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RESEARCH ARTICLE

Seasonality regulates the structure and biogeochemical impact of ectomycorrhizal fungal communities across environmentally divergent neotropical dry forests

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Abstract

1. Ectomycorrhizal (ECM) symbioses support forest functioning globally, yet both the structure and function of ECM fungal communities in seasonally dry neotropical forests (SDTFs), known for extreme heterogeneity in vegetation and edaphic properties, remain under characterized.
2. Here, we evaluated the relative influences of seasonal versus spatial variation in ECM fungal community structure in soils from four environmentally divergent SDTFs. We also assessed the importance of biotic and abiotic drivers of SDTF ECM fungal community structure at regional scales, as well as ECM impacts on soil carbon (C) and nitrogen (N) cycling.
3. ECM fungal frequency, relative abundance and richness all increased in the wet season, but spatial rather than seasonal effects explained more variation in community composition. Across the four SDTFs investigated, differences in tree communities drove ECM fungal community turnover more than geographic distances, site abiotic conditions or soil chemistry. Although soil moisture and ECM tree basal area were stronger predictors of soil biogeochemistry, incorporating ECM fungal community composition and relative abundance added explanatory power to models of soil C and N cycling in the wet season.
4. *Synthesis*: Our results highlight the importance of seasonality and plant community composition in shaping different aspects of SDTF ECM fungal community structure and diversity as well as the potential for both the plant and fungal components of ECM symbioses to impact soil functioning across heterogenous SDTFs. Furthermore, our findings suggest that alterations in SDTF plant community

composition due to climate or land-use change will have important consequences for ECM fungal diversity and associated effects on soil biogeochemical cycling.

KEYWORDS
ectomycorrhizal functioning, fungal community structure, neotropical dry forests, soil carbon and nitrogen cycling

1 | INTRODUCTION

Ectomycorrhizal (ECM) fungi play a key regulatory role in host plant productivity and soil biogeochemistry, contributing substantially to the diversity and functioning of microbial communities in many forest ecosystems (Averill et al., 2014; Bahram et al., 2020; Van Der Heijden et al., 2006). Although previously thought to be largely absent in tropical settings, there is growing evidence that ECM symbioses are regularly present in low-elevation tropical forests (Corrales et al., 2018, 2022). The most well-known ECM forests in tropical regions are the monodominant rainforests of Africa (Newberry et al., 1988; Tedersoo et al., 2012), Asia (Peay, Bidartondo, et al., 2010, Peay, Kennedy, et al., 2010) and the Americas (Smith et al., 2011, 2013). An increasing number of studies have also documented that ECM fungi are present in non-monodominant tropical rain forests (Alvarez-Manjarrez et al., 2018; Hayward & Horton, 2012; Tedersoo & Põlme, 2012; Tedersoo et al., 2010; Vasco-Palacios et al., 2020). In these hyperdiverse and more widespread tropical forests, ECM symbioses are characterized by hosts occurring in relatively low and patchy abundance and ECM fungi localized to areas surrounding individual host trees (Alexander, 2006; Bahram et al., 2013; Newbery et al., 2013). How different ecological factors affect the diversity and functioning of ECM fungi in non-monodominant tropical forests remains largely unknown, despite the potential for ECM symbioses to predict nutrient cycling in mixed forest environments (Fitch et al., 2020; Taylor et al., 2016; Waring et al., 2021).

Tropical forests occur across a wide spectrum of total annual precipitation, with many areas experiencing high variation in precipitation quantities by season (Allen et al., 2017). SDTFs are characterized by highly variable periods (2–7 months) of reduced rainfall (Murphy & Lugo, 1986; Pennington et al., 2018). Production of ECM fungal mycelium has also been shown to increase in response to greater water availability (Nilsen et al., 1998; Swaty et al., 2004; Taniguchi et al., 2018) and plant C allocation below-ground (Cavelier et al., 1999; Yavitt & Wright, 2001). Furthermore, the frequency and abundance of ECM fungal taxa can vary intra-annually, likely reflecting differing temporal strategies that avoid interspecific competition while maximizing access to host- and soil-derived resources (Bogar & Peay, 2017; Koide et al., 2007; Šťursová et al., 2020; Voříškova et al., 2014). Studies that have characterized the seasonal dynamics of tropical ECM fungi have found mixed support for seasonal shifts in ECM fungal community diversity and/or composition. Disyatat et al. (2016) found that ECM fungal richness was higher in the wet season, while Pachit et al. (2023) did not detect seasonal differences in ECM fungal richness or community composition in two deciduous dipterocarp forests. If host plants selectively partner with drought-tolerant ECM taxa that improve resilience to climate extremes within and between years, then temporal variability in ECM fungal communities may be low or non-existent (Bogar & Peay, 2017; Moeller & Neubert, 2016). Additionally, the distribution of rainfall throughout the year (rainfall seasonality) along with total mean annual precipitation (MAP) govern host plant distributions and soil properties, which in turn shape ECM fungal community composition (Dahlberg, 2001; Hayward & Horton, 2012; Tedersoo et al., 2012; Vasco-Palacios et al., 2020). Because SDTFs encompass notable plant-related and edaphic heterogeneity (Pennington et al., 2018; Waring et al., 2021), they represent a unique system to identify key environmental drivers of ECM fungal community composition across tropical forests.

With the rise of molecular-based identification, there has been growing recognition that ECM fungi exhibit biogeographic patterns driven by both dispersal limitation and environmental selection (Peay, Bidartondo, et al., 2010; Peay, Kennedy, et al., 2010). In contrast to the 'everything is everywhere' hypothesis postulated for organisms with microscopic propagules (Baas Becking, 1934), the dispersal of ECM fungal spores has been demonstrated consistently to be spatially limited (Galante et al., 2011; Peay et al., 2012), with ECM fungal communities in lowland neotropical forests showing significant turnover within just tens of meters (Bahram et al., 2013). Recent analyses of soil fungal communities also suggest that there is considerable turnover in fungal species across the SDTF biome in the neotropics (Tedersoo et al., 2022), which parallels similar biogeographic heterogeneity in plant community composition (Banda et al., 2016). ECM tree genera in the families Polygonaceae (*Coccoloba*, *Gymnopodium*), Nyctaginaceae (*Pisonia*, *Neea*, *Guapira*), Achatocarpaceae (*Achatocarpus*) and Fagaceae (*Quercus*) have been documented as the primary hosts of ECM fungi in SDTFs (Alvarez-Manjarrez et al., 2018; Desai et al., 2016; Hasselquist et al., 2011; Waring, Adams, et al., 2016; Waring, Gei, et al., 2016). Along with variation in tree community composition, edaphic environment may also shape tropical ECM fungal communities. Peay et al. (Peay, Bidartondo, et al., 2010; Peay, Kennedy, et al., 2010) demonstrated that soil nutrient status explained up to a quarter of the variation in ECM fungal community composition and other research in neotropical forests also suggests that soil fertility strongly influences the structure of ECM fungal communities (Corrales, Arnold, et al., 2016; Corrales, Mangan, et al., 2016). While studies in other tropical forests have found that tree community composition can act as a key factor controlling ECM fungal biogeography at regional scales (Kennedy et al., 2011), the extent to which tree community composition drives community turnover in SDTFs, particularly in

comparison with other factors such as geographic distance and soil environmental conditions, is not well understood.

The combination of high plant diversity and high heterogeneity in soil physical and chemical properties generates significant biogeochemical variation across the SDTF biome (Waring et al., 2015, 2021). A recent regional-scale study of soil biogeochemical cycling across neotropical SDTFs found that rates of carbon (C) and nitrogen (N) cycling were predicted in part by the relative abundance of ECM trees (Waring et al., 2021). Specifically, organic C and N pool sizes were positively correlated with the abundance of ECM trees and were greatest in forest stands where ECM trees comprised >20% of stand basal area (Waring et al., 2021). While these results indicate that ECM symbioses can significantly influence the soil C and N dynamics in mixed SDTFs, exactly how remains unresolved. It is possible that traits of ECM host plants (e.g. altered C:N:P ratios of litter and throughfall inputs relative to non-ECM host plants) may result in slowed soil C and N cycling (Chuyong et al., 2000, 2004). Instead, it may be that the overall abundance of ECM fungi in soils suppresses organic matter decomposition dynamics through N-related competition with saprotrophic fungi and bacteria (Fernandez & Kennedy, 2016; Orwin et al., 2011). There is also increasing recognition that the organic matter decomposition abilities of ECM fungi vary widely across taxa (Kohler et al., 2015; Pellitier et al., 2021; Shah et al., 2016), so altered soil C and N cycling may be driven specifically by higher abundances of particular ECM fungal lineages. Distinguishing among these different mechanisms requires characterization of the ECM fungal community across SDTF sites that vary in biotic and abiotic conditions.

In this study, we assessed both the seasonal and spatial variation in ECM fungal community structure across four neotropical SDTFs that vary widely in abiotic and biotic factors (Figure 1; Vargas G et al., 2021). Building off the recent study of Waring et al. (2021), we also examined the extent to which ECM fungal community abundance and composition predicted soil C and N cycling relative to ECM host tree abundances and soil properties. We outline three research questions with related hypotheses below. (1) How do different aspects of ECM fungal community structure respond to seasonality, including frequency, abundance, richness, and composition? We hypothesized that the frequency, abundance and richness of ECM fungi would all vary seasonally across SDTFs, being elevated in the wet season. (2) What ecological factors most strongly influence the composition of the ECM fungal community at regional scales, especially across SDTFs differing in tree community composition and edaphic properties? We hypothesized that spatial rather than temporal heterogeneity would have a stronger effect on ECM fungal community composition. Specifically, we predicted that large differences in vegetation and soil properties across sites would result in greater community turnover than changes in seasonality within a given site. (3) Does incorporating ECM fungal community abundance and composition significantly increase the ability to predict soil C and N cycling in SDTFs? Similar to other analyses accounting for the relative importance of microbial community composition (Graham et al., 2016), we hypothesized that including ECM fungal community abundance and composition would enhance the explanatory power of models predicting soil C and N cycling processes.

2 | MATERIALS AND METHODS

2.1 | Study sites and soil sampling

The four study sites were located in Colombia (5.06°N, 74.83°W), Costa Rica (10.72 N, 85.59 W), Mexico (21.02°N, 89.59°W), and Puerto Rico (17.97°N, 66.87°W). Collectively, these sites span major gradients of MAP, plant community structure, and soil properties (Figure 1). Within each country, four plots were established in intermediate to mature secondary forests recovering from agricultural land use. Plots were located within 4 km of each other in areas with fairly level slopes. For additional details regarding site establishment, calculation of seasonality index (SI) and measurement of forest composition, see Vargas G et al. (2021).

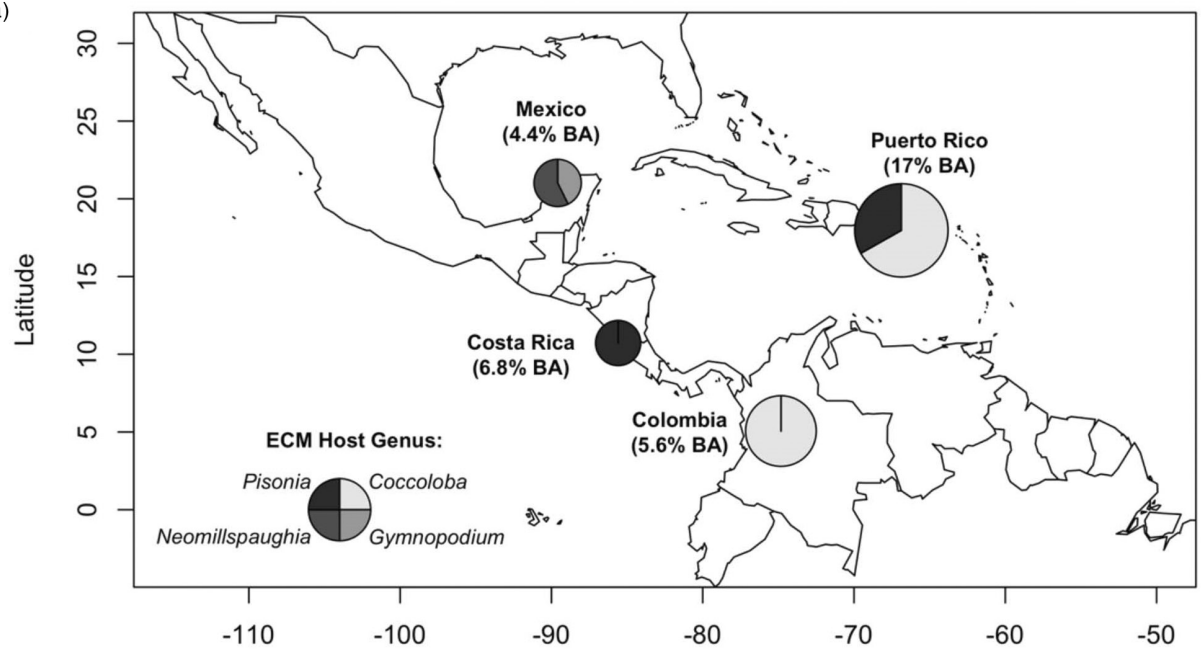
A 20 m transect was established through the middle of each plot and sampled every 5 m. Five unique soil samples were collected from the top 10 cm of mineral soil in each plot using a 2.5 cm diameter soil corer. Sampling was repeated twice along each transect; once in the wet season (October 2016) and once in the dry season (February 2017; $N = 160$). All soils were received at the University of Minnesota within 1 week of collection and then immediately processed for soil measurements or frozen at −20°C for later molecular analyses. For additional information on soil collection and processing, see Waring et al. (2021).

2.2 | Molecular analyses

Total genomic DNA was extracted from each sample using a DNEasy PowerSoil Kit (Qiagen) following manufacturer's instructions. All extractions were secondarily cleaned using a DNEasy PowerClean Pro Cleanup Kit (Qiagen) following manufacturer's instructions. The ITS1 rDNA subunit was PCR amplified using a barcoded fungal-specific ITS1F-ITS2 primer set and cycling conditions detailed in Smith and Peay (2014), with the exception of having 35 rather than 30 total cycles. Both negative and positive (Palmer et al., 2018) controls were included. All samples were cleaned and normalized using the Charm Just-A-Plate kit (Charm) following manufacturer's instructions. Samples were quantified on a Qubit fluorometer (Thermo Scientific), mixed at an equimolar concentration into a single library, and sequenced using Illumina MiSeq 2×250 bp v2 chemistry at the University of Minnesota Genomics Center.

The raw demultiplexed .fastq files were processed using the 'amptk' pipeline outlined (v1.5.4) in Palmer et al. (2018). Briefly, primers were removed, and sequences were trimmed to 250 bp. Based on initial quality control analyses of a mock community (using the 'synmock' community of Palmer et al., 2018), we found that including both forward and reverse reads resulted in both fewer reads per OTU as well as greater OTU inflation (likely due to the poorer quality of the reverse reads). As such, forward-only sequences were denoised using DADA2 algorithm (Callahan et al., 2016) under the default parameters (minLen = 50, maxN = 0, truncQ = 2, maxEE = 2) and clustered into operational taxonomic units (OTUs) at 97% similarity. Read

(a)



(b)

Country	MAT (°C)	MAP (mm)	No. dry months	SI	Soil Type	pH	Clay (%)	TOC (%)	TON (%)
Colombia	28	1833	4.3	0.17	Recent alluvial sediments that cover tuff	5.9 ± 0.2	22 ± 1	3.25 ± 0.15	0.277 ± 0.005
Costa Rica	25	1761	6.6	0.52	Inceptisol (Andic/ Typic Haplustept)	6.0 ± 0.1	50 ± 3	3.20 ± 0.21	0.273 ± 0.023
Mexico	27	1204	7.7	0.38	Mollisol (Lithic Haplustoll)	6.3 ± 0.2	51 ± 3	4.83 ± 0.18	0.465 ± 0.035
Puerto Rico	25	825	10.4	0.29	Mollisol (Aridic/ Typic Calciustoll)	7.2 ± 0.1	29 ± 5	14.08 ± 3.46	1.125 ± 0.396

FIGURE 1 (a). Map showing four neotropical dry forest sites with pie charts inset at sampling locations. The percentage of tree species belonging to ectomycorrhizal (ECM) associated host genera, by total basal area (% BA) is listed in parentheses next to each site location. Grayscale colours within pie charts show the proportion of total ECM BA occupied by the different ECM host genera present at each site. (b) Site climate information including mean annual temperature (MAT), mean annual precipitation (MAP), number of dry months and seasonality index (SI) along with average (± Standard Error) wet season soil clay content, total organic carbon (TOC) and total organic nitrogen (TON). For additional information on site soil characteristics and measurements see Waring et al. (2021).

counts in the OTU × sample matrix were adjusted to account for index bleed between samples, using 1% as the filter percentage. Taxonomy was assigned using a hybrid algorithm that integrates results from a USEARCH global alignment against the UNITE database (v8, Nilsson et al., 2019) and both UTAX and SINTAX classifiers. Raw sequences and associated metadata were deposited in the NCBI Short Read Archive (Bioproject ID #: PRJNA916723).

2.3 | Environmental variables

Tree community composition (including both arbuscular mycorrhizal [AM] and ECM-associated tree species) was previously reported by Waring et al. (2021). In brief, all tree or shrub stems 2.5 ≥ cm in diameter at breast height were identified by species, and diameters were recorded within each plot. The dominance of ECM-associated tree species was determined as a percentage of the total basal area of stems within a plot. ECM hosts were originally assigned according to Frioni et al. (1999), Wang and Qiu (2006) and Brundrett (2009) and then confirmed against the FungalRoot database (Soudzilovskaia et al., 2020).

We used soil data reported by Waring et al. (2021) and only included variables that were measured for both wet and dry seasons. In short, soil moisture (SM) was determined gravimetrically, and soil elemental concentrations (Al, Ca, Fe, K, P, S and Si) were determined using X-ray fluorescence spectrometry (Olympus). Inorganic-N pools (NO_3^- and NH_4^+) were extracted with 2 mol/L KCl and quantified colorimetrically in microplates using standard methods described by Waring, Adams, et al. (2016) and Waring, Gei, et al. (2016). Pools of C and N contained within microbial biomass (MBC and MBN) were measured via chloroform fumigation extraction (0.5 mol/L K_2SO_4 extractant) and quantified using a TOC/TN analyser (Shimadzu, Japan). Dissolved organic carbon (DOC) and nitrogen (DON) were equivalent to organic C and N contents of the unfumigated microbial biomass extracts (Waring & Powers, 2016). An ascorbic acid protocol was used to determine PO_4 concentrations colorimetrically (Murphy &

Riley, 1962). Using the methods of Saiya-Cork et al. (2002), extracellular enzyme activities were determined for two hydrolytic enzymes: β-glucosidase (BG), which breaks down cellulose and N-acetylglucosaminidase (NAG), which liberates C and N from organic matter (OM). Additionally, the activities of two oxidative enzymes: polyphenol oxidase (PPO) and peroxidase (PER), both of which are involved in the degradation of chemically complex OM (e.g. lignin).

2.4 | Pre-analysis data quality control

Only samples that had read totals in the 90% data quantile (more than 6160 reads) were included, leaving 117 out of the 130 samples that were successfully PCR amplified (Table S1). To account for differences in sequence reads among remaining samples, the OTU table was rarefied to 5977 sequences per sample. Based on the taxonomic assignments, fungal OTUs were assigned to saprotrophic, pathotrophic and symbiotrophic trophic modes using FUNGuild (Nguyen et al., 2016). The top 40 most abundant OTUs without guild assignments were checked manually in UNITE and reassigned when pairwise alignments were greater than 98% similarity (21 OTUs). When multiple fungal guilds were assigned to a single OTU, the primary or most commonly occurring lifestyle was determined using the FungalTraits database (Põlme et al., 2020). All OTUs assigned to the ECM guild with a 'possible' confidence score were manually checked by querying the top matching accession number against UNITE. All matches to the ECM fungal genus *Suillus* were eliminated (6 OTUs) due to laboratory contamination as determined by the presence in negative controls. ECM fungal lineages were assigned to genera according to Tedersoo and Smith (Tedersoo & Smith, 2013, 2017).

After rarefaction, 699,309 sequences representing 2941 fungal OTUs were assessed for functional guild membership. In total, 202 OTUs were assigned to ECM fungal taxa representing 21 lineages. Although OTU accumulation curves were variable across samples, the majority appeared to reach saturation (Figure S1). On average, soil samples contained 4 ECM fungal OTUs (range: 0–24; median = 3) and 287 sequences (range: 0–3648; median = 32).

2.5 | Statistical analyses

To address our first question—How do different aspects of SDTF ECM fungal community structure respond to seasonality?—we calculated ECM fungal frequency as the proportion of soil samples containing any ECM sequence reads, ECM fungal relative abundance as the number of ECM reads/total number of fungal reads per sample, and ECM fungal richness as the total number of ECM fungal OTUs in a given sample. These alpha diversity metrics were then used as response variables in linear mixed effects models (LME), with season, country and their interaction as fixed factors and soil cores taken along transects within countries (1|Country/Transect/Soil Core) as a nested random factor. Statistical analyses and data visualization were performed using R (R version 4.2.0; R Core Team, 2022) and PRIMER V7 (Primer-E Ltd). The models were run using the 'lmer()' function from the LME4 package (Bates et al., 2015) and then assessed the statistical significance of fixed effects using the analysis of variance (ANOVA) in the LMER TEST package (Kuznetsova et al., 2017); degrees of freedom were estimated using a Satterthwaite approximation and we utilized Type III sums of squares to test for significance. Post-hoc tests were carried out using Tukey's honestly significant difference (HSD) tests, using the package EMMEANS (Lenth et al., n.d.). We estimated marginal (variance explained by fixed factors) and conditional (variance explained by both fixed and random factors) R^2 values using the 'r2_nakagawa()' function from PERFORMANCE package (Nakagawa & Schielzeth, 2012). The contribution of our random factor to alpha diversity metrics was determined by subtracting the marginal R^2 from the conditional R^2.

We investigated differences in ECM fungal community composition across sites and seasonally (a.k.a. β-diversity) by calculating a Bray–Curtis dissimilarity matrix with log-transformed read-abundance data using the 'metaMDS()' function in the VEGAN package (Oksanen et al., 2022). Differences in community composition were visualized using nonmetric multidimensional scaling (*n*MDS). Prior to generating dissimilarity matrices, samples containing zero ECM fungal reads were eliminated as well as seven samples considered outliers in *n*MDS results indicated by a dubious stress value (close to zero; $N = 83$). To check if the results were robust regardless of the dissimilarity index, we also generated *n*MDS ordination plots using a Jaccard dissimilarity index. Clustering was similar for both Bray–Curtis and Jaccard dissimilarity indices (Figure S2), therefore only abundance-based data are presented. Permutational multivariate analyses of variance (PERMANOVA) were performed using PRIMER V7 (with PERMANOVA+) to assess the effect of fixed factors: season, country, and their interaction, and the nested random factors (1|Country/Transect/Soil Core) on ECM fungal community composition. To test the dispersion of samples in *n*MDS space, we used the PERMDISP distance-based test for homogeneity of multivariate dispersions in PRIMER V7.

To address our second question—how does ECM fungal community composition vary across SDTFs differing in their abiotic and biotic properties?—we utilized generalized dissimilarity modelling (GDM) to assess the relative effects of tree community, edaphic factors related to soil fertility and geographic distance on ECM fungal β-diversity. An extension of matrix regression, GDM is able to fit non-linear relationships between response and explanatory dissimilarity matrices by assuming a curvilinear relationship between community turnover and environmental and spatial distances (Ferrier et al., 2007). The VEGAN package was used to construct dissimilarity matrices (Bray–Curtis) for ECM fungal and tree communities along with Euclidean distances for selected edaphic variables (SM, NO_3^-, NH_4^+, PO_4, Al, Ca, Fe, K, P, S and Si) and geographic distance (spatial distance from latitude, and longitude). The variance in ECM fungal turnover explained by environmental variables was determined using the 'gdm.partition.deviance()' function included in the GDM package (Fitzpatrick et al., 2022). Simple linear regression analyses were used to assess relationships between ECM fungal richness or relative abundance and host tree richness or basal area. ECM fungal β-diversity was also calculated for each plot and regressed against tree β-diversity.

Given that environmental variables differed between seasons and across SDTFs, we used differential abundance analysis to detect seasonal shifts in ECM fungal lineages within countries. We also calculated the relative abundance of ECM fungal lineages across countries and explored correlations between ECM fungal lineage abundance and individual soil variables (SM, nutrient and elemental concentrations). Pairwise Wilcoxon tests were used to identify differentially abundant ECM fungal lineages via log2(fold-change) between seasons using the function 'wilcox.test()' in the STATS package. To better understand the ECM fungal lineages that might be driving distribution patterns across sites we correlated lineage abundances to *n*MDS ordination via the 'envfit()' function included in the VEGAN package in R.

To address our third question—does incorporating ECM fungal community abundance and composition increase our ability to predict soil C and N cycling in SDTFs?—we adapted the GDM approach to predict spatial patterns in a soil biogeochemistry dissimilarity matrix (including DOC, DON, MBC, MBN, NO_3^-, NH_4^+, N-mineralization, NAG, BG, PER and PPO activity) using tree (community composition and ECM tree basal area), fungal (ECM community composition and relative abundance) and soil (soil moisture, Al, Ca, Fe, K, P, S and Si concentrations) dissimilarity matrices as predictors. To assess the relative importance of individual soil, tree and fungal variables, we used matrix permutation ($n = 50$) to estimate the average loss in explanatory power or the percent decrease in deviance explained by the full model and the model fit without the variable of interest (Ferrier et al., 2007). To assess predictor importance, we used the 'gdm.varImp()' function in the GDM package (Fitzpatrick et al., 2022). We also partitioned the deviance from GDM into variance explained by the soil, tree and ECM fungal variable sets. GDMs were fitted using the 'gdm()' function in the GDM package with the default number of splines and knots (Fitzpatrick et al., 2022). To match ECM fungal community and soil C/N measurements, the model sample size was reduced to 67 (32 dry season samples and 35 wet season samples).

3 | RESULTS

3.1 | Seasonal and spatial variation in ectomycorrhizal fungal community structure

ECM fungi were detected in 77% of soil samples but made up a small portion of total fungal OTUs on average (<10%; Figure S3). All countries showed a marked increase in the frequency, relative abundance and richness of ECM fungi from the dry season to the wet season (Table 1; Figure 2). ECM fungal richness (Figure 2c) was ca. three times higher in the wet season, with the greatest seasonal increase occurring at the Mexican site (Figure S4). Ordination showed strong clustering of ECM fungal communities by country (Figure 2d), with visible separation between wetter (CR and CO) and drier sites (MX and PR) occurring along the first *n*MDS axis. Unlike alpha diversity, ECM fungal β-diversity was similar between wet (BC = 0.97 ± 0.003) and dry (BC = 0.99 ± 0.002) seasons (PERMANOVA: $p = 0.3$) but varied significantly across countries (PERMANOVA; $p = 0.001$). Although seasonal effects on β-diversity were not significant, compositional dispersion tended to be greater in the dry season, when fewer soil samples contained ECM fungal OTUs (Table 1).

Much of the variability in ECM fungal community structure could be attributed to individual soil cores and along transects within sites, with random effects explaining more than half of the variance in ECM fungal OTU relative abundance (59%) and richness (55%; Table S2).

TABLE 1 Analysis of variance (ANOVA) table for ectomycorrhizal (ECM) fungal community alpha diversity metrics including occurrence frequency (percentage of soil samples containing ECM amplicon reads), relative abundance (percentage of fungal amplicon reads categorized as ECM for a given soil sample) and ECM richness (total number of ECM OTUs). Permutational multivariate analysis of variance (PERMANOVA) and dispersion differences based on Bray–Curtis dissimilarities using abundance (count) data for ECM fungal community structure.

ANOVA	Frequency						Relative abundance					Richness				
	Num	Den					Den					Den				
	df	*df*	SS	MS	*F*	*p* (>*F*)	*df*	SS	MS	*F*	*p* (>*F*)	*df*	SS	MS	*F*	*p* (>*F*)
Alpha diversity																
Season	1	10	17	17	8.9	0.01		0.26	0.26	22	<0.001	67	18	18	60	<0.001
Country	3	20	4.9	1.6	0.88	0.5	42	0.03	0.01	0.84	0.48	56	0.15	0.05	0.17	0.90
Season × Country	3	9	9.0	3.0	0.25	0.3	36	0.10	0.03	2.8	0.05	62	9.3	3.1	10	<0.001

	PERMANOVA						Dispersion		
	Num	Den			Pseudo		Den	Pseudo	
	df	*df*	SS	MS	*F*	*p* (Perm)	*df*	*F*	*p* (Perm)
Beta diversity									
Season	1	4	3371	3371	1.22	0.30	81	8.42	<0.001
Country	3	18	34,567	11,522	2.44	0.001	79	1.19	0.42
Season × Country	3	12	11,950	3983	1.44	0.09	83	3.01	0.14

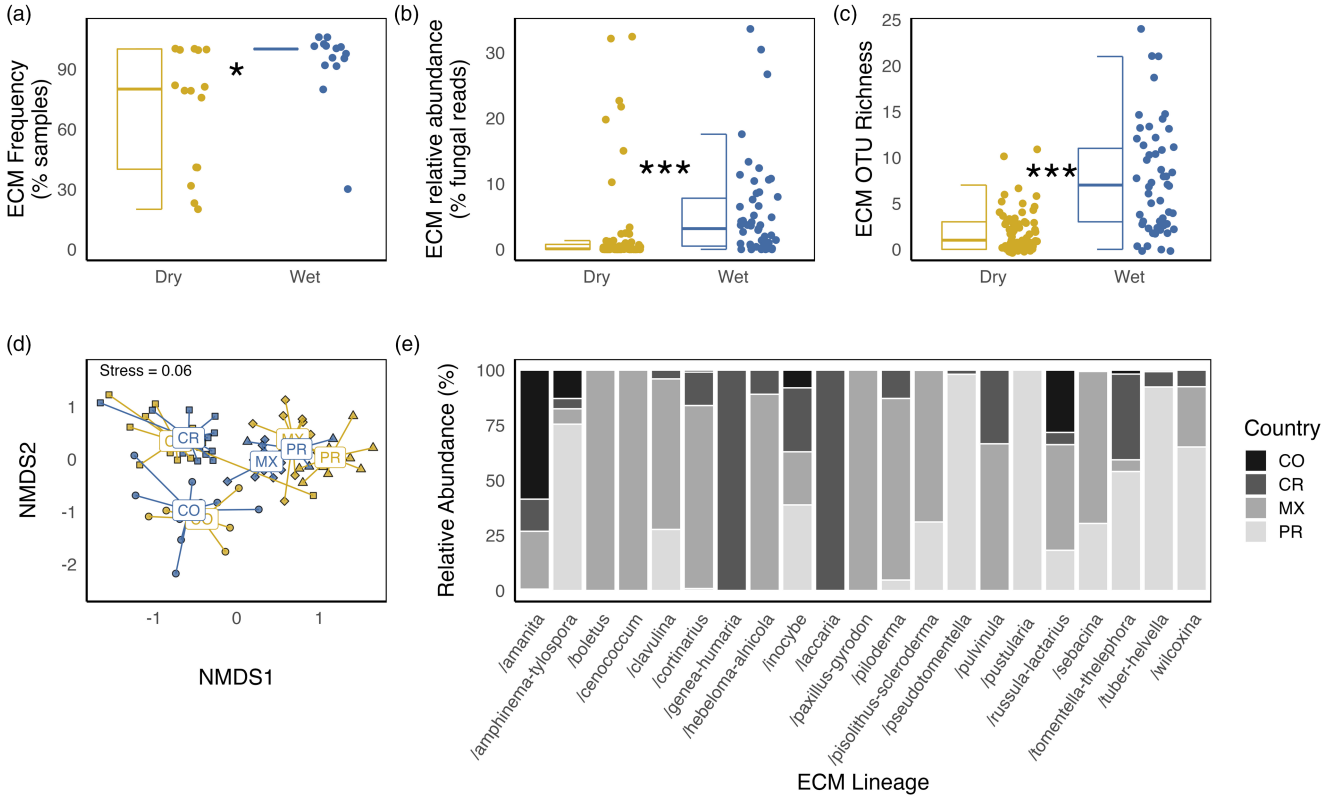


FIGURE 2 (a). Box and whisker plots of ectomycorrhizal (ECM) fungal occurrence frequency, (b) relative abundance and (c). OTU richness for wet and dry seasons. Asterisks denote significant differences in mean values according to ANOVA results (see Table 1). (d) Non-metric multidimensional scaling (*n*MDS) plot depicting similarity of fungal communities sequenced from soil samples at the Colombian (CO), Costa Rican (CR), Mexican (MX) and Puerto Rican (PR) sites. (e) Relative abundance of dominant ectomycorrhizal (ECM) fungal lineages present at the four sites. *, $p < 0.05$; ***, $p < 0.001$.

Notably, not a single ECM fungal OTU was shared among countries (Figure S5) and dominant ECM fungal lineages varied by country (Figure 2e). The /tomentella-thelephora lineage had the highest relative abundances in Puerto Rico and Costa Rica, while /sebacina, /clavulina and /pisolithus-scleroderma were dominant in Mexico and Puerto Rico (Figure S6). Colombian soils had the lowest overall ECM fungal relative abundances and contained a greater number of ECM fungal OTUs from the lineages /amanita and /russula-lactarius (Figure 2e; Figure S6). The ECM fungal lineages driving site differences in community composition included /pisolithus-scleroderma ($r = 0.31$; $p = 0.002$), and /sebacina ($r = 0.19$; $p = 0.003$; based on correlations to NMDS1; Figure S7a).

3.2 | Environmental drivers of ectomycorrhizal fungal community structure at regional scales

Tree community, selected soil variables and geographic distance together explained 37% of total deviance in ECM fungal species turnover. Tree community alone explained 11% of ECM turnover, which was more than both geographic distance (4%) and variables related to soil fertility (0.7%) alone (Table S3; Figure S8). ECM fungal OTU richness increased with host tree richness regardless of season (Figure S9a), while ECM fungal relative abundance was positively related to ECM tree basal area, but only in the wet season (Figure S9b). ECM fungal community dissimilarity increased with increasing tree community dissimilarity and the coupling of tree ECM fungal β-diversity was more pronounced in the wet compared with the dry season (Figure S9c). In Colombia, the /amanita and /amphinema-tylospora lineages more than doubled in the wet season, while /cortinarius increased in relative abundance at the Costa Rican and Mexican sites (Figure 3a). The relative abundance of the /tomentella-thelephora lineage was significantly higher in the wet season in Mexico but decreased in abundance between the dry and wet seasons in Puerto Rico. Across sites, the abundance of /amanita, /hebeloma-alnicola, /pseudotomentella, /pulvinula and /sebacina lineages were positively correlated with soil moisture and fertility variables (e.g. NO_3^-, NH_4^+, PO_4), which increased during the wet season (Figure 3b).

3.3 | Ectomycorrhizal effects on soil C and N cycling

Regardless of season, soil moisture was the best predictor of differences in soil C and N cycling across sites (Figure 4a; Figure S10). However, the importance of abiotic versus biotic predictors differed

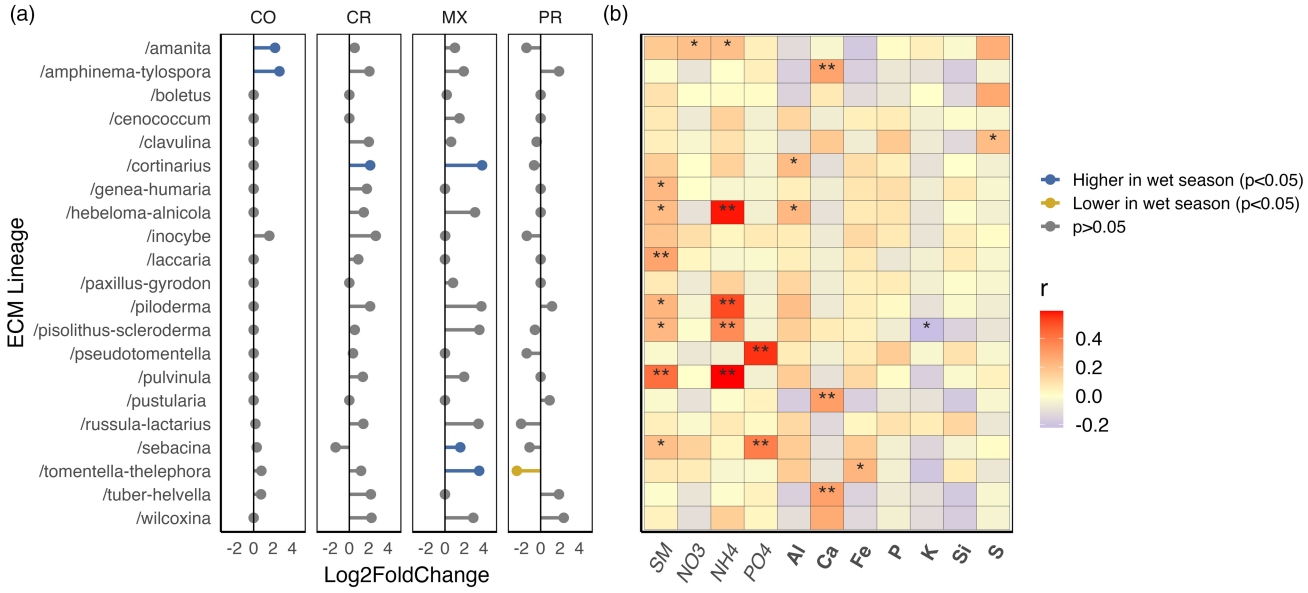
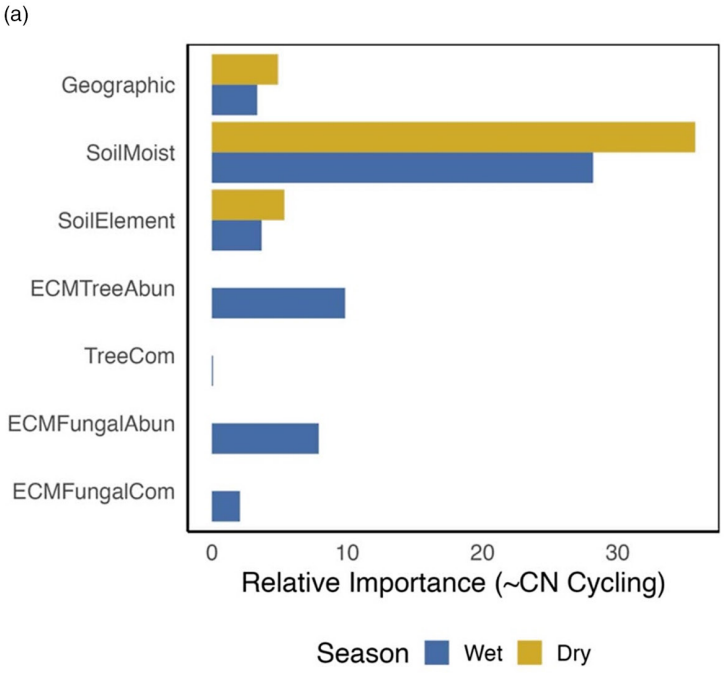


FIGURE 3 (a) Lollipop plots of the log2 fold change in ECM fungal lineage abundance between dry and wet season soils from each site (CO, Colombia; CR, Costa Rica; MX, Mexico; PR, Puerto Rico). Mann–Whitney Wilcoxon tests were used to determine the statistical significance of changes in ECM fungal lineage abundance in the wet season. (b) Spearman correlations between the relative abundances of ectomycorrhizal (ECM) fungal lineages and soil variables across seasons. SM, soil moisture. Bolded soil variables did not change seasonally, while italicized variables did change seasonally (see Waring et al., 2021 for more information). *, $p < 0.05$; **, $p < 0.01$.



(b)

	Deviance Explained	
Predictor Set	Dry	Wet
Soil alone	45.5	2.84
Tree alone	0.00	6.24
ECM alone	0.00	2.44
Soil + Tree	57.7	30.3
Soil + ECM	57.7	26.5
Tree + ECM	12.2	29.9
Soil +Tree + ECM	57.7	32.7
Unexplained	45.5	67.3

FIGURE 4 (a) Relative importance of different plant, soil and ectomycorrhizal (ECM) fungal variables for predicting soil carbon (C) and nitrogen (N) cycling in the dry and wet seasons. Predictors include geographic distance, soil moisture, a matrix of soil elemental composition dissimilarities, ECM tree abundance (% ECM tree basal area), ECM tree community composition (Bray–Curtis dissimilarity matrix), ECM fungal community composition (Bray–Curtis dissimilarity matrix) and ECM fungal relative abundances. (b) Variance partitioning of soil composition (elemental composition and moisture), tree community (composition and ECM tree abundance) and ECM fungal community (composition and ECM fungal relative abundance) individually and in combination.

between seasons with soil variables being more important in the dry season and tree and fungal variables increasing in importance in the wet season (Figure 4b; Table S4). Although soil and tree community variables tended to explain more variation in soil C and N cycling, the inclusion of ECM community metrics increased explanatory power in the wet season model. Specifically, the addition of ECM fungal

β-diversity and relative abundance increased deviance explained by 7% compared with soil and tree variables combined (Figure 4b). Additionally, the abundance of ECM tree hosts (% basal area) and fungi were of similar importance for explaining variation in soil C and N cycling in the wet season (Figure 4a).

4 | DISCUSSION

Plant host diversity, abiotic conditions and edaphic factors all contribute to the diversification of ECM fungal symbionts in forest ecosystems (Looney et al., 2016; Sánchez-Ramírez et al., 2015). To better understand the spatial and temporal controls on ECM fungal communities in seasonally dry neotropical forests (SDTFs), we characterized soil inhabiting ECM fungi in both wet and dry seasons in SDTFs at a regional scale (Figure 1). We hypothesized that ECM alpha diversity would be responsive to rainfall seasonality. In support of our hypothesis, we found ECM fungal frequency, abundance and richness all increased in the wet season (Figure 2). We also hypothesized that spatial rather than temporal heterogeneity would have a stronger effect on ECM fungal community composition. Spatial variability did exceed seasonal variability in explaining ECM fungal β-diversity, with community turnover being greater among sites than between seasons (Figure 2; Table 1). In support of our final hypothesis, we also found that ECM fungal abundance and community composition increased the explanatory power of models predicting soil C and N cycling, particularly in the wet season (Figure 4). We elaborate on each of these findings below.

4.1 | Ectomycorrhizal fungal frequency, relative abundance and richness increased in the wet season

In agreement with previous studies from temperate forests, we observed a significant increase in ECM fungal frequency, relative abundance, and richness during the wet season (Nilsen et al., 1998; Swaty et al., 2004; Taniguchi et al., 2018). In other systems, seasonal increases in ECM fungal abundance and richness have been shown to relate strongly to increase photosynthetic activity of host plants (Heinemeyer et al., 2007; Vořiškova et al., 2014). Plant photosynthetic rates are consistently higher in the wet season in SDTFs (Lugo et al., 1978), likely facilitating greater C allocation to ECM fungi. Incident precipitation in the tropics can also increase throughfall nutrient inputs to ECM fungal communities (Chuyong et al., 2004). We found that the abundance of several ECM fungal lineages increased with greater soil moisture and nutrient availability (Figure 3b), consistent with non-molecular assessments of fungal abundance patterns at these sites (Waring et al., 2021). Additionally, MAP has been identified as a key controller of fungal richness at the global scale (Tedersoo et al., 2014), which is consistent with greater water availability being critical for the turgor-driven lifestyle of hyphal growth. Regardless of specific mechanism (none of which are mutually exclusive above), our results highlight the potential for seasonal niche differentiation to help maintain ECM fungal diversity in SDTFs.

Despite the aforementioned cross-site trends, the magnitude of seasonal changes in ECM fungal relative abundance and richness varied by country (Table 1). Seasonal differences in alpha diversity were strongest in Mexico and weakest in Puerto Rico despite both sites having low MAP and dry seasons which can last over half the year. Compared with Mexico, sites in Puerto Rico experienced a longer dry season (up to 90% of the year) and less seasonal variability in soil moisture (Waring et al., 2021). Soil moisture more than doubled at the Mexican sites which experienced an abnormally dry season in 2017; this large increase in precipitation between wet (~100 mm) and dry (~2 mm) seasons might explain the particularly strong seasonal trends in Mexican soils (J. Dupuy-Rada, pers. obs.). A significant increase in the relative abundance of the /sebacina lineage is also consistent with reports of seasonal *sebacinoid* sporocarp production of taxa such as, *Tremelloscypha gelatinosa*, found under *Gymnopodium* trees in Mexican SDTFs during the wet season (Bandala & Montoya, 2015). In contrast, several ECM fungal lineages declined in relative abundance in Puerto Rico during the wet season, with taxa in the /tomentella–thelephora lineage decreasing six-fold in abundance (Figure 4a). Tomentelloid fungi have been shown to associate with osmotically stressed trees (Thiem et al., 2018) and may increase the efficiency of water uptake (Cabot et al., 2014). As such, it is possible that the more drought-tolerant *Tomentella* species decreased in relative abundance in the wet season at the Puerto Rican site. However, it is unclear why the opposite pattern was observed in Mexico, where abundance of the /tomentella–thelephora lineage increased in the wet season. Given this discrepancy, more studies are needed to better understand how seasonal variability in rainfall might interact with site-level conditions to select different functional groups of ECM fungi. As warmer and drier climate conditions may cause dry forests to expand into regions previously occupied by moist tropical forests (Siyum, 2020), it is important to study how ECM fungal communities are seasonally and spatially structured, particularly in tropical forests functioning at the edge of precipitation extremes (Maia et al., 2020).

4.2 | Spatial variation in ectomycorrhizal fungal community composition was linked to both abiotic and biotic factors

Our sampling locations captured substantial heterogeneity in soil moisture, texture and elemental composition (Waring et al., 2021), offering a variety of optimal growth conditions for different ECM fungal lineages (Smith & Read, 1997). Local-scale edaphic variation can play an important role in influencing ECM fungal community structure (Peay, Bidartondo, et al., 2010; Peay, Kennedy, et al., 2010; Read, 1991). Previous studies have shown that soil properties including moisture and nutrient availability are important drivers of ECM fungal community composition in tropical forests at local scales (Peay, Bidartondo, et al., 2010; Peay, Kennedy, et al., 2010; Schappe et al., 2020; Tedersoo et al., 2010; Waring et al., 2015). In support of these studies, we found that abundances of several

ECM fungal lineages were positively correlated with soil moisture, ammonium and phosphate concentrations (Figure 3b). Our findings also support the reported preference of *Hebeloma* species for forest soils with increased concentrations of ammonium (Sagara, 1992). In addition to capturing heterogeneity in the edaphic environment, our study locations represent 4 of the 12 floristic provinces that characterize the SDTF biome (Banda et al., 2016), and sites differed notably in their abundance and composition of ECM host trees (Figure 1). We found that tree composition explained more variation in ECM fungal community composition than soil properties and that ECM fungal community structure was significantly correlated with tree community composition and ECM host tree basal area. These findings support those of Schappe et al. (2020) who report greater host tree effects of ECM fungal communities compared with soil properties in mixed-AM-dominated lowland tropical forests.

Biotic links between plant and ECM fungal community structure could be the result of strong host preferences known to exist for certain tropical plant genera, including *Coccoloba* and *Pisonia* (Ishida et al., 2007; Põlme et al., 2017; Suvi et al., 2010; Tedersoo et al., 2010). Both *Pisonia* (Hayward & Hynson, 2014; Suvi et al., 2010) and *Coccoloba* spp. (Põlme et al., 2017) have been shown to form ECM associations with specific assemblages of *Tomentella* species and sites where *Pisonia* trees were present (Costa Rica and Puerto Rico) had the greatest relative abundances of the /tomentella–thelephora lineage followed by sites containing *Coccoloba* hosts (Puerto Rico and Colombia). In addition to site differences in host tree incidence, the patchy distribution of host trees along transects likely explained the large within-site variation in ECM fungal community composition (Table S2) as well as the overall low ECM fungal relative abundances found in soil cores (John et al., 2007; Tedersoo et al., 2010). This within-site variation highlights the importance of studying ECM fungal communities in non-monodominant tropical forests (Corrales et al., 2022; Schappe et al., 2020), especially given the potential for low-abundance species to serve as reservoirs of microbial diversity (Dawson et al., 2017) and for individual ECM fungal taxa to influence biogeochemical processes at the forest scale (Lindahl et al., 2021).

4.3 | Ectomycorrhizal symbioses impact soil C and N cycling via plant and fungal effects

Communities of plants and fungi are known to influence soil biogeochemistry individually, but their relative contributions and interactive effects are not well known, particularly in tropical forests. Despite representing a small fraction of tropical plant diversity (6%–20% of species; Brundrett, 2009; Fukami et al., 2017), trees that associate with ECM fungi can have disproportionate effects on soil C and N cycling in tropical forests (Corrales et al., 2017; Waring et al., 2021). In a common garden study, Lin et al. (2017) found that soil C:N ratio and rates of N cycling were lower beneath tropical ECM trees relative to AM trees. As a result, soils beneath ECM trees are thought to have more 'closed' N cycles, that is, lower N loss relative to the N that is recycled (Mushinksi et al., 2020). In the study of Lin et al. (2017), the more 'closed' N cycling under ECM trees was largely attributed to lower leaf litter decomposability (but see Keller & Phillips, 2019) and less resorption of leaf N compared with AM tree species. Chuyong et al. (2000) suggest that root mats under ECM trees may help trap the nutrients contained within ECM leaf litter by preventing leaching of mobile nutrients during the wet season. In support of greater nutrient recapture by tropical ECM trees, Lin et al. (2018) also found that ECM trees produced more root length per soil volume and had greater rhizosphere effects on N transformations. To determine the ECM plant traits that most influence soil biogeochemistry in tropical dry forests, future studies should compare leaf and root traits of ECM plant species growing outside of mono-dominant stands with those of nearby AM-associated plant species (Barceló et al., 2022).

Although ECM fungal predictors alone had low explanatory power compared with ECM host tree basal area, the inclusion of ECM fungal relative abundance and community composition improved the explanatory power of models predicting soil C and N cycling across SDTFs (Figure 4b). Similar to ECM tree effects, we found that ECM fungal effects on soil biogeochemistry were stronger in the wet compared with the dry season. The wet season also showed greater abundance of ECM fungi from the /pisolithus-scleroderma lineages, which were positively correlated with concentrations of soil inorganic nitrogen (Figure S10b). Gao et al. (2022) recently found that the abundance of ECM fungi in the genus *Pisolithus* increased in response to irrigation and N fertilization in a tropical *Eucalyptus* plantation and these increases were associated with enhanced growth of host trees. Inorganic N pools were also larger in the wet season, as greater precipitation likely accelerated microbial nutrient uptake and soil N cycling (Waring et al., 2021; Waring & Powers, 2016). It could be that 'nitrophilic' ECM fungi that are better at foraging for inorganic sources of N are more abundant in the wet season (Lilleskov et al., 2001; Pellitier et al., 2021). However, it is not yet clear if nitrophilic ECM fungi can influence soil C and N processes directly by priming microbial activity (Lindahl & Tunlid, 2015) or indirectly via increased growth of host trees. Thus, SDTFs serve as an interesting system to further study nitrophilic ECM fungal species and their effects on soil processes (Lilleskov et al., 2011).

4.4 | Caveats

While our results indicate that SDTF ECM fungal communities present are clearly dynamic in both time and space, we encountered some methodological issues that merit discussion. Sampling soils instead of root tips directly may have biased our ability to detect active ECM fungi (Bruns, 1995). Despite applying a secondary DNA purification step following DNA extraction as well as multiple PCR attempts under different settings, we were unable to successfully amplify a number of samples (30 of the 160 soil samples), particularly from the organic-rich soils of Puerto Rico. This remains a challenge facing microbial community analyses in tropical areas (Frostegård et al., 1999) and indicates that optimization is still needed for tropical soil molecular-based analyses. The sequence read counts we obtained for the ECM fungal communities were also relatively low, which we suspect parallels a generally lower abundance of this guild in SDTF

soils. The within-site read count patterns for individual ECM fungal OTUs in samples with low and high read count totals was often similar (data not shown), however, suggesting our low total read count samples were able to capture the biological signal. We also recognize that shifts in other fungal guilds by season or site might have influenced our ECM-focused results because the community measures of fungal abundance were relativized. The across-site trends were, however, variable for other guilds (Figure S3), suggesting there was not a consistent directionality in those non-ECM fungal shifts that skewed the larger ECM fungal relative abundance trends that emerged. Finally, subsetting our data to only include samples that contained ECM fungal reads reduced our sample size, potentially limiting our ability to actually infer links between biogeochemical processes and different plant, soil and fungal predictors. Despite the reduced sample size, our findings align with those of the companion study Waring et al. (2021), which reported a significant effect of ECM tree abundance on soil C/N cycling across the same SDTF sites in the wet season.

5 | CONCLUSIONS

The extreme heterogeneity in plant and soil properties that exists within SDTFs provides a unique context in which to study spatiotemporal variability in communities of ECM fungi. We found that multiple ECM fungal community metrics were strongly responsive to rainfall seasonality, suggesting that seasonal water limitation in SDTFs acts as an important ecological control on ECM fungal community structure. Despite the importance of seasonality on ECM fungal richness and frequency relative abundances, we also determined that tree species community composition rather than geographic distance and soil edaphic factors was the dominant driver of the ECM fungal community variation across the neotropical dry forest biome. Additionally, we found that ECM tree abundance explained more variation in wet season soil C and N cycling than ECM fungal community metrics, highlighting the importance of the plant side of ECM associations to influence soil biogeochemistry. At the same time, we also found that the addition of ECM fungal community metrics did improve the power to predict soil biogeochemical processes in the wet season. These findings demonstrate the potential for ECM associations to influence soil biogeochemistry even within mixed non-monodominant tropical forests where ECM hosts and fungi exist in relatively low abundance.

AUTHOR CONTRIBUTIONS

Individual author contributions are as follows: study conception and design: Jennifer S. Powers and Peter G. Kennedy; data collection: Jennifer S. Powers and German Vargas G, data analysis and draft manuscript preparation: Katilyn V. Beidler and Peter G. Kennedy; manuscript review and interpretation of results: all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14112.

DATA AVAILABILITY STATEMENT

Raw sequences and associated metadata have been deposited in the NCBI Sequence Read Archive under the project accession PRJNA916723. Plant and soil data from Waring (2021) are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v15dv41vf.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Distribution of missing samples across sites and seasons from original 160 soil samples.

Table S2. Random effect contributions from alpha and beta diversity models.

Table S3. Variance partitioning results from GDM analyzing drivers of ectomycorrhizal fungal community turnover[1].

Table S4. Variance partitioning results from GDM analyzing soil carbon and nitrogen cycling[1]

Figure S1. Sample-based rarefaction curve for ectomycorrhizal (ECM) fungi found in seasonally dry tropical forests. Following initial quality filtering, a total of 2,132,526 fungal ITS sequences were obtained from 117 soil samples.

Figure S2. Non-metric multidimensional scaling (*n*MDS) ordination plots of Jaccard and Bray-Curtis community dissimilarities for ectomycorrhizal (ECM) fungal communities across dry forest sites in Colombia (CO), Costa Rica (CR), Mexico (MX) and Puerto Rico (PR) in wet and dry season.

Figure S3. Relative abundance of fungal guilds across dry forest sites in Colombia (CO), Costa Rica (CR), Mexico (MX) and Puerto Rico (PR) in wet and dry season.

Figure S4. Boxplots of ectomycorrhizal (ECM) fungal relative abundance (A), frequency (B) and OTU richness (C) for dry forest sites in Colombia (CO), Costa Rica (CR), Mexico (MX) and Puerto Rico (PR). Blue boxes represent wet season samples and yellow boxes represent dry season samples.

Figure S5. Venn-Diagrams displaying the number unique and shared OTUs across sites (A) and between seasons (B).

Figure S6. Relative abundance of ectomycorrhizal (ECM) fungal lineages in in Colombia (CO), Costa Rica (CR), Mexico (MX) and Puerto Rico (PR).

Figure S7. Dominant ECM lineages across sites (A) Relationship between /Pisolothus-Scleroderma abundance with inorganic N (B; concentration of NH4+). Only significant relationships are displayed ($p < 0.05$).

Figure S8. Results of generalized dissimilarity modeling (GDM). The partial or marginal effect (f()) of each predictor plotted against the level of a given predictor while holding all other predictors constant (B–D). Bray–Curtis dissimilarity was calculated for ectomycorrhizal (ECM) fungal and tree communities and Euclidean distances were calculated for soil fertility metrics (elemental composition and soil moisture). Geographic distance is in km.

Figure S9. Relationships between ectomycorrhizal (ECM) fungal and host tree richness (A) ECM fungal and tree abundance (B), and ECM fungal and tree beta diversity (C). Only significant relationships are displayed ($p < 0.05$).

Figure S10. Results of generalized dissimilarity modeling (GDM). The partial or marginal effect (f ( )) of each predictor plotted against the level of a given predictor while holding all other predictors constant (B–H). Bray–Curtis dissimilarity was calculated for ectomycorrhizal (ECM) fungal and tree communities and Euclidean distances were calculated for soil fertility metrics (elemental composition and soil moisture). Geographic distance is in km.

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