ECOLOGICAL DRIVERS OF MICROBIOME ASSEMBLY IN A PANAMANIAN RAINFOREST

by

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Fungal pathogens in soil have been hypothesized to drive the maintenance of plant communities through population density-dependent feedbacks. For this to be the case, however, different species of fungi must show patterns of favoring certain tree host species. In this study, I analyzed metagenomic sequencing data to determine whether fungi formed distinct communities across 11 tree species. Soil and leaf litter samples were obtained from Gigante, a peninsula of Barro Colorado National Monument, Panama. I used FUNGuild, an online taxonomic database, to classify amplicon sequence variants (ASVs) into three ecological guilds: mutualists, pathogens, and decomposers. Using a pairwise PERMANOVA test, I found pathogenic fungi (in soil) and decomposer fungi (in soil and in litter) to show the strongest patterns of community divergence (for most tree species, $p < 0.05$), and mutualistic fungi had the weakest (for most tree species, $p > 0.10$). Findings were limited by a high percentage of unidentified taxa (60% – 63% unclassified ASVs for all tree species). Together, these results suggest that fungal pathogens and decomposers show strong patterns of community divergence across tree species, thereby potentially validating their roles in shaping aboveground plant community structure.

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Table of Contents

Accompanying Materials

My R code is online on a GitHub repository (Malamud 2022):

https://github.com/Gromulus-Romulus/2022-Panama-ASV-Analysis

List of Figures

List of Tables

In addition, **Tables A1-A6** in **Appendix A** contain *p*-values from the pairwise PERMANOVA test applied to three separate ecological guilds of fungi across soil and litter layers.

1. Introduction

Bacteria and fungi play an incredible and understudied role in shaping the diversity of tropical rainforests. Through field surveys in the tropics, ecologists have shown that soil microbes are largely responsible for shaping plant communities (Mangan *et al.* 2010; Comita *et al.* 2010; Eck *et al.* 2019). Through their interactions with plant roots, seedlings, and organic detritus, microbes mediate plant fitness and dispersal through a complex set of interactions referred to collectively as plant-soil feedbacks (Van der Putten *et al.* 2016; Friesen *et al.* 2011). Microbes can have many types of interactions with plants, ranging on a continuum from mutualism to parasitism. As a result, plant-soil feedbacks have been shown to have a range of effects (from positive to negative) on the population dynamics of tropical tree species (Van der Putten *et al.* 2016; Deniau *et al.* 2018).

The role of different microbial groups in the maintenance of tropical rainforests has been implicated for several decades, but direct tests of microbial assembly mechanisms across different tree species are sparse. The *Janzen-Connell hypothesis*, formed independently by Janzen (1970) and Connell (1970), explains that plant predators maintain the diversity of plant communities by targeting areas of high seedling density. In their hypothesis, Janzen (1970) and Connell (1970) propose that species-specific herbivores and pathogens prevent the dominance of any one tree species by targeting seedlings at the base of the parent trees. The targeting of seedlings around parent trees leads to a phenomenon often referred to as negative density-dependence: as a population grows larger (denser), negative pressures exerted by pathogens and herbivores become greater, and the growth of the entire population is

inhibited as a result (Comita *et al.* 2010). This phenomenon has been shown to be present in tropical rainforests (Wright 2002) and has been assumed to be regulated primarily by microbial pathogens (Mangan *et al.* 2010). Recent studies have also been able to update the Janzen-Connell hypothesis to account for the effects of microbial mutualists and decomposers on the structure of plant communities (Deniau *et al.* 2018).

Previous studies have shown evidence of negative density-dependence operating in Barro Colorado National Monument, a famous long-term ecological research site in Panama (Mangan *et al.* 2010; Comita *et al.* 2010; Eck *et al.* 2019). However, a key assumption of the Janzen-Connell hypothesis, microbe-host specificity, is lacking evidence. Negative density dependence has been observed in Barro Colorado tree species (Comita *et al.* 2010; Eck *et al.* 2019), and the underlying cause has been attributed to microorganisms (Mangan *et al.* 2010). Despite our expectation that different plant populations should have a distinct associated microbiome, the reality is not so straightforward. There appear to be strong correlations between microbiome assembly and above-ground plant composition, but species-specific patterns of plant-microbe feedbacks have not been sufficiently investigated (Barberan *et al.* 2015; McGuire *et al.* 2012).

Despite their importance for tropical rainforest ecology, the mechanisms driving microbiome assembly are still not well understood. Environmental gradients involving soil pH, moisture, and geologic structure have profound roles in structuring bacterial communities (Fierer 2017). In contrast, fungal dispersal appears to be driven more by complex biotic ecological factors. Pathogens and saprotrophic fungi appear to co-evolve in response to plant anti-herbivory defense strategies (Gallery *et al.* 2010; Marden *et al.*

2017). This variation leads to a very familiar case of a co-evolutionary "arms race": as plants become better at developing different defense strategies, different groups of pathogens become better at overcoming specific defenses (de Vries *et al*. 2020). For saprotrophic fungi, the driver for co-evolution comes not from variation in plant defenses, but instead from structural diversity in organic compounds (such as lignins and polyphenols) that are being degraded by the microbes (Osono 2020; Proß *et al*. 2021). Arbuscular mycorrhizae (an entire clade of fungi that form mutualisms with plants) on the other hand, appear to be well conserved across plant species (Öpik *et al.* 2002; Mangan *et al.* 2004), yet still appear to play a role in density-dependent population dynamics (Deniau *et al.* 2018).

To reveal species-specific relationships across microbial taxa in soil and above-ground plant communities, I analyzed genomic sequencing data from tree-adjacent soil and litter samples to describe the distribution of three ecological guilds of fungi (each guild containing many identified and unidentified species strains) across eleven tree species in a tropical Panamanian rainforest. The work done for this thesis is part of a more extensive collaboration between the University of Oregon (USA), the Smithsonian Tropical Research Institute (USA), and the University of Haifa (Israel). The following research questions (Q) were addressed:

Q1. How do soil fungal communities vary across tree species?

Q2. How do fungi in mineral soil (0-20 cm) compare to fungi in litter (O^{i-e} horizons) in their assembly patterns across different tree species?

Q3. Do different fungal functional groups show unique assembly patterns across individual tree species?

A set of ten key terms used throughout this thesis are given in **Table 1**.

Term	Definition
Barro Colorado Nature Monument (BCNM)	A Long-Term Ecological Research (LTER) site run by the Smithsonian Institute for Tropical Research. Contains *Barro Colorado Island (BCI)* along with 4 other peninsulas in the Panama Canal.
Community Assembly	Used interchangeably with *community composition* to refer to the overall abundance of species (microbial or plant) within a region.
Ecological Guild	A group of species that exploit different resources in different ways. These are also referred to as *functional guilds* and *functional groups.*
Herbivore	An animal (microbial, insect, mammal, or otherwise) that feeds on plants or plant material, such as seeds.
Litter	Leaf detritus found on the forest floor. Often referred to as the O^{i-e} horizons, indicating the topmost organic layers of the soil.
Pathogen	An organism (usually a microbe) that causes disease in a host. Can be plant or animal specific.
Plant Soil Feedbacks	The complex set of interactions that occur between soil microbes and plants.
Metagenomics	Techniques and methodologies for studying microbial DNA isolated from environmental samples, such as soil or water.
Mycorrhiza	A mutual symbiotic association between a fungus and a plant. The plural term is *mycorrhizae.* In tropical rainforests, these relationships show up most often in the form of *arbuscular mycorrhiza*, in which the fungal symbiont penetrates the root cells to exchange soil nutrients for sugars produced by the plant.
Negative Density Dependence	A phenomenon predicted by the *Janzen-Connell hypothesis* in which host-specific herbivores and pathogens regulate the growth of a plant population.

Table 1. Ten key terms and definitions used in this thesis.

2. Methods

2.1 Site description, Tree Species Surveyed, Soil and Litter Sampling

The analysis used in my thesis draws upon prior collected soil and litter sample cores from Gigante – a peninsula of Barro Colorado National Monument, Panama (9° 5' N, -79° 52' W). Barro Colorado is one of the most intensively studied tropical rainforests in the world (Anderson-Teixeira *et al.* 2015). In a permanent research plot (800 × 480 m) on Gigante, 11 different tree species were surveyed. Soil (0-20 cm) and litter (O^{i-e} horizons) were separately collected from the four cardinal directions of each tree and pooled for each sample. Soil was collected using a soil corer (sterilized with ethanol between subsequent samplings) and litter was collected using a 5 cm × 5 cm square. In total, there were 126 soil samples and 118 leaf litter samples (**Table 2**).

Species	**Family**	**Code**	**# Soil**	**# Litter**
Alseis blackiana	*Rubiaceae*	ALBL	7	7
Cordia bicolor	*Boraginaceae*	COBI	18	18
Dialium guianense	*Fabaceae*	DIGU	20	19
Heisteria concinna	*Olacaceae*	HECO	20	16
Hirtella triandra	*Chrysobalanaceae*	HITR	6	6
Jacaranda copaia	*Bignoniaceae*	JACO	7	7
Prioria copaifera	*Fabaceae*	PRCO	20	17
Simarouba amara	*Simaroubaceae*	SIAM	8	7
Tabebuia guayacan	*Bignoniaceae*	TAGU	5	5
Tetragastris panamensis	*Burseraceae*	TEPA	8	9
Virola sebifera	*Myristicaceae*	VISE	7	7

Table 2. The 11 tree species surveyed in my thesis data listed with their 4-digit identification codes and the number of soil (total 126) and leaf litter (total 118) samples taken for each (samples provided by the McGuire lab).

2.2 Metagenomic Sequencing

Fungal DNA was extracted from the soil and litter cores at the University of Oregon using single-tube and high-throughput extraction kits (Qiagen, Inc., Düsseldorf, Germany). Following DNA extraction and PCR amplification, the ITS (internal transcribed spacer) marker gene was sequenced using the Illumina HiSeq platform (Illumina Inc., San Diego, CA, USA). Bioinformatic analysis was done to separate the ITS sequence reads into groupings of amplicon sequence variants (ASVs). The resulting ASV table allowed me to use the ITS marker gene variants as proxies for microbial species. The ITS region served as a molecular "barcode" that allowed the McGuire lab to identify strains of fungi solely from analyzing sequencing data on a computer. This is often necessary because not all microbial species have been identified or are even culturable in a lab setting (Perez-Cobaz *et al.* 2020; Liu *et al.* 2021).

2.3 Identification of Ecological Guilds

The resulting ASV table was provided as input into FUNGuild (Nguyen *et al.* 2016) – an online research-curated database that determines which ecological "guild" each sequenced microbial taxon falls into. A guild can be thought of as a microbial life strategy: whether a microbe makes its living by supporting the plant, harming the plant, or some mixture of both. There were many different functional guilds present in the ASV table, but my subsequent analysis just focused on three: mutualists, decomposers, and pathogens. These three guilds are very abundant in the tropics and are often the primary focus of many pertinent studies (Van der Putten *et al.* 2016).

2.4 Statistical Analysis in R

ASV tables, sample metadata, and guild classifications were all analyzed using the R programming language. The phyloseq package was used for managing data within the ASV tables (McMurdie & Holmes 2002) and the vegan and EcolUtils packages were used for statistical analyses (Dixon 2002; Salazar 2019). A pairwise PERMANOVA (Permutational Analysis of Variance) test evaluated differences in fungal communities across tree species. Statistical assumptions of the pairwise PERMANOVA test were tested prior to using a test for Beta-dispersion (homogenous dispersion of groups). The PERMANOVA test evaluated compositional differences in fungal taxa across tree samples using the Bray-Curtis metric (Bray & Curtis 1957).

2.5 Visualization Techniques

Stacked bar charts were used to show the relative abundances of microbial guilds and fungal genera across all samples for each separate tree species. Ordination plots, generated by applying NMDS (non-metric multidimensional scaling) to the ASV table, were used to visualize divergence in fungal communities. One ordination plot was generated to show that fungal community assembly diverges across litter and soil samples. Separate ordination plots were then also generated to show divergence across tree species for each functional guild in soil and litter samples.

My R code is online on a GitHub repository (Malamud 2022): https://github.com/Gromulus-Romulus/2022-Panama-ASV-Analysis

3. Results

3.1 Diversity of Fungal Guilds across Tree Species

ITS sequencing followed by bioinformatic analysis yielded an amplicon sequence variant (ASV) table with 16,648 sequence variants. Each variant served as a distinguishable barcode for a different family, genus, or species of fungi. FUNGuild classified around 40% of these ASVs into 10 different ecological guilds, and the remaining taxa were listed as unidentified (**Figure 1**).

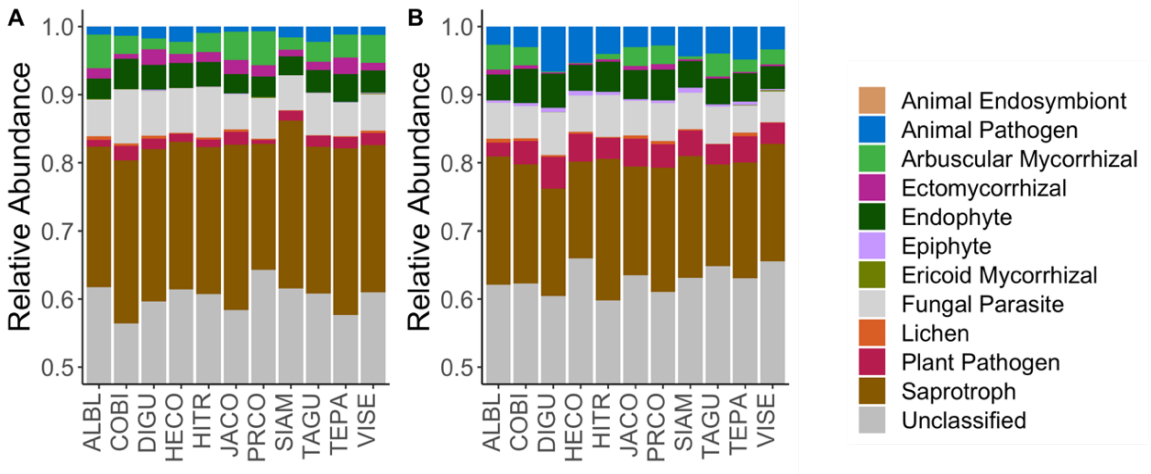

Figure 1. Relative abundance of 10 fungal guilds (plus a category for unclassified taxa), as given in the legend across 11 tree species (listed as 4-letter identification codes along the *x*-axis, which are given in **Table 2**). Separate stacked bar charts were made to show differences in (A) soil samples and (B) litter samples. Note that the relative abundance on the *y*-axis starts at 0.5, with 0.0 to 0.5 part of the category 'unclassified'. From 60% to 63% of all alternative sequence variants (ASV) were unclassified and not assigned a guild.

As shown in **Figure 1**, Relative abundances for saprotrophic fungi (decomposers) were slightly higher in soil than in litter. Arbuscular mycorrhizae (AMF), or mutualists, were much more prevalent in soil, but still showed up consistently in litter samples. Plant pathogens, which are of particular interest to the

Janzen-Connell hypothesis, made up a significantly smaller percentage of all fungal taxa and showed up more in litter than in soil (along with animal pathogens, lichens, and fungal epiphytes).

3.2 Diversity of Fungal Genera across Tree Species

To further investigate differences between soil and litter composition, separate bar charts were made for known mutualists, decomposers, and pathogens across soil and litter samples (**Figure 2A–F**). Fifteen total AMF genera were present, along with 457 saprotrophic genera and 141 pathogenic genera across all samples. Many saprotrophs and pathogens had low read counts in the ASV table (abundance of ≈ 0.000), so they were grouped into "other" categories and the top 15 most abundant in soil and litter were visualized. Bar charts were color coded so that the same color represented genera that showed up in both soil and litter.

Genus *Acaulospora* was ubiquitous across all litter samples (**Figure 2B**) and showed up consistently in soil (**Figure 2A**). *Rhizoglomus* was second most abundant and was found more in litter than in soil. Several AMF taxa were much more abundant in soil (*Glomus*, *Corymbiglomus*, *Scutellospora*), but some were more abundant in litter (*Funneliformis*, *Rhizoglomus*). Similar patterns can be seen for decomposers in soil (**Figure 2C**) and litter (**Figure 2D**), as well as for pathogens in soil (**Figure 2E**) and litter (**Figure 2F**). Some genera were classified by FUNGuild as both pathogens and decomposers (e.g., *Acremonium*, *Marasmius, Trichoderma*), which is why they show up twice in some of the subfigures.

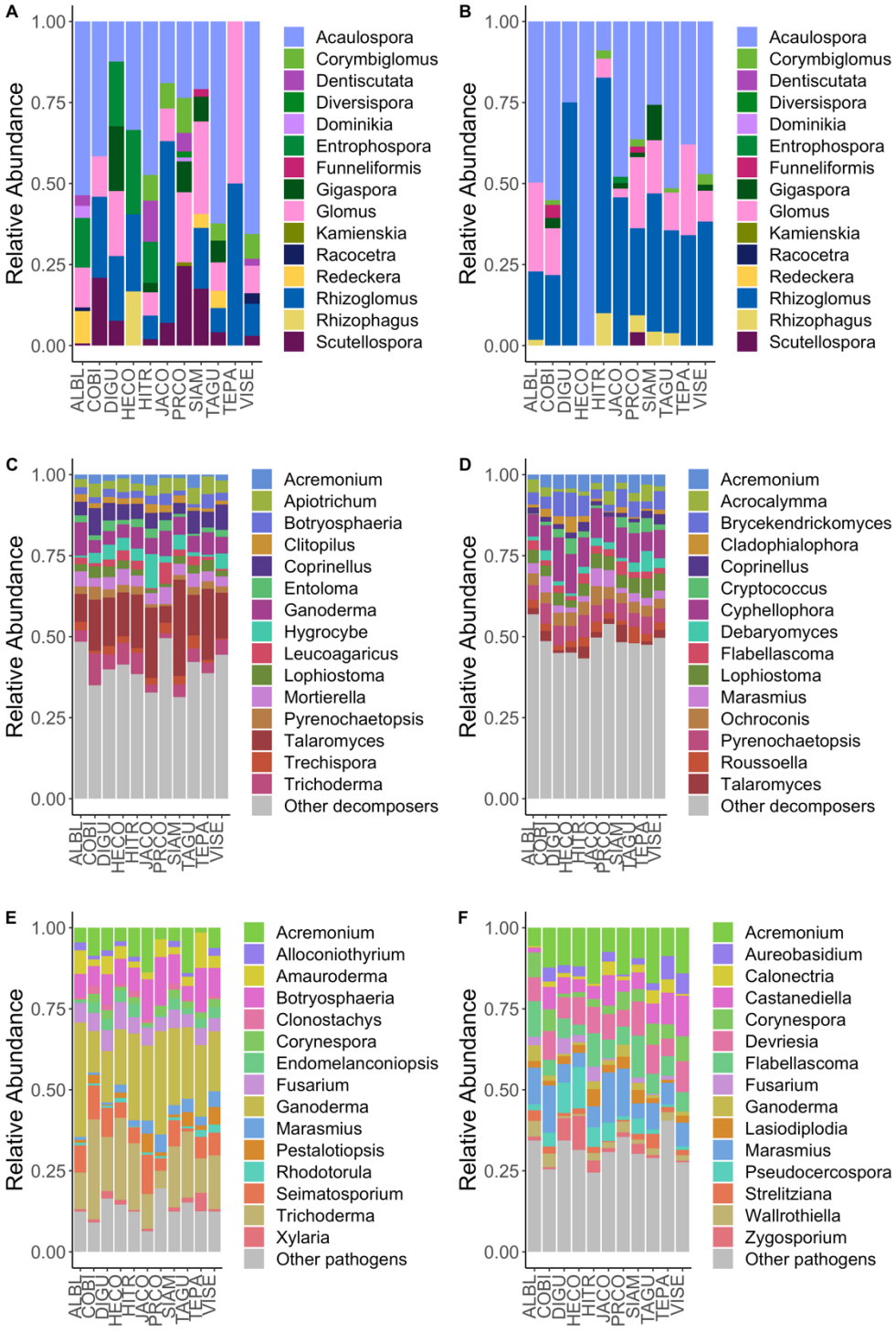

Figure 2. Stacked bar charts visualizing relative abundances of fungal genera within each separate fungal guild. The figures are listed as follows: arbuscular mycorrhizae (AMF) in (A) soil and (B) litter; decomposers in (C) soil and (D) litter; pathogens in (E) soil and (F) litter.

3.3 Analysis of Variance between Tree Microbiomes

Non-metric multidimensional scaling allowed fungal community divergence to be viewed on a two-dimensional grid (**Figure 3**). Distances between distinct clusters of points formed on the ordination plots were tested using permutational analysis of variance (PERMANOVA).

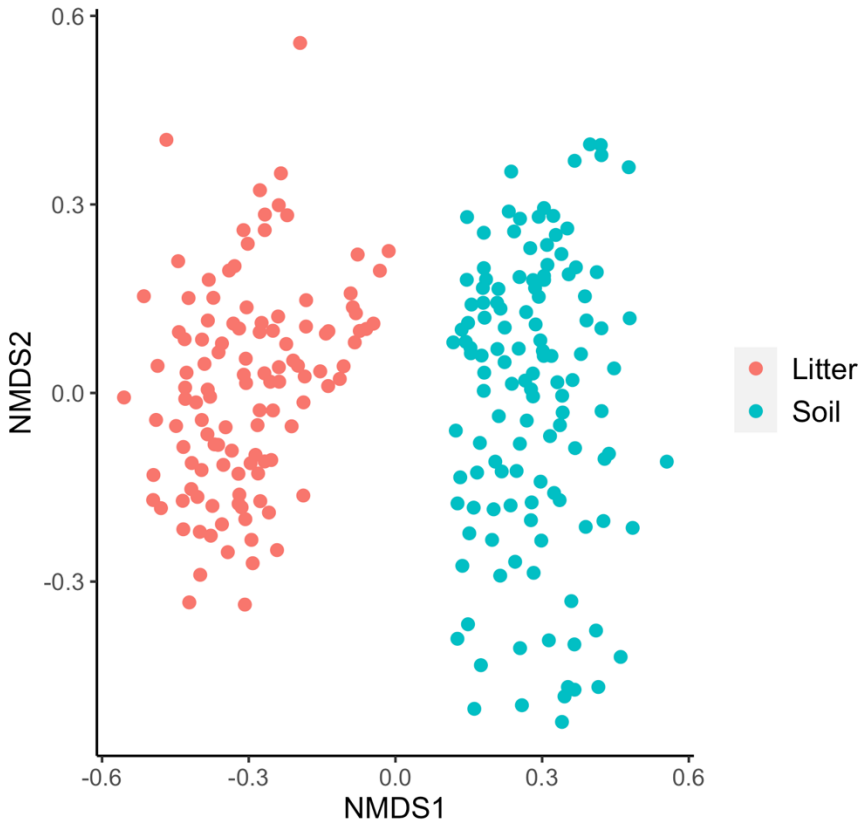

Figure 3. Ordination plot visualizing divergence of all fungal taxa across soil and litter layers. The results shown in this figure were confirmed by a permutational analysis of variance (PERMANOVA) test across litter and soil ($F = 25.846, p \approx 0.001$).

In addition, a separate bar chart was made to visualize the community divergence of the three fungal guilds across soil and litter separately (**Figure 4A–F**).

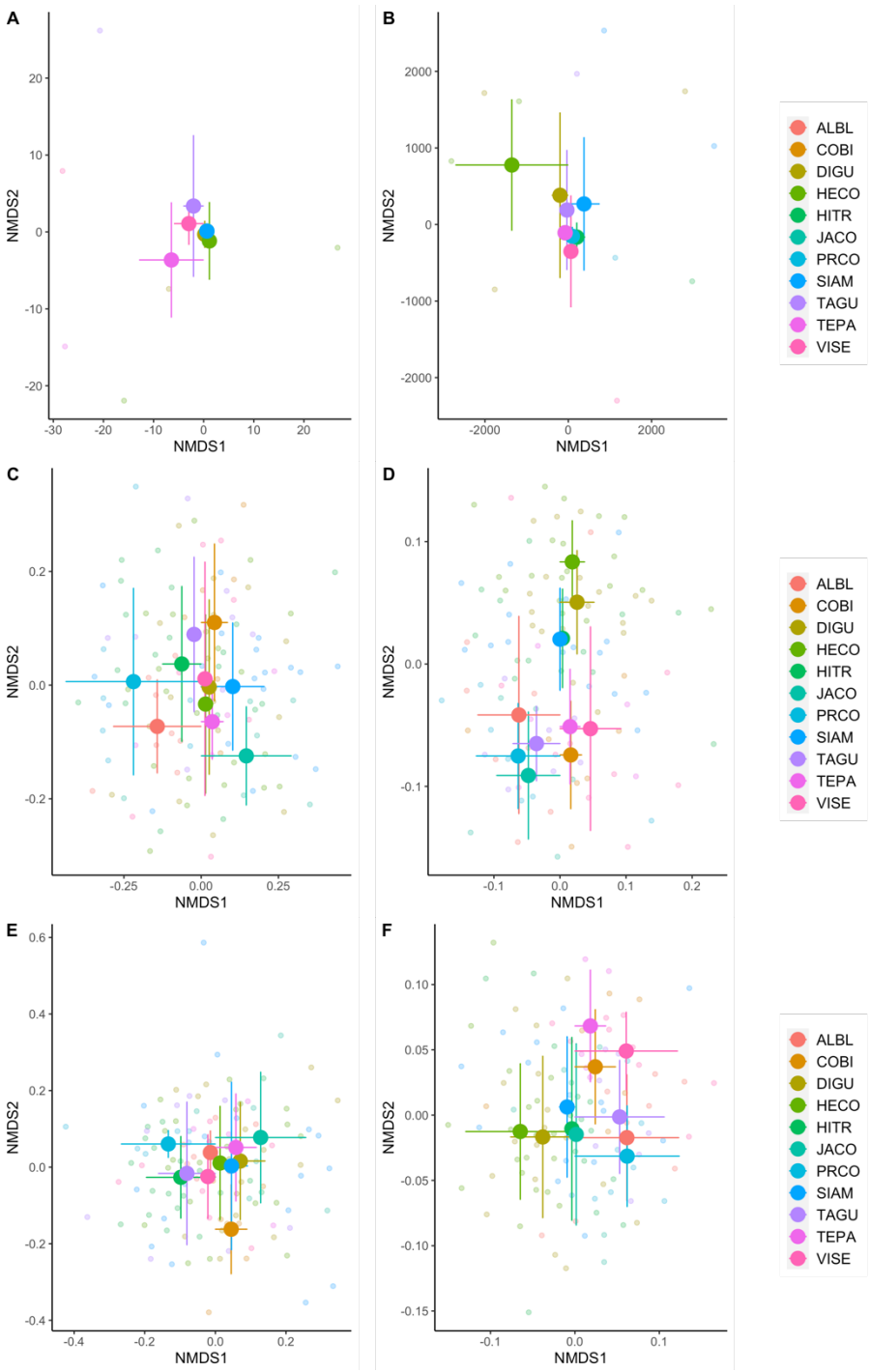

Figure 4. Ordination plots visualizing separation of fungal guilds across all tree species: AMF in (A) soil and (B) litter; decomposers in (C) soil and (D) litter; pathogens in (E) soil and (F) litter. Note that *y*-axis (NMDS2) and *x*-axis (NDMS1) scales are given over different overall ranges for A to F. Results of pairwise statistical tests are given in **Appendix A**.

Separation of fungal ASVs varied depending on what fungal guild was being considered and whether the samples were derived from the soil or leaf litter layer. Beta-dispersion showed that distances between clustered points and their centroids were equivalent enough to warrant the use of a pairwise PERMANOVA test. The results of this test, which evaluated community divergence between each pair of tree species in soil and litter, are listed in the attached appendix document (**Appendix A)**.

4. Discussion

My statistical analyses have revealed some interesting large-scale patterns that may aid in the future identification of species-level relationships between tropical tree species and fungal symbionts. Ordination plots have shown that the forest floor's soil and leaf litter layers harbor distinct fungal communities, with some overlapping genera. Plant pathogens were more abundant in litter samples than in soil samples, AMF (arbuscular mycorrhizae) were more abundant in soil samples than in litter samples, and saprotrophic fungi (decomposers) were roughly equal across both layers. The degree to which fungal communities diverge depends on what ecological guild is being considered, what layer of the soil is sampled, and even what tree species are being compared.

Pathogenic and saprotrophic fungi (decomposers) appear to exhibit the strongest patterns of tree host-specificity. Ordination plots for these groups exhibited a high degree of within-group clustering and inter-group separation across the 11 tree species. These charts are further supported by the table of *p*-values from the pairwise PERMANOVA test (**Appendix A**). Clustering was observed and statistically confirmed in 3 out of the 6 possible categories: decomposers in soil, decomposers in litter, and pathogens in litter. Clustering was not observed amongst pathogens in soil, although that may be explained by the overwhelmingly high relative abundances of *Trichoderma* and *Ganoderma* within litter samples.

Previous studies have investigated the underlying evolutionary and genetic causes for pathogen-host specificity in tropical ecosystems (Gallery *et al.* 2010; Marden *et al*. 2017) and have found soil pathogens to be tied strongly to density-dependent

effects (Mangan *et al.* 2010). My analysis has shown that to view the role of pathogens in negative density-dependence, we need to investigate what is going on in the litter layer, in addition to the soil layer. Decomposers are also likely to play a strong role in shaping plant communities, given that they are (a) overwhelmingly abundant in both soil and litter samples and (b) show a higher degree of community divergence. In addition, the assignment of ecological guilds is somewhat restricting since certain species of microorganisms can employ a variety of different life strategies. *Trichoderma* and *Acremonium* showed up both as pathogens and decomposers in the top 15 most prevalent fungal genera for each of the two guilds.

Species in the genera *Acremonium* and *Marasmius* were particularly prevalent in litter when viewing taxa that were classified as both pathogenic and saprotrophic fungi. Across all tree litter samples, *Acremonium* taxa made up <25% of all saprotrophic taxa and <12.5% of all pathogenic taxa. In addition to their apparent affinity for degrading tree matter, they have also been shown to form endophytic relationships with mangrove trees (Hammerschmidt *et al*. 2014). Fungal strains of *Marasmius* were highly abundant pathogens in leaf litter and their representation in the stacked bar charts was highest among tree species *Alseis blackiana* (ALBL), *Cordia bicolor* (COBI), *Jacaranda copaia* (JACO), and *Prioria copaifera* (PRCO). *Marasmius* strains can have especially detrimental effects on different tree species. A research article on plant pathology from Ghana shows that *Marasmius* can cause blight in Cacao trees (Amoako-Attah *et al.* 2020). Depending on whether species within *Marasmius* and *Acremonium* form more pathogenic relationships, more saprotrophic relationships, or a different kind of

relationship not being considered, they could have varying effects on the dispersal of the plant species surveyed in Barro Colorado.

While saprotrophic and pathogenic fungi showed strong patterns of community divergence across tree species, AMF fungi did not appear to have the same patterns. There were only 15 AMF genera sampled across all sites (compared to over 400 decomposer genera and over 100 pathogen genera). The PERMANOVA test did not reveal any two tree species that had sufficiently distinct compositional differences in AMF taxa (all p-values were $p > 0.10$). Some of this could be explained by sequencing bias: perhaps the PCR primers for the ITS region favored AMF less than other types of fungi. However, even that would not make much difference since AMF fungal partners appear to be highly conserved across plant species. *Glomus* and *Scutellospora* species were among the most prevalent genera in a meta-analysis of 26 molecular surveys worldwide (Öpik *et al.* 2006). Another survey restricted in scope to Panama found *Acaulospora* and *Glomus* to be the most prevalent amongst fragmented forest habitats (Mangan *et al.* 2004). Nevertheless, even if AMF species form a predictable oligarchy across Panamanian rainforests, their role in shaping community structure should not be neglected in future studies (Deniau *et al.* 2018).

This study is limited by (a) a lack of data for temporal changes in microbiome assembly and (b) classification of ecological guilds was not able to account for unidentified taxa in the ASV table. Changes in microbiome assembly over time are important to study because changing climatic conditions may have an influence on ecological relationships (Fierer 2017). In addition, around 60% to 63% of ASVs at each sample site were unable to be classified into an ecological guild. If future advances are

made in assigning ASVs to known species, then the results of analyzing relationships within separate ecological guilds may be made even more clear. That said, unclassified taxa are not expected to significantly affect the results of the NMDS and PERMANOVA tests, as these tests were done using ASV table abundances instead of overall guild abundances.

Nevertheless, decomposer and pathogenic fungi appear to form distinct communities around separate tree species. This confirms the underlying assumption of the Janzen-Connell hypothesis and indicates that these microbes may play an important role in maintaining tropical tree coexistence (Mangan *et al.* 2010). More work will need to be done to see how prevalent genera in overlapping guild classifications, such as *Acremonium* and *Marasmius*, impact the growth of tree species in Barro Colorado. In addition, arbuscular mycorrhizae (AMF) should not be neglected even though they appear to be more generalist. Future studies may be able to better evaluate the role that AMF fungi play in shaping forest community structure. Broader studies may even be able to show how the impact of fungi works in tandem with other herbivores like insects in shaping plant community structure (Becerra 2015). In an even broader context, bioinformatic analyses and data-driven studies like the one I have carried out for my thesis will allow researchers to better understand the infinite complexity of relationships between plants, soil, and microbes.

5. Appendix

Appendix A: Pairwise PERMANOVA corrected *p*-values rounded to 3 decimal places. Each analysis was done with *N*=999 random permutations. Reproducing these results may not yield the exact same values given the inherent element of randomness within the test itself.

Table A1: Community Divergence across AMF in Soil.

	COBI	DIGU	HECO	HITR	JACO	PRCO	SIAM	TAGU	TEPA	VISE
ALBL	0.255	0.106	0.167	0.162	0.106	0.464	0.339	0.148	0.572	0.106
COBI		0.210	0.533	0.190	0.533	0.106	0.573	0.644	0.55	0.533
DIGU			0.831	0.106	0.147	0.106	0.553	0.533	0.533	0.106
HECO				0.106	0.106	0.106	0.673	0.831	0.573	0.106
HITR					0.106	0.106	0.533	0.162	0.673	0.106
JACO						0.106	0.522	0.351	0.190	0.117
PRCO							0.533	0.190	0.533	0.126
SIAM								0.673	0.833	0.167
TAGU									0.553	0.573
TEPA										0.313

Table A2: Community Divergence across AMF in Litter.

	COBI	DIGU	HECO	HITR	JACO	PRCO	SIAM	TAGU	TEPA	VISE
ALBL	0.750	0.595	0.595	0.750	0.709	0.874	0.874	0.891	0.68	0.874
COBI		0.055	0.532	0.532	0.532	0.646	0.532	0.532	0.874	0.595
DIGU			1.000	0.750	0.595	0.595	0.874	0.595	0.778	0.595
HECO				0.750	0.595	0.642	0.848	0.595	0.750	0.646
HITR					0.595	0.750	0.874	0.642	0.631	0.750
JACO						1.000	0.620	0.774	0.595	0.750
PRCO							0.874	0.750	0.750	0.874
SIAM								0.750	0.870	0.750
TAGU									0.874	0.874
TEPA										0.646

Legend

Dark orange	$p \geq 0.20$
Light orange	$0.20 > p \geq 0.10$
White	$0.10 > p \geq 0.05$
Light green	$0.05 > p \geq 0.01$
Dark green	$p < 0.01$

Table A3: Community Divergence across Decomposers in Soil.

	COBI	DIGU	HECO	HITR	JACO	PRCO	SIAM	TAGU	TEPA	VISE
ALBL	0.003	0.003	0.003	0.005	0.008	0.012	0.003	0.003	0.019	0.008
COBI		0.008	0.003	0.003	0.003	0.003	0.005	0.006	0.006	0.303
DIGU			0.739	0.006	0.009	0.003	0.005	0.022	0.226	0.154
HECO				0.009	0.006	0.003	0.003	0.008	0.083	0.056
HITR					0.006	0.003	0.005	0.003	0.076	0.008
JACO						0.013	0.070	0.008	0.260	0.011
PRCO							0.003	0.012	0.014	0.005
SIAM								0.003	0.129	0.005
TAGU									0.075	0.065
TEPA										0.075

Table A4: Community Divergence across Decomposers in Litter.

	COBI	DIGU	HECO	HITR	JACO	PRCO	SIAM	TAGU	TEPA	VISE
ALBL	0.008	0.003	0.003	0.011	0.086	0.036	0.004	0.007	0.022	0.007
COBI		0.003	0.003	0.036	0.014	0.009	0.019	0.101	0.128	0.078
DIGU			0.070	0.008	0.003	0.003	0.003	0.003	0.003	0.003
HECO				0.004	0.003	0.003	0.003	0.003	0.006	0.003
HITR					0.003	0.003	0.077	0.004	0.031	0.004
JACO						0.004	0.003	0.013	0.079	0.019
PRCO							0.003	0.004	0.022	0.003
SIAM								0.003	0.012	0.003
TAGU									0.053	0.007
TEPA										0.221

Legend

Dark orange	$p \geq 0.20$
Light orange	$0.20 > p \geq 0.10$
White	$0.10 > p \geq 0.05$
Light green	$0.05 > p \geq 0.01$
Dark green	$p < 0.01$

Table A5: Community Divergence across Pathogens in Soil.

	COBI	DIGU	HECO	HITR	JACO	PRCO	SIAM	TAGU	TEPA	VISE
ALBL	0.028	0.082	0.175	0.086	0.086	0.745	0.175	0.028	0.522	0.380
COBI		0.086	0.039	0.028	0.06	0.039	0.049	0.156	0.196	0.807
DIGU			0.777	0.028	0.741	0.086	0.741	0.218	0.807	0.909
HECO				0.142	0.66	0.186	0.608	0.266	0.807	0.807
HITR					0.039	0.224	0.049	0.041	0.150	0.235
JACO						0.307	0.807	0.175	0.766	0.807
PRCO							0.370	0.199	0.472	0.741
SIAM								0.184	0.741	0.807
TAGU									0.545	0.661
TEPA										0.766
VISE										

Table A6: Community Divergence across Pathogens in Litter.

	COBI	DIGU	HECO	HITR	JACO	PRCO	SIAM	TAGU	TEPA	VISE
ALBL	0.432	0.004	0.004	0.060	0.090	0.347	0.250	0.045	0.021	0.04
COBI		0.007	0.004	0.155	0.506	0.432	0.060	0.347	0.316	0.923
DIGU			0.025	0.008	0.007	0.004	0.045	0.004	0.006	0.004
HECO				0.004	0.006	0.004	0.004	0.004	0.004	0.004
HITR					0.034	0.012	0.552	0.028	0.016	0.004
JACO						0.033	0.137	0.006	0.037	0.025
PRCO							0.008	0.007	0.041	0.004
SIAM								0.006	0.007	0.004
TAGU									0.007	0.070
TEPA										0.036

Legend

Dark orange	$p \geq 0.20$
Light orange	$0.20 > p \geq 0.10$
White	$0.10 > p \geq 0.05$
Light green	$0.05 > p \geq 0.01$
Dark green	$p < 0.01$

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