USA) followed an adjusted protocol. All DNA extracts were stored at 20°C until molecular analyses. Fungal communities were amplified using ITS1 (CTTGGTCATTTAGAGGAAGTAA) and ITS1-F (GCTGCGTTCTTCATCGATGC) primers and Nextera barcodes (TAAGGCGA, CGTACTAG) on the forward primer. Successful amplicons were quantified using fluorometry with the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Waltham, MA) on a SpectraMax M5E Microplate Reader (Molecular Devices, San Jose, CA, USA). Amplicons were pooled in equimolar concentrations and purified using the QIAquick PCR Purification Kit (Qiagen). The Illumina HiSeq platform (150BP) was used to sequence ITS samples. The libraries were sequenced at the University of Oregon Genomics and Cell Characterization Core Facility (Eugene, OR).

### *Sequence Processing and Bioinformatics*

ITS sequence data was demultiplexed using QIIME v.1.9.1 (Caporaso et al., 2010) and primers were removed using cutadapt (v.1.10.1, Martin 2011). It was then passed through the DADA2 pipeline to assemble amplicon sequence variants (ASVs). ASVs were assigned taxonomy using the UNITE database (Nilsson et al., 2019) and

normalized using variance stabilization. Fungal ASVs were parsed into functional guilds using the FUNGuild database (Nguyen et al., 2016).

### *Statistical Analyses*

To examine the differences in fungal ASVs between year, tree species, and land use permutational multivariate analysis of variance (PERMANOVA) was conducted using the Adonis function in the Vegan package (Oksanen et al., 2020). All ASVs were converted to Bray-Curtis distances prior to analyses. Bray Curtis counts were then plotted over distances to visualize overall dissimilarity before and after hurricane Maria.

Compositional differences of soil and litter communities between sampling years was visualized using nonmetric dimensional scaling (NMDS) using Bray Curtis distances in the Phyloseq package (McMurdie and Holmes, 2013) . To visualize potential tree species specific microbial signatures the soil and litter samples, average NMDS scores for each species were calculated and plotted as centroids.

The FUNGuild program was used to give fungal ASVs functional guild identification. For this paper, arbuscular mycorrhizal (AM) fungi were singularly selected for analysis and agglomerated at the genus level. Changes in relative abundance of AM fungi, by year and land use were investigated using a Kruskal-Wallis test and visualized using stacked bar charts filtered by the top 15 genera. All figures were created using the ggplot2 package (Wickam, 2016). Pairwise PERMANOVA comparisons of AM fungal communities were used to examine compositional differences amongst tree species. Bonferroni multiple comparisons correction was used to generate adjusted p-values.

### *Network analyses*

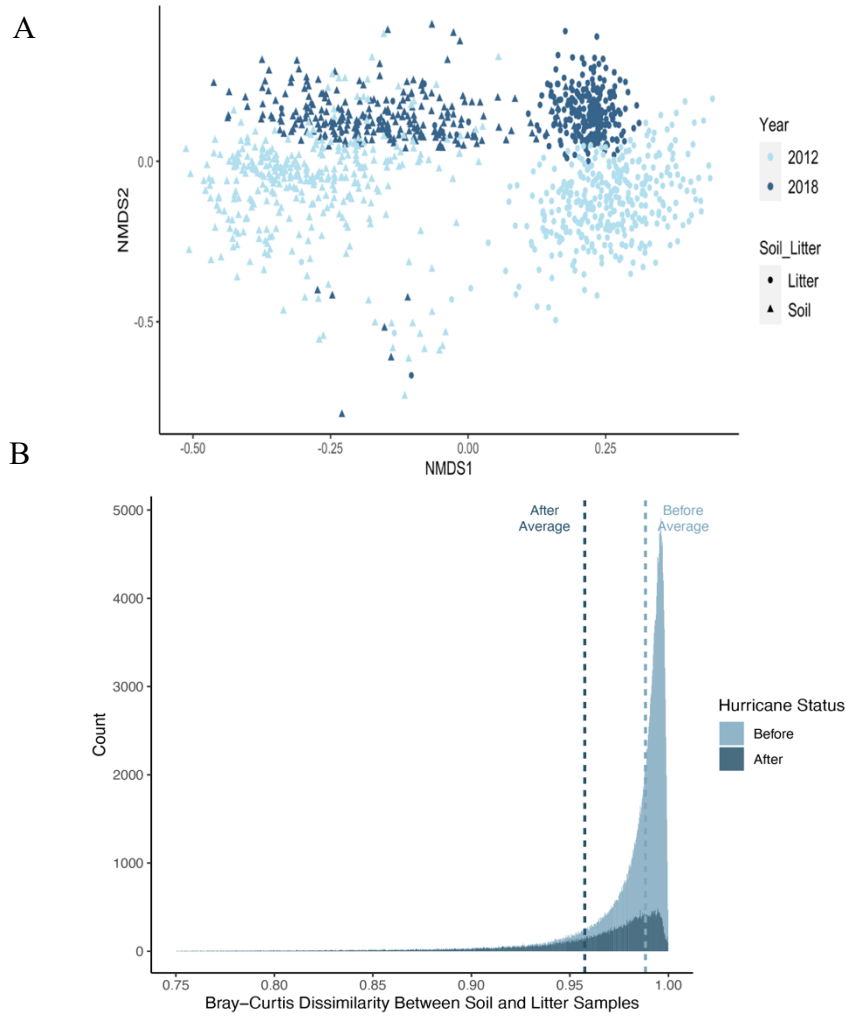
Data were parsed into their respective year and land use categories prior to building bipartite networks using the ‘bipartite’ package. We calculated Beckett’s modularity index to compute the modularity of each network, which detects interacting sets of species within networks. We also calculated  $c$  and  $z$  values for each AM fungal taxon, where  $c$  = ‘participation coefficient’ aka *between*-module connectivity (Guimera and Nunes Amal, 2005) and  $z$  = within module degrees/connectivity. Taxa that have high  $c$  and  $z$  values have been considered ‘hubs’. Modularity ( $Q$ ) was calculated which measures how well interactions can be parsed into modules. A module contains species that interact more within modules than between them; for instance, a completely modular network would have clusters of interacting organisms that do not interact with those outside of their module. Further, you can consider how modularity correlates with other network indices such as degree of specialization, where more specialist organisms will form modules in an interaction network, and very generalist communities are not modular.



**CHAPTER III**  
**RESULTS**

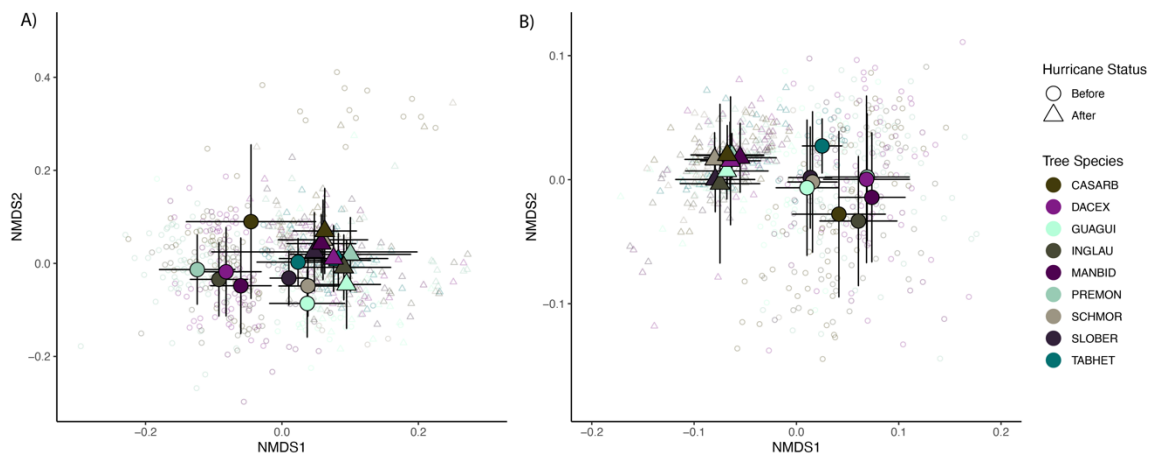
*Hurricane Disturbance on Fungal Communities*

We found hurricane status, substrate, land use history, and tree species all to have a significant effect on overall fungal community composition. Fungal communities were distinct between soil, litter, and year ( $F=16.33$ ,  $R^2 = 0.012$ ,  $P < 0.001$ , Fig. 1A).



**Figure 1.** A. Compositional differences of fungal communities across year and substrate. B. Histogram of all pairwise Bray-Curtis dissimilarities between soil and litter samples grouped by year.

Soils also differed by land use before ( $F = 4.59$ ,  $R^2 = 0.013$ ,  $P < 0.001$ , Fig. 3) and after ( $F = 3.99$ ,  $R^2 = 0.015$ ,  $P < 0.001$ , Fig. 3) the hurricane. Further analyses were done separately by year and land use due to these differences. Pre-hurricane microbial signatures of the overall fungal community resulted in 59 out of 72 significant comparisons ( $P < 0.05$ ) with only low land use only having 2 insignificant pairs. Comparisons of post-hurricane soils resulted in only 31 out of 72 of the comparisons which were equal between land use. Overall, Bray Curtis dissimilarity between soil and litter was reduced post hurricane. Post hurricane dissimilarity counts also had a greater range than pre hurricane counts (Fig. 1B). Tree species centroids appeared to be structured by year for both soil and litter communities (Fig. 2). Distance from base of the tree yielded no significant effects for both soil and litter communities.

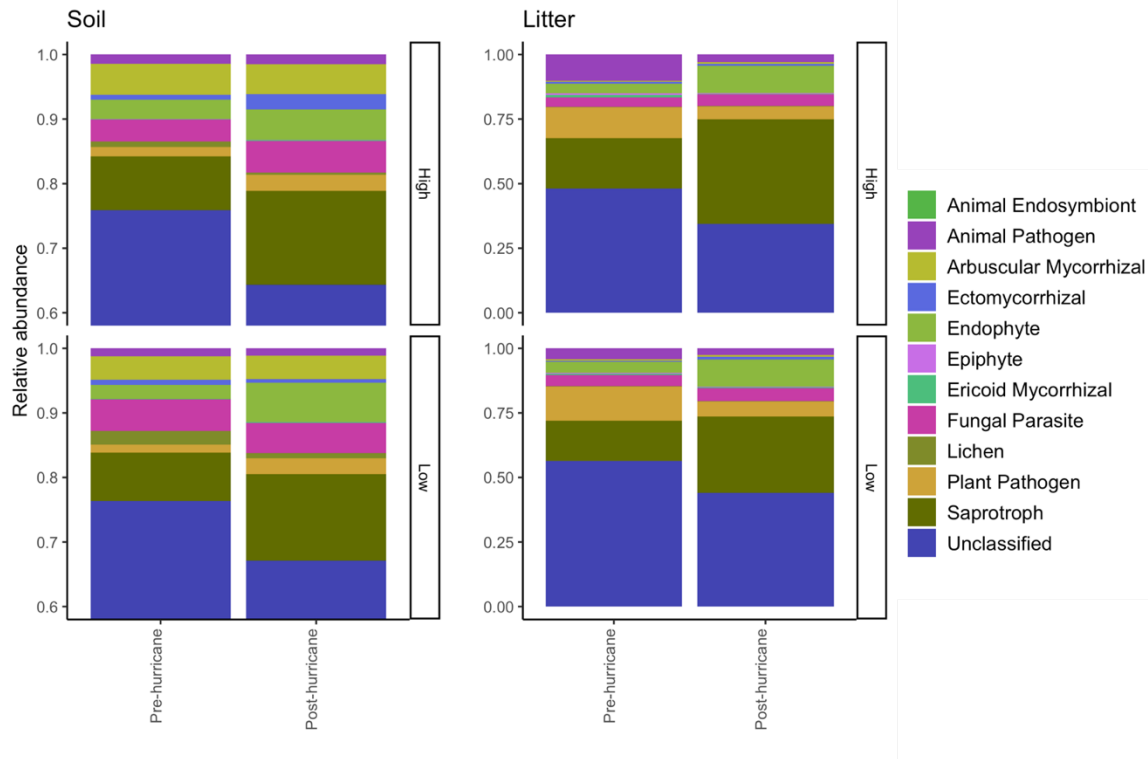


**Figure 2.** NMDS plots of soil (A) and litter (B) communities with centroids by tree species.

### *Fungal functional guilds*

FunGUILD was used to separate taxa into functional guilds. FunGUILD identified 84458 out of 119098 ASVs (71%). Unclassified fungi represented the largest

group among all samples (Fig. 3). Hurricane status significantly structured both saprotroph ( $F = 4.33$ ,  $R^2 = 0.007$ ,  $P < 0.001$ , Fig. 3) and plant pathogen ( $F = 4.26$ ,  $R^2 = 0.006$ ,  $P < 0.001$ , Fig. 3) composition. Saprotroph and endophyte relative abundance significantly increased in post hurricane soils and litter ( $P < 0.001$ , Fig. 3). Plant pathogen relative abundance significantly increased in post hurricane soils ( $P < 0.001$ , Fig. 3).



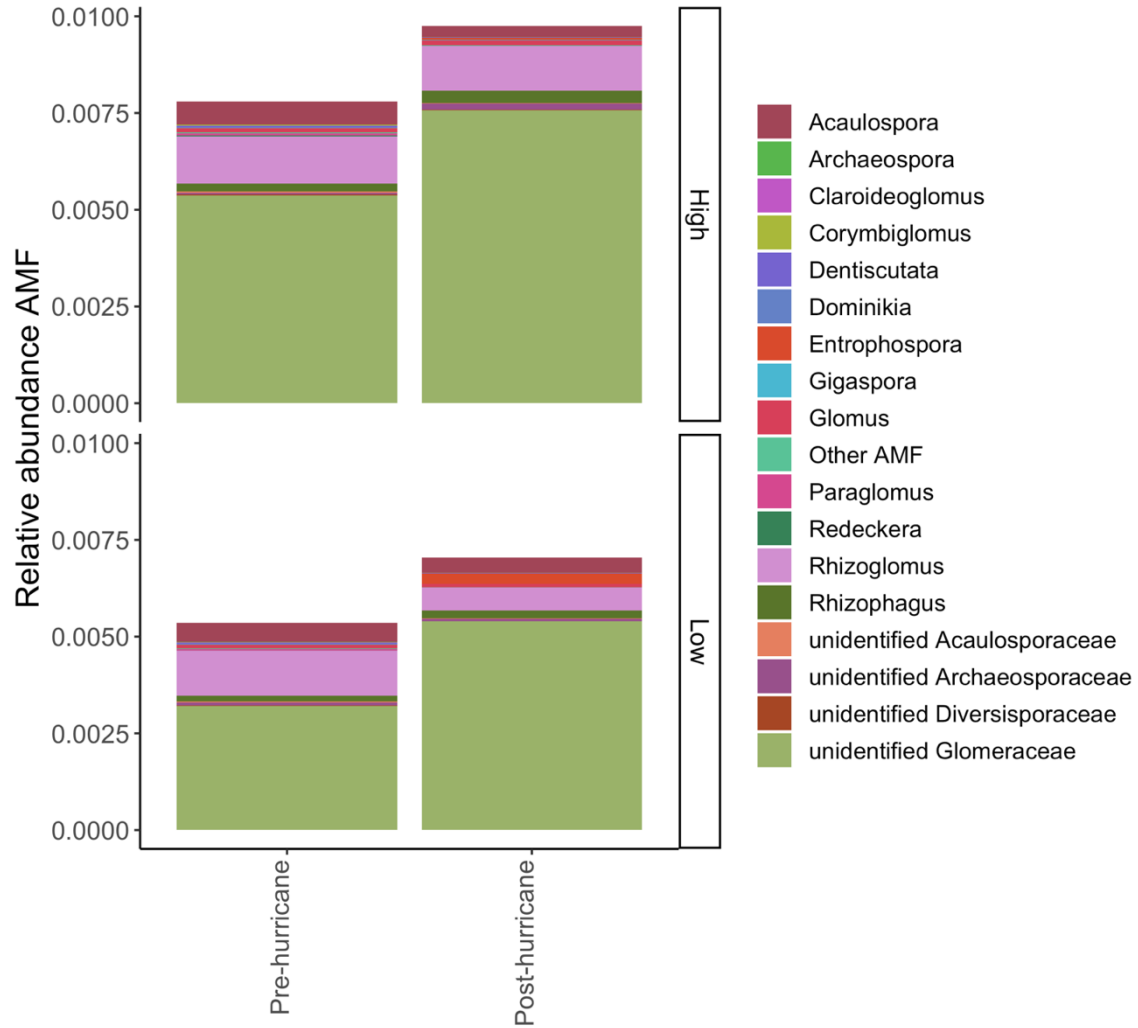
**Figure 3.** Relative abundance of fungal functional guilds in soil and litter by year and land use history.

### *Arbuscular Mycorrhizal Composition*

Arbuscular mycorrhizal composition was affected by year ( $F = 6.11$ ,  $R^2 = 0.01$ ,  $P < 0.001$ ) and there was a significant interaction between land use and tree species ( $F = 1.64$ ,  $R^2 = 0.02$ ,  $P < 0.001$ ). Only soil samples were used in these analyses AMF are found in very low abundances in leaf litter since they are root symbionts. Mycorrhizal relative abundance was significantly greater in high land use plots than low land use ( $P < 0.001$ ) (Fig. 4), but not by hurricane status. The Shannon diversity index for AM

fungi in soil was significantly higher in low land use than in high land use ( $P=0.015$ ).

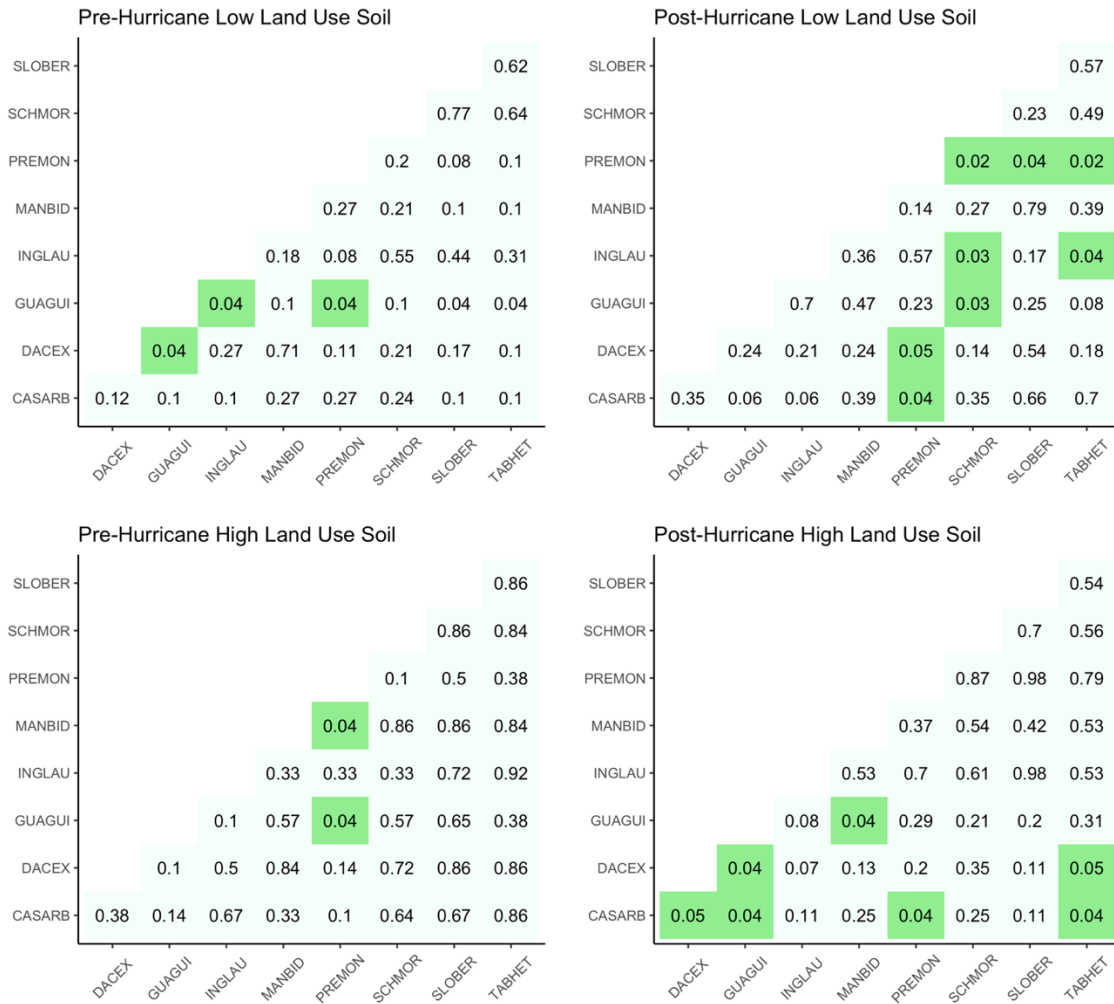
Unidentified Glomeraceae was the most abundant genus for both 2012 and 2018 samples.



**Figure 4.** Relative abundances of arbuscular mycorrhizal fungi genera by year and land use history.

Pairwise comparisons of AM fungal communities showed significant differences between tree species. In high land use areas, pre-hurricane soils had 2 out of 36 significant comparisons while post hurricane there were 6 out of 36 ( $P$  adjusted $<0.05$ )

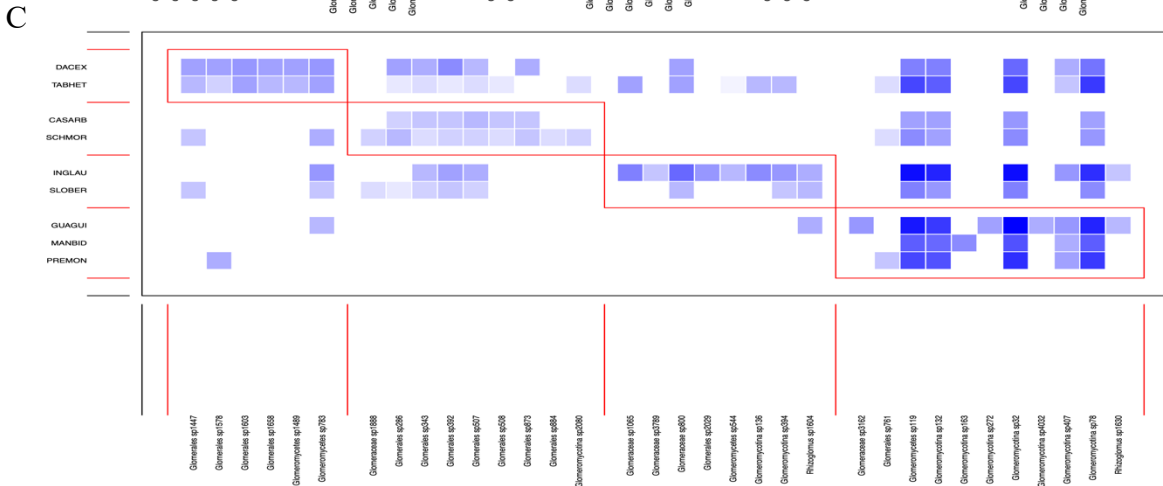
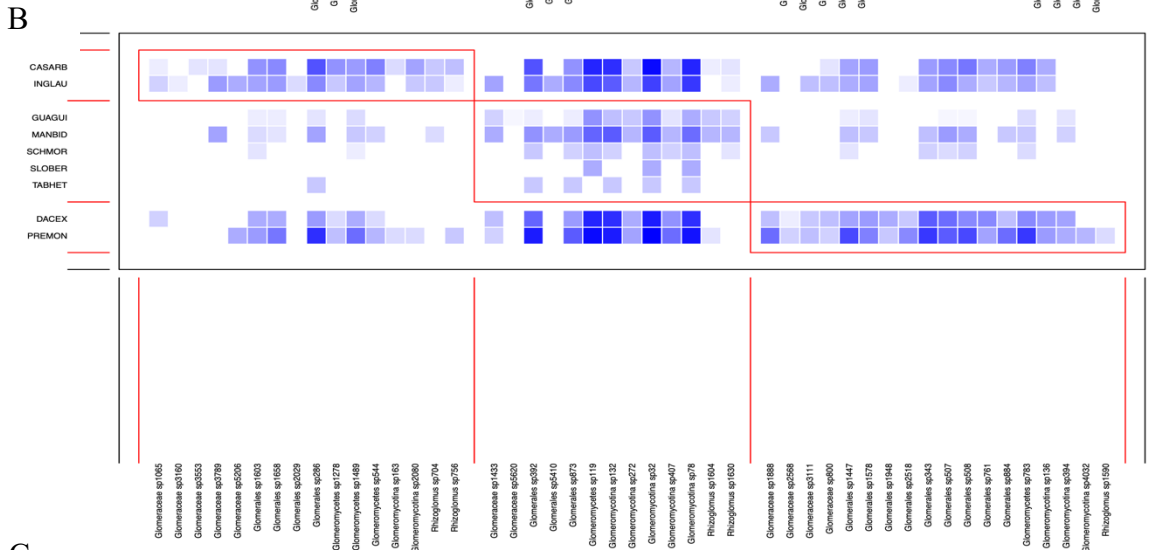
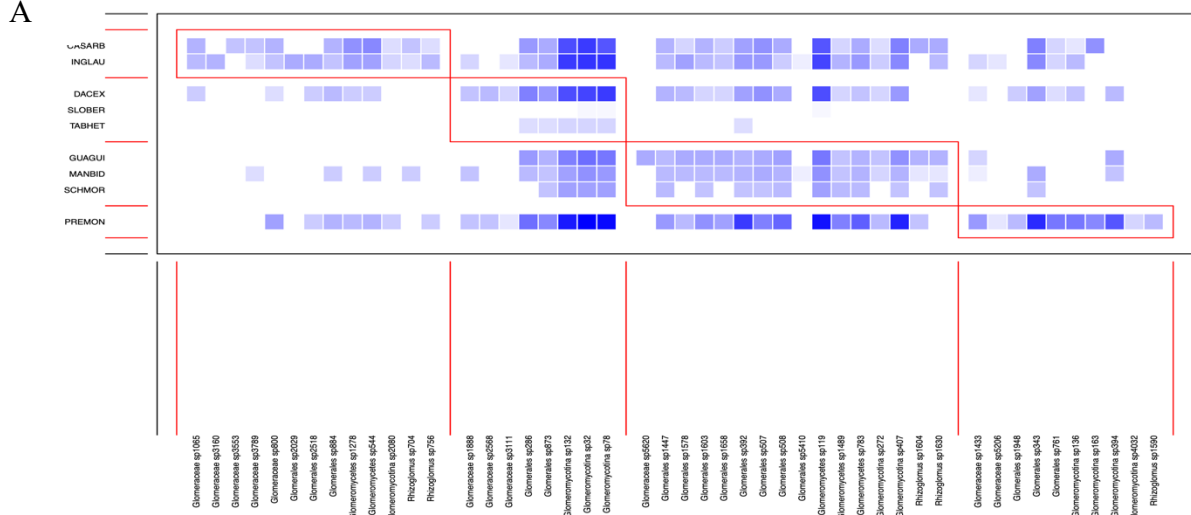
(Fig. 5). For low land use, only 3 of 36 pairs were significant pre hurricane while there were 8 out of 36 pairs post hurricane ( $P_{\text{adjusted}} < 0.05$ ) (Fig. 5).



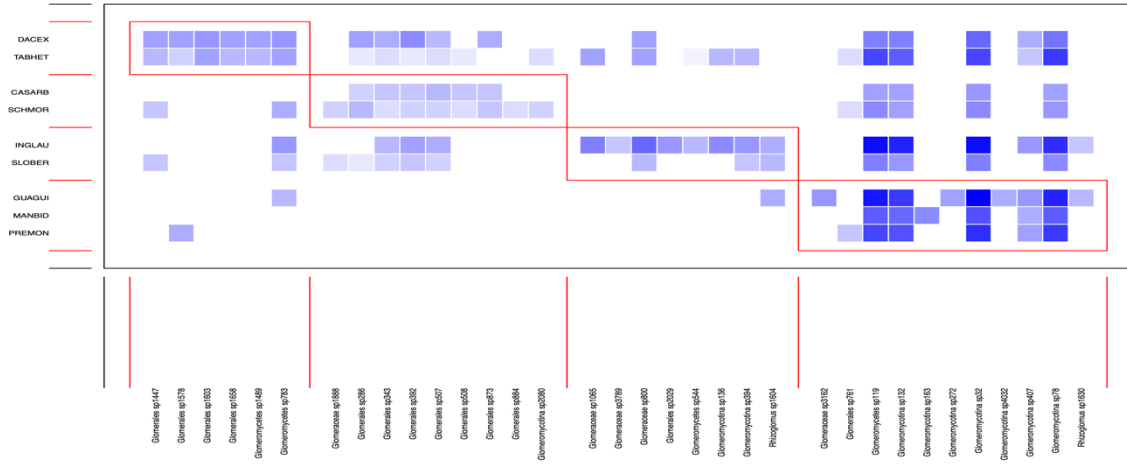
**Figure 5.** Pairwise PERMANOVAs of AM fungal communities for tree species by year and land use. P adjusted values are shown for each comparison with  $P < 0.05$  in green.

Our bipartite network analyses revealed significantly modular communities compared to our null model. Low land use matrix resulted in  $Q = 0.122$  and  $z = 9.677$ , meaning the interaction network is 9.6 standard deviations more modular than the null model. Post-hurricane low land use  $Q = 0.195$   $z = 11.822$  and high land use  $Q = 0.240$   $z = 22.72$ . Tree species were parsed into separate models for each separate community (Fig. 6

A-D). Overall high and low land use had similar modularity values before the hurricane, both of which increased after the hurricane and with greater modularity in high land use after hurricane.



D



**Figure 6.** Modularity matrices of plant-AM fungal bipartite networks by year and land use. (A. 2012 Low land use, B. 2018 Low land use, C. 2012 High land use, D. 2018 High land use) Red groupings denote separate modules while blue boxes represent ASV abundance.

## CHAPTER IV

### DISCUSSION

Distinct compositional differences such as homogenization in tree fungal signatures indicate the magnitude hurricane disturbance has on fungal communities which has implications for forest coexistence mechanisms. We also found changes in composition and abundance of fungal functional guilds like fungal pathogens and mycorrhizae which are influential in tree and seedling performance. The Janzen-Connell (JC) hypothesis, one of the leading mechanisms explaining the maintenance of tropical tree diversity, posits that species specific enemies increase seedling mortality near conspecifics adults to allow rare species to establish. JC mechanisms could be weakened from the hurricane as fungal pathogens were dispersed further across the forest through strong wind which results in seedling mortality being largely driven by generalist pathogens. Common seedling mortality would increase and reduce tree diversity as rare species cannot rely on enemy specificity.

A land use legacy was still apparent post hurricane which is consistent with our hypothesis that historical context is important in determining how fungi respond to large natural disasters. Land use alters soil physiochemical properties and plant community composition which in turn influences soil microbial composition. Since land use practices ended in this forest 80 years ago, the current fungal communities in high land use areas could reflect a secondary state that is both compositionally and functionally different than low land use. Glomeraceae and *Rhizophagus* were found in post hurricane soils and are considered to contain ruderal species. Efforts to sort AM fungi by functional traits has been proposed to give greater insight into the functionality and assembly of



these organisms (Chagnon et al., 2013; Zanne et al., 2020). Many of these classifications follow a competitor-stressor-ruderal framework that is commonly used in plant databases (Grime, 1977). Ruderal species are characterized as being disturbance tolerant by being able to quickly produce and regenerate hyphae (Chagnon et al., 2013). Competitor species like in the genus *Gigaspora* seemed to decrease in 2018. In high land use areas, these ruderal fungi could have overtaken slower growing competitive fungi after repeated disturbances much like secondary forest successional patterns therefore altering community composition (Guariguata and Ostertag, 2001). These communities could be selected to be able to withstand large disturbances and maintain their abundance which would explain greater abundances in high land use plots. Functional traits need to be further investigated to help understand successional and assemblage patterns of AM fungi.

AM fungi diverge from overall fungal microbial signature patterns as unique AM microbial signatures increased post hurricane. AM fungi have been shown to counteract Janzen-Connell effects by providing benefits like resource acquisition and pathogen protection to seedlings near conspecific adults. While these mechanisms are complex and involve both abiotic and biotic variables, an increase in the specificity of mycorrhizal communities under adult trees could potentially offer more benefits to conspecific seedlings rather than rare species growing nearby. This trend was seen regardless of land use, which suggests there is recruitment of plant species-specific fungi post disturbance. Plant traits and AM phylogeny have been shown to be significant factors in AM fungal-plant networks (Chagnon 2015). In congruence with the intermediate disturbance hypothesis (Connell 1978), hurricane disturbance could have removed general species

and allowed for opportunistic and ruderal fungi to compete for resource space. It will be interesting to see how if mycorrhizae maintain distinct trajectories or if this an early successional period.

Tree defoliation was predicted to be a driver in decreased mycorrhizal abundance through photosynthetic carbon limitations and shifts soil properties, however we did not find this in our results. Rapid litter decomposition has also been previously shown to occur in post hurricane (Ostertag et al., 2003; Vargas et al., 2010) which allows for a pulse of nutrients to be recycled back into soil (May and Oberbauer, 2021; Xu et al., 2004). Mycorrhizae decrease in abundance in soils with high nutrients (Liu et al., 2020; Soonvald et al., 2019), however trees still need mycorrhizae to help source limiting nutrients such as P, K, and N. Reduction in abundance could have also been buffered by the increased pathogen abundance in soils. Mycorrhizae stimulate a plant immune response called priming in their plant hosts to reduce infection (Jung et al., 2012; Song et al., 2015). Primed plants have higher survival rates when introduced to pathogens. In this study mycorrhizae could be enhancing disease resistance from the influx of pathogens from leaf litter which is beneficial for plant hosts to maintain the symbiosis.

While our initial sampling time was several months after the hurricane hit, we can still infer trends from our data that were potentially due to the hurricane. Temporal shifts occur in ecosystems, however if our results were due only due to these changes, we should see similar trends or only fine scale variation (Lauber et al., 2013). But as our data is showing significant differences between pre- and post-hurricane in soil and litter, we infer this is due to the disturbance, as has been found with other trophic groups in this system (Hu and Smith, 2018; Meléndez-Vazquez et al., 2019; Schowalter et al., 2021).

Here we show homogenization of tree microbial signatures while AM fungi with changes in taxonomy and abundance for AM fungi after a major hurricane disturbance in Puerto Rico. This study examines how litter mixture and deposition on soils selects for homogenous fungal communities. The emergence of differences by land use, show the toll previous practices have on belowground communities. Contrary to expectations, AM fungal abundance and diversity did not change post hurricane which highlights the differences in disturbance response among functional guilds which offers different mechanisms of disturbance resilience for plant mutualists. As natural disasters are thought to increase due to climate change and hurricanes will increase in frequency and intensity. Understanding how microbial communities respond to disturbances along with other environmental factors is essential to disentangling future fungal assembly patterns, function, and implications for plant-soil feedbacks as they relate to the maintenance of diversity.

## REFERENCES CITED

- Alvarez-Manjarrez, J., Garibay-Orijel, R., 2021. Resilience of soil fungal community to hurricane Patricia (category 4). *For. Ecol. Manage.* 498, 119550. <https://doi.org/10.1016/j.foreco.2021.119550>
- Bachelot, B., Uriarte, M., Zimmerman, J.K., Thompson, J., Leff, J.W., Asaii, A., Koshner, J., McGuire, K., 2016. Long-lasting effects of land use history on soil fungal communities in second-growth tropical rain forests. *Ecol. Appl.* 26, 1881–1895. <https://doi.org/10.1890/15-1397.1>
- Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* 57, 233–266. <https://doi.org/10.1146/annurev.arplant.57.032905.105159>
- Balaguru, K., Foltz, G.R., Leung, L.R., 2018. Increasing Magnitude of Hurricane Rapid Intensification in the Central and Eastern Tropical Atlantic. *Geophys. Res. Lett.* 45, 4238–4247. <https://doi.org/10.1029/2018GL077597>
- Bennett, A.E., Classen, A.T., 2020. Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias. *Ecology* 101, 1–11. <https://doi.org/10.1002/ecy.2978>
- Buma, B., 2015. Disturbance interactions: Characterization, prediction, and the potential for cascading effects. *Ecosphere* 6, 1–15. <https://doi.org/10.1890/ES15-00058.1>
- Buma, B., Wessman, C.A., 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2, 1–13. <https://doi.org/10.1890/ES11-00038.1>
- Calderón, K., Philippot, L., Bizouard, F., Breuil, M.C., Bru, D., Spor, A., 2018. Compounded disturbance chronology modulates the resilience of soil microbial communities and N-cycle related functions. *Front. Microbiol.* 9, 1–11. <https://doi.org/10.3389/fmicb.2018.02721>
- Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Peña, A.G., Goodrich, J.K., Gordon, J.I., Huttley, G.A., Kelley, S.T., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C.A., McDonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Turnbaugh, P.J., Walters, W.A., Widmann, J., Yatsunenko, T., Zaneveld, J., Knight, R., 2010. correspondence QIIME allows analysis of high-throughput community sequencing data Intensity normalization improves color calling in SOLiD sequencing. *Nat. Publ. Gr.* 7, 335–336. <https://doi.org/10.1038/nmeth0510-335>
- Chagnon, P.L., Bradley, R.L., Maherali, H., Klironomos, J.N., 2013. A trait-based framework to understand life history of mycorrhizal fungi. *Trends Plant Sci.* 18, 484–491. <https://doi.org/10.1016/j.tplants.2013.05.001>

- Chandler, R.B., Royle, J.A., King, D.I., 2011. Soil microbes drive the classic plant diversity-productivity pattern. *Ecology* 92, 1429–1435.
- Classen, A.T., Sundqvist, M.K., Henning, J.A., Newman, G.S., Moore, J.A.M., Cregger, M.A., Moorhead, L.C., Patterson, C.M., 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere* 6. <https://doi.org/10.1890/ES15-00217.1>
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. *Bioscience* 53, 77–88. [https://doi.org/10.1641/0006-3568\(2003\)053\[0077:TIOLUL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2)
- Gavito, M.E., Sandoval-Pérez, A.L., del Castillo, K., Cohen-Salgado, D., Colarte-Avilés, M.E., Mora, F., Santibáñez-Rentería, A., Siddique, I., Urquijo-Ramos, C., 2018. Resilience of soil nutrient availability and organic matter decomposition to hurricane impact in a tropical dry forest ecosystem. *For. Ecol. Manage.* 426, 81–90. <https://doi.org/10.1016/j.foreco.2017.08.041>
- Grime, J.P., 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *Am. Nat.* 111, 1169–1194. <https://doi.org/10.1086/283244>
- Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. *For. Ecol. Manage.* 148, 185–206. [https://doi.org/10.1016/S0378-1127\(00\)00535-1](https://doi.org/10.1016/S0378-1127(00)00535-1)
- Guimera, R., Nunes Amal, L.'s A., 2005. Functional cartography of complex metabolic networks. *Nature* 433, 895–900. <https://doi.org/10.1038/nature03286.1>
- Gutiérrez del Arroyo, O., Silver, W.L., 2018. Disentangling the long-term effects of disturbance on soil biogeochemistry in a wet tropical forest ecosystem. *Glob. Chang. Biol.* 24, 1673–1684. <https://doi.org/10.1111/gcb.14027>
- Hu, T., Smith, R.B., 2018. The impact of Hurricane Maria on the vegetation of Dominica and Puerto Rico using multispectral remote sensing. *Remote Sens.* 10. <https://doi.org/10.3390/rs10060827>
- Jung, S.C., Martinez-Medina, A., Lopez-Raez, J.A., Pozo, M.J., 2012. Mycorrhiza-Induced Resistance and Priming of Plant Defenses. *J. Chem. Ecol.* 38, 651–664. <https://doi.org/10.1007/s10886-012-0134-6>
- Lauber, C.L., Ramirez, K.S., Aanderud, Z., Lennon, J., Fierer, N., 2013. Temporal variability in soil microbial communities across land-use types. *ISME J.* 7, 1641–1650. <https://doi.org/10.1038/ismej.2013.50>

- Lima, M.M., Hurduc, A., Ramos, A.M., Trigo, R.M., 2021. The Increasing Frequency of Tropical Cyclones in the Northeastern Atlantic Sector. *Front. Earth Sci.* 9, 1–14. <https://doi.org/10.3389/feart.2021.745115>
- Liu, J., Zhang, J., Li, D., Xu, C., Xiang, X., 2020. Differential responses of arbuscular mycorrhizal fungal communities to mineral and organic fertilization. *Microbiologyopen* 9, 1–10. <https://doi.org/10.1002/mbo3.920>
- May, J.L., Oberbauer, S.F., 2021. Simulated hurricane-induced changes in light and nutrient regimes change seedling performance in Everglades forest-dominant species. *Ecol. Evol.* 11, 17762–17773. <https://doi.org/10.1002/ece3.8273>
- McMurdie, P.J., Holmes, S., 2013. Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. *PLoS One* 8. <https://doi.org/10.1371/journal.pone.0061217>
- Meléndez-Vazquez, F., Olmeda-Saldaña, M., Cruz, J., Arcila, D., Betancur, R., 2019. Effects of Hurricane Maria in hamlet communities (Serranidae: *Hypoplectrus* spp.) in Puerto Rico. *Ecol. Indic.* 107, 1–4. <https://doi.org/10.1016/j.ecolind.2019.105591>
- Moor, M., Davison, J., Öpik, M., Metsis, M., Saks, Ü., Jairus, T., Vasar, M., Zobel, M., 2014. Anthropogenic land use shapes the composition and phylogenetic structure of soil arbuscular mycorrhizal fungal communities. *FEMS Microbiol. Ecol.* 90, 609–621. <https://doi.org/10.1111/1574-6941.12420>
- Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol.* 20, 241–248. <https://doi.org/10.1016/j.funeco.2015.06.006>
- Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D., Kennedy, P., Picard, K., Glöckner, F.O., Tedersoo, L., Saar, I., Kõljalg, U., Abarenkov, K., 2019. The UNITE database for molecular identification of fungi: Handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res.* 47, D259–D264. <https://doi.org/10.1093/nar/gky1022>
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, E.S. and H., 2020. *vegan: Community Ecology Package*.
- Ostertag, R., Scatena, F.N., Silver, W., 2003. Forest Floor Decomposition Following Hurricane Litter Inputs in Several Puerto Rican Forests. *Ecosystems* 261–273. <https://doi.org/10.1007/s10021-002-0203-8>
- Parniske, M., 2008. Arbuscular mycorrhiza: The mother of plant root endosymbioses. *Nat. Rev. Microbiol.* 6, 763–775. <https://doi.org/10.1038/nrmicro1987>

- Powell, J.R., Rillig, M.C., 2018. Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytol.* 220, 1059–1075. <https://doi.org/10.1111/nph.15119>
- Prescott, C.E., Grayston, S.J., 2013. Tree species influence on microbial communities in litter and soil: Current knowledge and research needs. *For. Ecol. Manage.* 309, 19–27. <https://doi.org/10.1016/j.foreco.2013.02.034>
- Schowalter, T.D., Pandey, M., Presley, S.J., Willig, M.R., Zimmerman, J.K., 2021. Arthropods are not declining but are responsive to disturbance in the Luquillo experimental forest, Puerto Rico. *Proc. Natl. Acad. Sci. U. S. A.* 118. <https://doi.org/10.1073/PNAS.2002556117>
- Shi, Z., Li, K., Zhu, X., Wang, F., 2020. The worldwide leaf economic spectrum traits are closely linked with mycorrhizal traits. *Fungal Ecol.* 43. <https://doi.org/10.1016/j.funeco.2019.100877>
- Song, Y., Chen, D., Lu, K., Sun, Z., Zeng, R., 2015. Enhanced tomato disease resistance primed by arbuscular mycorrhizal fungus. *Front. Plant Sci.* 6, 1–13. <https://doi.org/10.3389/fpls.2015.00786>
- Soonvald, L., Loit, K., Runno-Paurson, E., Astover, A., Tedersoo, L., 2019. The role of long-term mineral and organic fertilisation treatment in changing pathogen and symbiont community composition in soil. *Appl. Soil Ecol.* 141, 45–53. <https://doi.org/10.1016/j.apsoil.2019.05.003>
- Trivedi, P., Delgado-Baquerizo, M., Anderson, I.C., Singh, B.K., 2016. Response of soil properties and microbial communities to agriculture: Implications for primary productivity and soil health indicators. *Front. Plant Sci.* 7, 1–13. <https://doi.org/10.3389/fpls.2016.00990>
- Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., Murphy, L., Sabat, A.M., Fetcher, N., Haines, B.L., 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: Results from a forest simulator. *Ecol. Monogr.* 79, 423–443. <https://doi.org/10.1890/08-0707.1>
- Uriarte, M., Thompson, J., Zimmerman, J.K., 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nat. Commun.* 10, 1–7. <https://doi.org/10.1038/s41467-019-09319-2>
- Van Der Heijden, M.G.A., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* 11, 296–310. <https://doi.org/10.1111/j.1461-0248.2007.01139.x>

- Van Der Heijden, M.G.A., Martin, F.M., Selosse, M.A., Sanders, I.R., 2015. Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytol.* 205, 1406–1423. <https://doi.org/10.1111/nph.13288>
- van der Heyde, M., Ohsowski, B., Abbott, L.K., Hart, M., 2017. Arbuscular mycorrhizal fungus responses to disturbance are context-dependent. *Mycorrhiza* 27, 431–440. <https://doi.org/10.1007/s00572-016-0759-3>
- Vargas, R., Hasselquist, N., Allen, E.B., Allen, M.F., 2010. Effects of a hurricane disturbance on aboveground forest structure, arbuscular mycorrhizae and belowground carbon in a restored tropical forest. *Ecosystems* 13, 118–128. <https://doi.org/10.1007/s10021-009-9305-x>
- Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhardt, F., Hermy, M., 2007. Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *J. Ecol.* 95, 565–573. <https://doi.org/10.1111/j.1365-2745.2007.01233.x>
- Waldrop, M.P., Holloway, J.M., Smith, D.B., Goldhaber, M.B., Drenovsky, R.E., Scow, K.M., Dick, R., Howard, D., Wylie, B., Grace, J.B., 2017. The interacting roles of climate, soils, and plant production on soil microbial communities at a continental scale. *Ecology* 98, 1957–1967. <https://doi.org/10.1002/ecy.1883>
- Wickam, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Wiley, E., Casper, B.B., Helliker, B.R., 2017. Recovery following defoliation involves shifts in allocation that favour storage and reproduction over radial growth in black oak. *J. Ecol.* 105, 412–424. <https://doi.org/10.1111/1365-2745.12672>
- Xu, X., Hirata, E., Shibata, H., 2004. Effect of typhoon disturbance on fine litterfall and related nutrient input in a subtropical forest on Okinawa Island, Japan. *Basic Appl. Ecol.* 5, 271–282. <https://doi.org/10.1016/j.baae.2004.01.001>
- Yuan, Z., Ali, A., Loreau, M., Ding, F., Liu, S., Sanaei, A., Zhou, W., Ye, J., Lin, F., Fang, S., Hao, Z., Wang, X., Le Bagousse-Pinguet, Y., 2021. Divergent above- and below-ground biodiversity pathways mediate disturbance impacts on temperate forest multifunctionality. *Glob. Chang. Biol.* 27, 2883–2894. <https://doi.org/10.1111/gcb.15606>



Zanne, A.E., Abarenkov, K., Afkhami, M.E., Aguilar-Trigueros, C.A., Bates, S., Bhatnagar, J.M., Busby, P.E., Christian, N., Cornwell, W.K., Crowther, T.W., Flores-Moreno, H., Floudas, D., Gazis, R., Hibbett, D., Kennedy, P., Lindner, D.L., Maynard, D.S., Milo, A.M., Nilsson, R.H., Powell, J., Schildhauer, M., Schilling, J., Treseder, K.K., 2020. Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biol. Rev.* 95, 409–433. <https://doi.org/10.1111/brv.12570>