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Fungi

# Diversity and Distribution of Soil Fungi in Neotropical Mexican Forests

Bernardo Águila[1] | Julieta Alvarez-Manjarrez[1] | Leho Tedersoo[2] | Mohammad Bahram[3,4] | Ana E. Escalante[5] | Roberto Garibay-Orijel[1]

[1]Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico | [2]Mycology and Microbiology Center, University of Tartu, Tartu, Estonia | [3]Department of Agroecology, Faculty of Technical Sciences, Aarhus University, Slagelse, Denmark | [4]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden | [5]Laboratorio Nacional de Ciencias de la Sostenibilidad, Instituto de Ecología, Universidad Nacional Autónoma de México, Mexico City, México

**Correspondence:** Roberto Garibay-Orijel (rgaribay@ib.unam.mx)

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## ABSTRACT

Soil fungal diversity in the Neotropics remains poorly understood, despite growing evidence of high endemism and many undescribed taxa. Here, we analyzed the Global Soil Mycobiome dataset from 55 sites across the Mexican Neotropics, integrating community composition with alpha- and beta-diversity metrics. Cluster and ordination analyses revealed eight distinct community groups largely explained by vegetation type and ecogeographic patterns. Tropical rainforests and temperate conifer forests harbored the highest richness (mean > 1500 OTUs), whereas coastal dunes showed the lowest (< 400 OTUs). Xeric shrublands, despite reduced richness, exhibited high evenness, suggesting niche differentiation under stressful conditions. Prevalence and indicator species analyses highlighted the role of ectomycorrhizal taxa in coniferous and coastal systems, soil saprotrophs in *Pinus–Quercus* forests, and plant pathogens in xeric shrublands, while many tropical lineages remained unclassified. Multivariate redundancy analysis identified pH, mean annual precipitation and elevation as the strongest independent drivers of fungal turnover, with soil nutrients (N, P, $\delta^{15}N$) explaining finer-scale variation. Together, these results demonstrate that broad climatic gradients and vegetation types structure fungal communities in the northern Neotropics, while local soil properties refine community assembly. Our findings underscore the importance of tropical rainforests, temperate montane forests, and xeric shrublands as key reservoirs of soil fungal diversity, and provide a predictive framework for the conservation and monitoring of Neotropical ecosystems within initiatives such as the Soil Biodiversity Atlas of Mexico.

## 1 | Introduction

Soil fungi are essential for ecosystem function, providing a wide range of ecosystem services, such as nutrient cycling (Dai et al. 2021; Read and Perez-Moreno 2003), organic matter decomposition (Nicolás et al. 2019), soil structure and stability (Miller and Jastrow 2000), plant nutrition (Smith and Smith 2012; Vassileva et al. 2022), disease suppression (Deliopoulos et al. 2010; Latz et al. 2018), and carbon sequestration (Treseder and Holden 2013). They also sustain soil biodiversity by acting as food for other organisms and mediating multi-trophic interactions (Fodor 2012; Tekwa et al. 2023; Zhang et al. 2018). Despite this importance, fungal diversity remains poorly documented in tropical ecosystems.

Understanding soil fungal diversity and its drivers is fundamental for conservation strategies and sustainable land management (Spurgeon et al. 2013). Fungal communities are shaped by multiple abiotic factors, including climate, pH, soil texture, and topography (Boddy et al. 2014; Carrino-Kyker et al. 2016; Marian et al. 2019; Větrovský et al. 2019). Vegetation type and plant species composition are among the most influential biotic variables, since root exudates and litter inputs provide distinct carbon sources for fungi (Brundrett and Tedersoo 2018; Nilsson et al. 2019). In addition, fungal dispersal strategies and lifestyles contribute to shaping diversity across space and time (Tedersoo et al. 2014).

Metabarcoding has enabled unprecedented insights into soil fungal communities, capturing cryptic, non-fruiting, and dormant taxa (Tedersoo et al. 2015). However, most studies have concentrated on temperate ecosystems of Europe and North America (Bieker et al. 2020), while regional-scale surveys in the Neotropics remain scarce (Corrales et al. 2016; Vaz et al. 2017; Garibay-Orijel et al. 2020; Alvarez-Manjarrez and Garibay-Orijel 2021).

The Neotropical region encompasses the central and southern portions of Mexico, Central and South America (Morrone 2014), southern Florida, and parts of the Caribbean. It is recognized as a global biodiversity hotspot, with exceptionally high levels of vegetation endemism (Berndt 2012) and outstanding richness of both flora and fauna. Within this region, Mexico harbors a complex mosaic of ecosystems shaped by the interaction of Nearctic and Neotropical biotas. Its forests span from tropical rainforests to xeric shrublands and high-elevation coniferous ecosystems; however, their belowground fungal diversity remains largely understudied (Del Olmo-Ruiz et al. 2017; García-Guzmán et al. 2017).

Understanding the ecological patterns of Neotropical soil fungi and their abiotic and biotic drivers is essential for predicting how fungal communities may respond to global change, including climate shifts (Andrew et al. 2016; Větrovský et al. 2019) and anthropogenic disturbances (Compant et al. 2010). The aim of this study was to analyze fungal diversity patterns across the Mexican Neotropics and to identify the main environmental and biotic drivers of fungal community structure in this region.

We hypothesized that fungal community structure in the northern Neotropics is primarily driven by broad climatic and elevational gradients, coupled with local soil nutrient concentrations. Importantly, we predicted that these patterns would diverge from global fungal biogeographical trends because Mexico's extreme topographic heterogeneity amplifies the role of elevation as a key predictor of diversity and community composition (Ramírez-Barahona and Eguiarte 2013).

Building on this rationale, we developed an explicit predictive framework to guide our analyses: (1) Habitat area and vegetation complexity should predict fungal richness and evenness, with structurally complex systems such as tropical rainforests and temperate conifer forests expected to harbor higher diversity, while environmentally extreme habitats (e.g., coastal dunes, xeric shrublands) are predicted to sustain lower diversity and have stronger dominance (Tedersoo et al. 2014; Bahram et al. 2021; Ochoa-Hueso et al. 2018); (2) Host mycorrhizal status should strongly structure community composition, with ectomycorrhizal-dominated forests (*Abies*, *Pinus*, *Quercus*) enriched in ECM fungi relative to arbuscular-mycorrhizal tropical systems enriched in saprotrophs and other symbionts (Brundrett and Tedersoo 2018; Corrales et al. 2022; Garibay-Orijel et al. 2020); (3) Regional climatic and elevational gradients should primarily drive beta diversity (Peay et al. 2016; Tedersoo et al. 2014), while local nutrient concentrations should explain within-habitat turnover (Leff et al. 2015; Camenzind et al. 2018).

Finally, this predictive framework is the basis for the national-scale initiative "Soil Biodiversity Atlas of Mexico" (Martínez-Ugalde et al. 2025), which seeks to integrate metabarcoding data on fungi, bacteria, and soil fauna into a comprehensive platform for monitoring, conservation, and sustainable management of soil in Mexico. Establishing which variables best predict fungal biodiversity is therefore not only ecologically relevant but also a critical step for making belowground biodiversity visible and actionable for policy and climate adaptation.

## 2 | Methods

This regional-meta analysis is based on a subset (Neotropical Mexican sites) of the data published by the Global Soil Mycobiome consortium (GSMc) (Tedersoo et al. 2021) and constitutes the first data set "MxA" of the Soil Biodiversity Atlas of Mexico.

### 2.1 | Bioinformatic Data Collection and Filtering

The Global Soil Mycobiome (GSM) dataset consists of PacBio long-read sequences targeting the full internal transcribed spacer (ITS1–5.8S–ITS2) region and the 18S-V9 variable region of the nuclear ribosomal DNA, amplified with the universal eukaryotic primers ITS9mun and ITS4ngsUni (Tedersoo and Lindahl 2016; Tedersoo and Anslan 2019) clustered at 98% similarity, with assigned taxonomic classifications and functional annotations (Tedersoo et al. 2021). Data from GSM included sample metadata abundance tables and OTU sequences.

First, samples from Mexico (73 sites) were queried and extracted from the GSM dataset using Python 3.12 within a Jupyter Notebook environment (Kluyver et al. 2016). Next, sites corresponding to the Neotropical Region (Morrone 2014) were selected, resulting in 56 sites (most excluded sites were from Sierra Madre Oriental). Finally, one site with a high relative abundance of common fungal contaminants (Eurotiales, Mortierellales, Mucorales, Trichoderma, and Umbelopsidales) was excluded from the analysis making a final data set of 55 sites. The python script used for data extraction and processing is openly available in GitHub at https://github.com/Burn121212/FungiMX.git.

For an updated taxonomic annotation, we reclassified GSM sequences by BLAST annotation in Pipecraft v 1.1 using the latest UNITE all Eukaryotes database version 04.04.2024 (Abarenkov et al. 2024). Later, annotated genera were used to assign primary lifestyles using the Fungal Traits database (Põlme et al. 2020). Unique species numbers (SpN) were assigned to each GSM-OTU identifier and fasta headers to facilitate taxa visualization. SpN identifiers were used to construct abundance and classification tables (taxonomy and primary lifestyle).

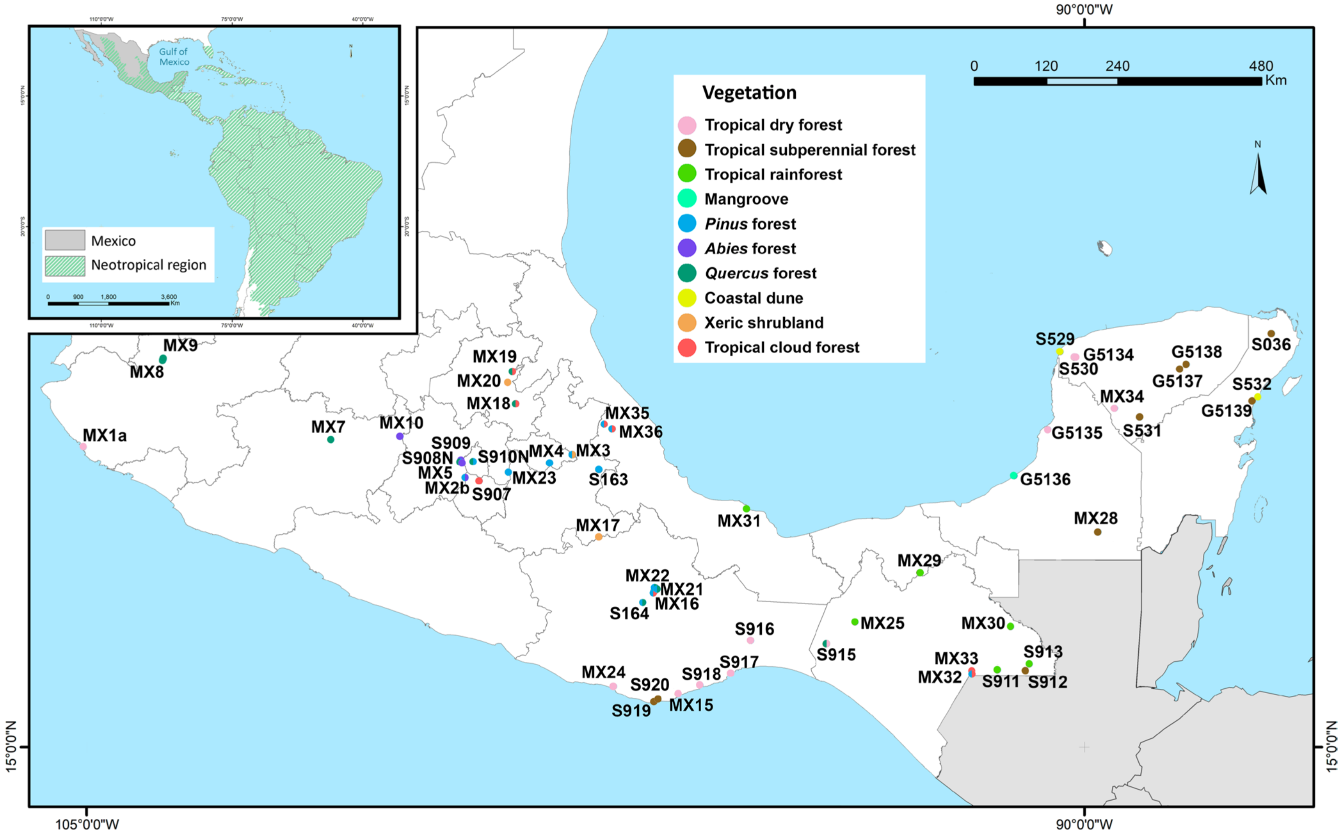


**FIGURE 1** | Map showing the location and associated vegetation of the 55 sites across central and southern Mexico (northern Neotropics) studied for their fungal composition. Sites with mixed vegetation were supplemented with secondary vegetation (colored circles).

## 2.2 | Local Environmental Data Collection and Filtering

Environmental and physicochemical data were obtained from two complementary sources. Total nitrogen, total phosphorus, and $\delta^{15}N$ values were directly extracted from the Global Soil Mycobiome consortium metadata (Tedersoo et al. 2021), where soil analyses were performed at the University of Tartu following standardized protocols, including isotope ratio mass spectrometry (IRMS) for $\delta^{15}N$ determination. $\delta^{15}N$ represents the isotopic ratio of $^{15}N/^{14}N$ in total soil nitrogen expressed as a per-mil (‰) deviation from atmospheric $N_2$, which reflects the relative enrichment or depletion of $^{15}N$ in the nitrogen pool due to biogeochemical processes such as mineralization, denitrification, or biological fixation.

The remaining environmental and edaphic variables were obtained from the "Portal de Geoinformación" (CONABIO 2025). Specifically, we extracted data from the following layers: "Uso del suelo y vegetación, escala 1:250000, serie VII continuo nacional" (for associated vegetation); "Precipitación media anual 11-03-2008" (for mean annual precipitation); "Temperatura media anual 18-04-2008" (for mean annual temperature); "Modelo digital de elevaciones resolución 1 km 31-05-2016" (for elevation); "pH 0–05 cm Predicción escala: 1:4000000 edición: 1.0 01-02-2020" (for pH), and Terrestrial Ecoregions of the World (Olson et al. 2001) for ecoregions. Data was query extracted from shape files with sample locations using the intersect function in Qgis v3.36 (QGIS Development Team 2023); data was used to complement GSM sample metadata. Additionally, we validated vegetation and secondary vegetation metadata with field observations. A map (Figure 1) and a table (Table S1) with the 55 locations, 10 vegetation types and several transitional ecotones are presented.

## 2.3 | Statistical Analysis

A total of 44,403 fungal OTUs, belonging to 1951 genera, 736 families, 282 orders, 98 classes, and 21 phyla, within 55 sites in 15 Mexican states, 14 ecoregions, and 7 biomes were extracted from the GSM database (Tedersoo et al. 2021).

The analyses were implemented using the R packages *phyloseq* (McMurdie and Holmes 2013), *vegan* (Oksanen et al. 2013), *ampvis2* (Andersen et al. 2018), *indicspecies* (De Cáceres and Legendre 2009), and *ggplot2* (Wickham et al. 2016). Our statistical workflow was designed to test the predictive framework that fungal community structure in the northern Neotropics is shaped by (i) vegetation type and habitat complexity, (ii) host mycorrhizal status, and (iii) climatic and edaphic gradients.

Beta diversity was assessed using Jaccard (presence/absence) and Bray–Curtis (relative abundance) dissimilarities. Hierarchical clustering defined eight major community groups (Bray Groups I–VIII), which were validated with non-metric multidimensional scaling (NMDS). Principal Component Analysis (PCA) was also performed as a supplementary ordination to confirm clustering patterns.

Alpha diversity was quantified using observed richness, Shannon diversity, Simpson diversity, and Pielou's evenness index. Taxonomic composition was examined at the phylum, order, and family levels, while functional composition was evaluated using trophic guilds/primary lifestyles (see Methods Section 2.1). Relative abundances were summarized in barplots by Bray Group, and heatmaps were generated using the *amp_heatmap* function which aggregates taxa by relative abundance of OTUs and prevalence across samples. To identify taxa significantly associated with Bray Groups, an Indicator species analysis was conducted using the *multipatt* function in the *indicspecies* package. *p*-values were adjusted for multiple comparisons using the Benjamini–Hochberg False Discovery Rate (FDR) correction, and taxa with adjusted FDR $\leq 0.05$ were considered significant indicators. Finally, to test the influence of environmental variables on fungal community composition, we performed a redundancy analysis (RDA) with Hellinger-transformed OTU data (Legendre and Gallagher 2001). Predictor variables included elevation, pH, mean annual temperature, mean annual precipitation (mm year$^{-1}$), total N (g kg$^{-1}$) and total P (mg kg$^{-1}$) concentrations, $\delta^{15}$N, OTU abundance, and OTU richness. Model significance was evaluated with permutation tests (999 permutations). Both sequential tests were conducted (by = "term") which estimates the additional variance explained as predictors enter the model, and marginal tests (by = "margin")—which quantifies the unique effect of each variable while controlling for the others. For each predictor, we report the F and permutation-based *p*-values along with partial adjusted $R^2$ and variance inflation factors (VIF) to assess multicollinearity. The total and axis-wise explained variances were also calculated.

## 3 | Results

### 3.1 | Fungal Beta Diversity and Ecogeographic Clustering

To explore patterns of community composition across sites, we first performed cluster analyses using Jaccard (presence/absence) and Bray–Curtis (relative abundance) distances. Both distance metrics yielded similar topologies. Using a branch cut-off of 0.55, the Bray–Curtis dendrogram grouped the 55 sites into eight clusters (hereafter Bray Groups I–VIII). These groups captured not only differences in vegetation type but also broader ecogeographic patterns, reflecting the combined influence of vegetation, climate, and geography (Figure 2a).

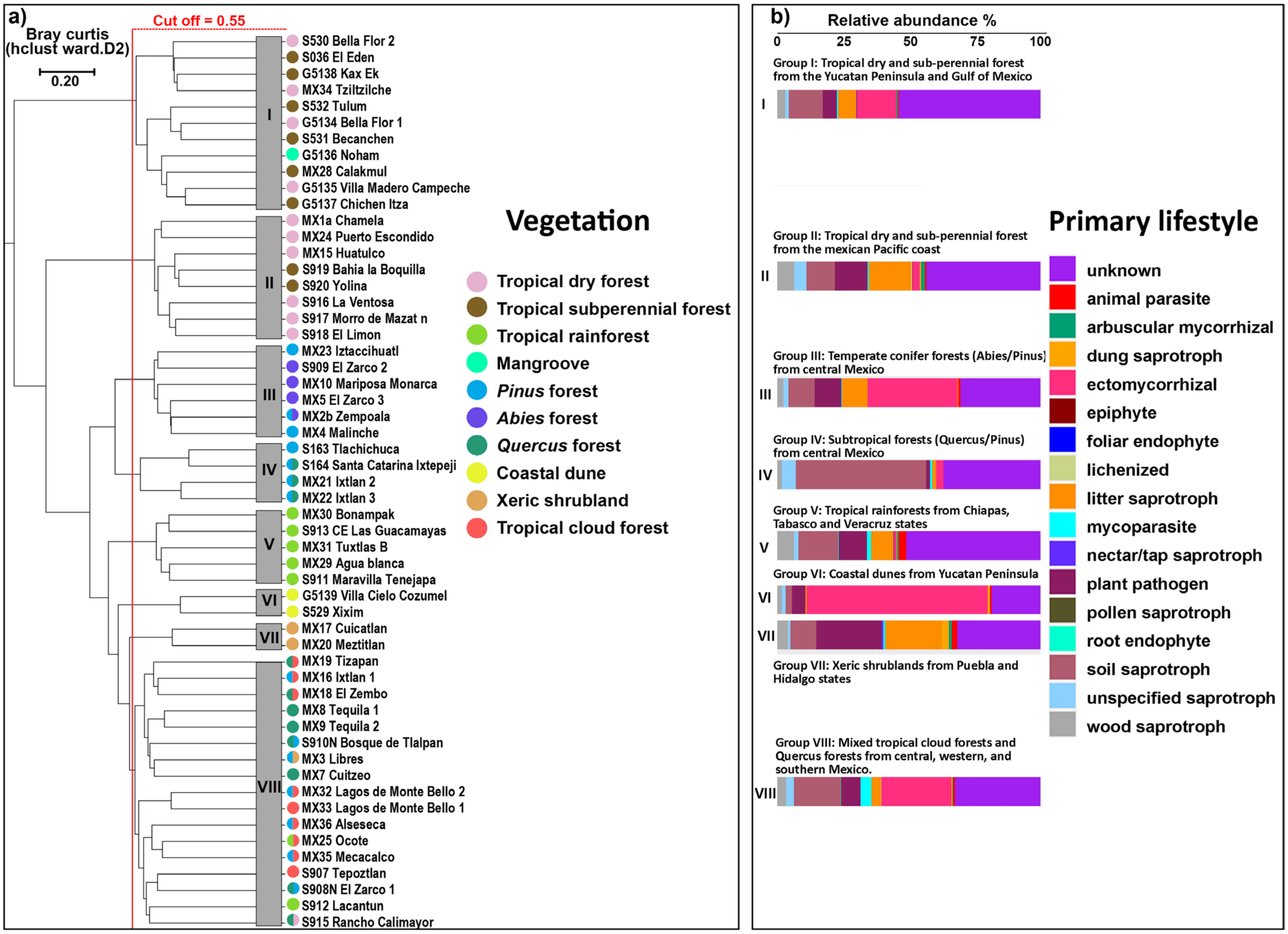


**FIGURE 2** | Beta diversity analysis and fungal primary lifestyle composition across different vegetation types. (a) in central and southern Mexico (the northern Neotropics). Hierarchical clustering dendrogram based on Bray–Curtis dissimilarity, with clusters defined at a cutoff of 0.55. Sites are color-coded according to their vegetation type (colored circles). (b) Bar plots showing the mean relative abundance of fungal primary lifestyles for each Bray–Curtis group (colored bars).

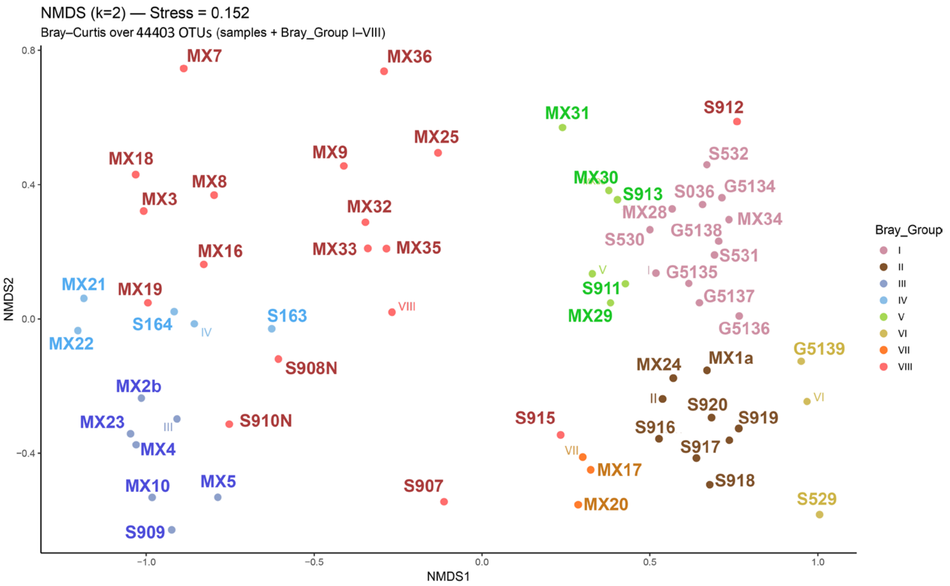


**FIGURE 3** | Non-metric multidimensional scaling (NMDS) ordination ($k=2$, stress $=0.152$) based on Bray–Curtis dissimilarities (Bray group) of 44,403 fungal OTUs across 55 sites in central and southern Mexico (the northern Neotropics). Colors indicate the eight Bray Groups (I–VIII) defined by hierarchical clustering (see Figure 2a). Roman numerals denote the centroid (mean position) of each group in the ordination space.

Group I comprised tropical dry and sub-perennial forests from the Yucatán Peninsula and Gulf of Mexico; Group II included tropical dry and sub-perennial forests along the Pacific coast; Group III encompassed temperate conifer forests dominated by *Abies religiosa* and *Pinus* species in central Mexico; Group IV contained subtropical forests dominated by *Pinus* and *Quercus* species in central Mexico. Group V included tropical rainforests from Chiapas, Tabasco, and Veracruz states; Group VI consisted of coastal dune systems in the Yucatán Peninsula, primarily associated with *Coccoloba* species; Group VII represented xeric shrublands in the states of Puebla and Hidalgo; and Group VIII was represented by a heterogeneous group of mixed tropical cloud forests and *Quercus* forests from central, western, and southern Mexico.

To corroborate these groups, we performed a non-metric multidimensional scaling (NMDS) analysis (Figure 3) based on the full OTU table (44,403 taxa). The two-dimensional ordination ($k=2$) had a stress value of 0.152, indicating a good fit for community dissimilarities. The NMDS confirmed the separation among most Bray Groups, with tropical systems (Groups I, II, and V) clustering apart from temperate conifer and oak forests (Groups III and IV), xeric shrublands (Group VII), and coastal dunes (Group VI) (Figure 2b). Group VIII showed no consistent pattern, with several sites dispersed across the ordination space; notably, three sites assigned to Group VIII clustered closely with Group III, suggesting that these communities are compositionally more similar to temperate ectomycorrhizal systems than to the heterogeneous assemblages that defined the rest of Group VIII. Principal Component Analysis (PCA) was also conducted as a supplementary validation of community clustering (Figure S1). Together, the cluster and ordination analysis support the Groups I–VIII as the comparative framework for subsequent analyses.

## 3.2 | Fungal Primary Lifestyles Across Groups

In tropical systems (Groups I, II, and V), a large fraction of the community remained unclassified into trophic guilds (Group I = 52.5%, Group II = 41.9%, Group V = 49.9%), reflecting the prevalence of uncharacterized and potentially new lineages in these ecosystems. Within the annotated guilds, tropical dry forests of the Yucatán (Group I) showed notable contributions of ectomycorrhizal fungi (14.9%), soil saprotrophs (12.6%), and litter saprotrophs (6.7%). Pacific dry forests (Group II) were characterized by litter saprotrophs (15.6%), plant pathogens (12.1%), and soil saprotrophs (10.4%). Rainforests (Group V) displayed a more balanced distribution among annotated guilds, with soil saprotrophs (14.7%), plant pathogens (10.4%), and litter saprotrophs (8.3%) contributing at comparable levels, suggesting no single guild dominated community composition (Figure S2).

Temperate conifer *Abies–Pinus* forests (Group III) were strongly enriched in ectomycorrhizal fungi (33.5%), accompanied by plant pathogens (10.0%) and litter saprotrophs (9.5%). In contrast, *Pinus–Quercus* subtropical forests (Group IV) were dominated by soil saprotrophs (48.3%), while other guilds remained comparatively minor (< 10%). Coastal dune systems (Group VI) showed a striking prevalence of soil saprotrophs (67.8%), together with moderate contributions from plant pathogens (4.9%) and litter saprotrophs (4.9%). Xeric shrublands (Group VII) were enriched in plant pathogens (24.0%) and litter saprotrophs (20.8%), with soil saprotrophs (9.6%) as secondary contributors. Finally, the heterogeneous Group VIII (tropical cloud forests and *Quercus* forests) showed greater variability across sites, with soil saprotrophs (17.3%), ectomycorrhizal fungi (26.0%), and plant pathogens (7.3%) as the most consistent guilds (Figure 2b), although site MX33 stood out for its greater relative abundance of mycoparasitic fungi (Figure S3). Restricted guilds, each representing less than 5% of relative abundance across all groups, included dung and wood saprotrophs, moss symbionts, mycoparasites, and lichen parasites. It is important to note that guild assignments were inferred primarily at the genus level and therefore should be interpreted with caution. Although this approach may obscure fine-scale functional diversity, it remains valuable for identifying broad ecological patterns and for testing our predictive framework. By aggregating taxa into trophic guilds, we can directly evaluate whether fungal functional composition aligns with expectations based on vegetation type, host mycorrhizal status, and environmental gradients.

### 3.3 | Fungal Alpha Diversity and Taxa Composition

We did not apply rarefaction to homogenize sequencing depth, as PacBio HiFi sequencing generates fewer but longer and highly accurate reads, which provide strong taxonomic resolution despite relatively shallow depth. However, PacBio data often contain many singletons, which can inflate observed richness estimates. Therefore, we report observed richness but interpret it with caution, and we emphasize Shannon and Simpson diversity indices as more robust descriptors of alpha diversity in our dataset.

At the site level, the richest communities were recorded in MX2b and MX23 (Group III, temperate conifer forests) and MX24 (Group II, Pacific dry forests), each surpassing 1800 OTUs. In contrast, the lowest observed richness was found in S529 and GS139 (Group VI, coastal dunes), with fewer than 500 OTUs, confirming the reduced diversity of these environmentally harsh systems (Figure 4a,b; Table S2).

When alpha diversity was averaged by Group (Table 1), tropical rainforests (Group V) exhibited the greatest mean richness (1542 ± 261 OTUs) and Shannon diversity (6.08 ± 0.35). Temperate conifer forests (Group III) showed a comparable richness (1540 ± 585 OTUs) but lower evenness (Pielou 0.737 ± 0.090) relative to rainforests (Pielou 0.829 ± 0.038). At the opposite extreme, coastal dunes (Group VI) had the lowest richness (368 ± 105 OTUs) and the lowest evenness (Pielou 0.526 ± 0.134), while xeric shrublands (Group VII) displayed moderate richness (1082 ± 424 OTUs) but high evenness (Pielou 0.834 ± 0.023) despite being represented by only two sites.

Other groups fell intermediately within ranges noted above: Pacific dry forests (Group II) had high evenness (Pielou 0.801 ± 0.034) and Shannon diversity (5.63 ± 0.30), Yucatán/Gulf dry forests (Group I) were slightly lower (Pielou 0.793 ± 0.062, Shannon 5.42 ± 0.56), while *Pinus–Quercus* forests (Group IV) showed the lowest diversity among forested systems (richness 798 ± 196 OTUs, Shannon 4.76 ± 0.48, Pielou 0.714 ± 0.056), and the heterogeneous Group VIII (*Quercus* forests and cloud forests) had intermediate richness (1175 ± 462 OTUs) but reduced evenness (Pielou 0.726 ± 0.077).

Across all 55 sites, Ascomycota and Basidiomycota were the dominant phyla, together representing more than 60% of relative abundance (Figure S4). Sites with atypical phylum-level profiles included MX2b and MX7, where Zoopagomycota accounted for ~29% of total reads. Mortierellomycota were particularly enriched in conifer forests (Groups III and IV), with relative abundances of 8.7% and 11.7%, respectively. Tropical dry forests (Groups I and II) and rainforests (Group V) had low but consistent contributions by Glomeromycota (up to 2%).

At the order level, clear ecological differentiation was observed across Groups (Figure 4c). Agaricales were consistently prevalent (13.7%–18.5%) in tropical dry forests (Groups I–II), conifer forests (16.2%, Group III), and rainforests (18.5%, Group V), but markedly reduced in *Pinus–Quercus* forests (1.4%, Group IV). Umbelopsidales reached high abundance in Group IV (25.6%, *Pinus–Quercus* forests), while Thelephorales were strongly enriched in coastal dunes (34.9%, Group VI). Russulales were well represented in conifer forests (10.1%, Group III) and cloud/oak forests (6.9%, Group VIII). Pleosporales were characteristic of xeric shrublands (31%, Group VII), whereas Hypocreales showed greater abundance in Groups V and VII (15.8% and 16.4%, respectively).

### 3.4 | Prevalent Taxa and Indicator Species Analysis

Patterns of species prevalence across Groups revealed distinct dominant genera (Figure 5). In tropical dry forests of the Yucatán Peninsula (Group I), prevalent taxa included *Tomentella* (4.1%), *Agaricomycetes* incertae sedis (6.5%), and *Sebacina* (2.9%). In contrast, Pacific dry forests (Group II) were characterized by greater relative abundance of *Fusarium* (3.0%) and *Geastrum* (5.3%). Temperate conifer forests (Group III) showed a prevalence of ectomycorrhizal lineages such as *Russula* (9.6%) and *Inocybe* (6.5%), while Group IV (*Pinus–Quercus* forests) was enriched in *Umbelopsis* (25.6%) and *Geminisbasidium* (7.7%). Rainforests (Group V) displayed a more balanced distribution, with *Geastrum* (1.7%) and *Sebacina* (2.3%) among the most abundant taxa. Coastal dunes (Group VI) were dominated by *Tomentella* (29.4%) and *Scleroderma* (25.9%), whereas xeric shrublands (Group VII) showed a high prevalence of *Fusarium* (8.8%) and *Cladophialophora* (1.5%). Finally, Group VIII (tropical cloud and oak forests) was enriched in *Russula* (6.1%) and *Trichoderma* (3.7%). For detailed patterns at the species level, including the top 50 most prevalent OTUs across all sites, see Figure S5.

Indicator species analysis further supported these compositional differences, identifying significant associations (FDR ≤ 0.05) between particular taxa and vegetation types. For example, *Geastrum* and *Scleroderma* were significant indicators of tropical dry forests (Groups I–II), *Russula* and *Gymnopus nubicola* of temperate conifer forests (Group III), *Umbelopsis* of *Pinus–Quercus* subtropical forests (Group IV), and *Dermoloma* of tropical rainforests (Group V). In coastal dunes (Group VI), *Tomentella* was confirmed as a strong indicator, while xeric shrublands (Group VII) were characterized by indicator species such as *Fusarium* and *Trichoderma* (Table S3). No significant indicator taxa were detected for Group VIII, likely reflecting its heterogeneous composition across mixed tropical cloud and oak forests.

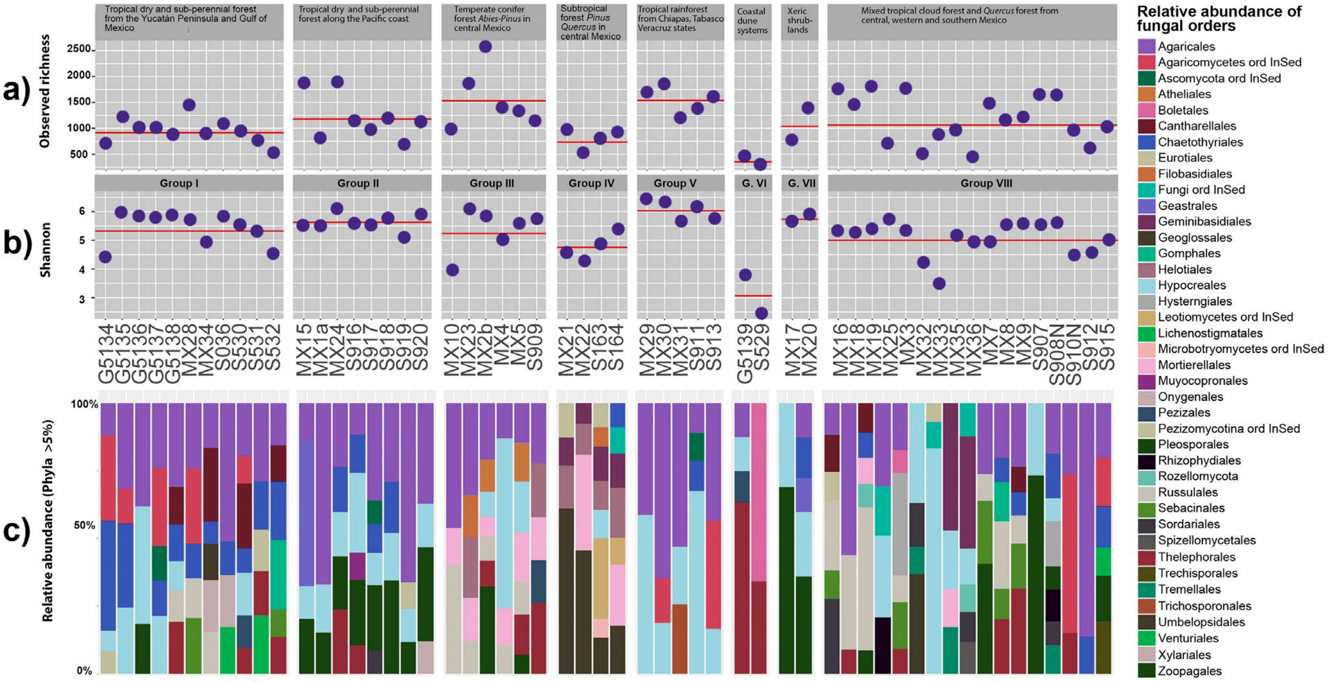


**FIGURE 4** | Fungal diversity and community composition across 55 sites in central and southern Mexico (the northern Neotropics) grouped by Bray groups (I–VIII). (a) Observed richness of fungi across sites, with red trend lines indicating the mean value within each cluster. (b) Shannon diversity index across sites, showing mean values within each cluster. (c) Relative abundance of fungal orders (only orders with >5% abundance shown) across sites.

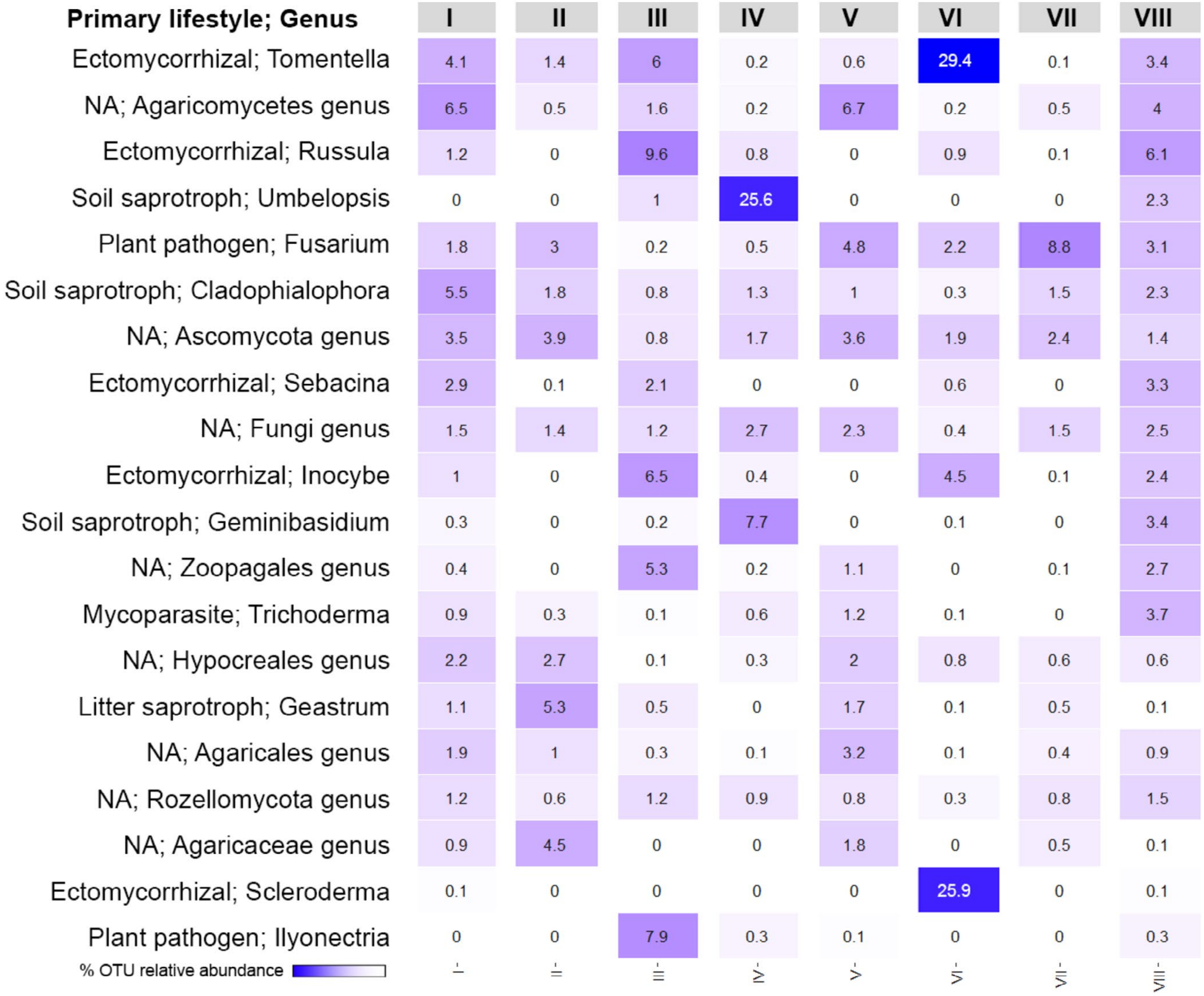
**TABLE 1** | Mean alpha diversity index for Bray groups composed of soil samples collected from 55 sites in central and southern Mexico (the northern Neotropics) and studied for their fungal composition.

| Group | Observed_ mean | Shannon_ mean | Simpson_ mean | Pielou_ mean |
|---|---|---|---|---|
| I | 948 | 5.419 | 0.978 | 0.793 |
| II | 1202 | 5.628 | 0.978 | 0.800 |
| III | 1540 | 5.378 | 0.964 | 0.736 |
| IV | 798 | 4.757 | 0.971 | 0.714 |
| V | **1542** | **6.079** | 0.987 | 0.829 |
| VI | 368 | 3.115 | 0.811 | 0.525 |
| VII | 1082 | 5.789 | **0.989** | **0.834** |
| VIII | 1175.294 | 5.066 | 0.953 | 0.725 |

## 3.5 | Multivariate Analysis of Environmental Drivers of Fungal Communities

To test whether regional climatic gradients and local edaphic conditions explained fungal community composition, we performed a redundancy analysis (RDA) with Hellinger-transformed OTU data. The model including elevation, pH, temperature, precipitation, total phosphorus concentrations ($\mathrm{mg\,kg^{-1}}$), total nitrogen concentrations ($\mathrm{g\,kg^{-1}}$), $\delta^{15}$N, OTU abundance (sequencing reads), and observed richness explained 23.8% of the total variance (adjusted $R^2 = 4.1\%$ Adj. $R^2 \approx 0.0406$) (Figure 6). Environmental and physicochemical variables are summarized in Table S4. Sequential permutation tests (by = "term") indicated that elevation ($F = 3.32$, $p = 0.001$) and pH ($F = 1.80$, $p = 0.001$) were the strongest initial predictors, followed by precipitation, soil phosphorus and nitrogen concentrations, $\delta^{15}$N, and richness (all $p \leq 0.005$). However, marginal tests (by = "margin")—which estimate the unique contribution of each variable while controlling for the others—identified pH ($F = 1.70$, $p = 0.002$) and precipitation ($F = 1.62$, $p = 0.001$) as the most influential independent predictors, with smaller but significant effects of nutrient concentrations, $\delta^{15}$N, elevation, and richness ($p \leq 0.01$). Variance inflation factors (VIF) indicated low collinearity among most predictors (VIF $< 3$), except for elevation (VIF = 9.2) and temperature (VIF = 8.5), which are expectedly correlated given their climatic interdependence. Although the marginal effect of elevation was reduced by this collinearity, its vector remained among the longest in the RDA ordination, reflecting a clear compositional turnover along the elevational gradient. This supports the interpretation of elevation as an integrative variable that encompasses both climatic and edaphic influences on soil fungal communities. Complete statistics for both sequential and marginal tests are provided in Table S5.

While the correlation analysis (Figure S6) suggested positive associations of richness with elevation and among abundance with both elevation and precipitation, and negative associations with pH, temperature, $\delta^{15}$N, and phosphorus concentration, the RDA provided a multivariate perspective that disentangled these effects. Once all predictors were considered simultaneously, elevation and pH emerged as the strongest independent



| Primary lifestyle; Genus | I | II | III | IV | V | VI | VII | VIII |
|---|---|---|---|---|---|---|---|---|
| Ectomycorrhizal; Tomentella | 4.1 | 1.4 | 6 | 0.2 | 0.6 | 29.4 | 0.1 | 3.4 |
| NA; Agaricomycetes genus | 6.5 | 0.5 | 1.6 | 0.2 | 6.7 | 0.2 | 0.5 | 4 |
| Ectomycorrhizal; Russula | 1.2 | 0 | 9.6 | 0.8 | 0 | 0.9 | 0.1 | 6.1 |
| Soil saprotroph; Umbelopsis | 0 | 0 | 1 | 25.6 | 0 | 0 | 0 | 2.3 |
| Plant pathogen; Fusarium | 1.8 | 3 | 0.2 | 0.5 | 4.8 | 2.2 | 8.8 | 3.1 |
| Soil saprotroph; Cladophialophora | 5.5 | 1.8 | 0.8 | 1.3 | 1 | 0.3 | 1.5 | 2.3 |
| NA; Ascomycota genus | 3.5 | 3.9 | 0.8 | 1.7 | 3.6 | 1.9 | 2.4 | 1.4 |
| Ectomycorrhizal; Sebacina | 2.9 | 0.1 | 2.1 | 0 | 0 | 0.6 | 0 | 3.3 |
| NA; Fungi genus | 1.5 | 1.4 | 1.2 | 2.7 | 2.3 | 0.4 | 1.5 | 2.5 |
| Ectomycorrhizal; Inocybe | 1 | 0 | 6.5 | 0.4 | 0 | 4.5 | 0.1 | 2.4 |
| Soil saprotroph; Geminibasidium | 0.3 | 0 | 0.2 | 7.7 | 0 | 0.1 | 0 | 3.4 |
| NA; Zoopagales genus | 0.4 | 0 | 5.3 | 0.2 | 1.1 | 0 | 0.1 | 2.7 |
| Mycoparasite; Trichoderma | 0.9 | 0.3 | 0.1 | 0.6 | 1.2 | 0.1 | 0 | 3.7 |
| NA; Hypocreales genus | 2.2 | 2.7 | 0.1 | 0.3 | 2 | 0.8 | 0.6 | 0.6 |
| Litter saprotroph; Geastrum | 1.1 | 5.3 | 0.5 | 0 | 1.7 | 0.1 | 0.5 | 0.1 |
| NA; Agaricales genus | 1.9 | 1 | 0.3 | 0.1 | 3.2 | 0.1 | 0.4 | 0.9 |
| NA; Rozellomycota genus | 1.2 | 0.6 | 1.2 | 0.9 | 0.8 | 0.3 | 0.8 | 1.5 |
| NA; Agaricaceae genus | 0.9 | 4.5 | 0 | 0 | 1.8 | 0 | 0.5 | 0.1 |
| Ectomycorrhizal; Scleroderma | 0.1 | 0 | 0 | 0 | 0 | 25.9 | 0 | 0.1 |
| Plant pathogen; Ilyonectria | 0 | 0 | 7.9 | 0.3 | 0.1 | 0 | 0 | 0.3 |

**FIGURE 5** | Heatmap of the most prevalent fungal genera across Bray Groups (I–VIII) across 55 sites in central and southern Mexico (the northern Neotropics), classified by primary lifestyle. Values represent the relative abundance (%) of OTUs assigned to each genus within groups. Color intensity indicates increasing abundance (light purple to dark blue).

drivers of community turnover, with precipitation and nutrient concentrations explaining finer-scale within-group variation. This contrast highlights that some bivariate associations reflect indirect effects better captured in a multivariate framework.

These results confirm that fungal communities in the northern Neotropics are primarily structured by broad climatic and elevational gradients, with additional turnover explained by local soil properties. In particular, richness tended to increase with elevation, whereas pH and temperature were negatively associated with community structure. Precipitation and soil nutrient availability (P and N) further explained within-group variation. This was especially evident in tropical dry forests of the Yucatán and Pacific regions (Groups I and II), which occur at low elevation, warm climates, and low precipitation, yet differ in their nitrogen and phosphorus availability. Conversely, Groups III, IV, and VIII (conifer and cloud forests) occur at higher elevations with cooler and wetter conditions, where soil nutrients and $\delta^{15}N$ contributed to further compositional turnover.

## 4 | Discussion

### 4.1 | Vegetation Types and Ecogeography as Primary Drivers of Soil Fungal Communities in the Northern Neotropics

The organization of communities into eight Groups confirmed that vegetation type and geography jointly structured soil fungal assemblages across the northern Neotropics. These results echo global evidence that vegetation and ecoregions filter fungal diversity (Bahram et al. 2021; Tedersoo et al. 2021) but provide novel regional insight: in Mexico, topographic heterogeneity amplifies this effect, creating ecogeographic clusters even within a relatively narrow latitudinal range.

This directly supports our first prediction—structurally complex habitats such as rainforests (Group V) and conifer forests (Group III) harbor richer fungal communities, while extreme systems like dunes (Group VI) and xeric shrublands (Group VII)

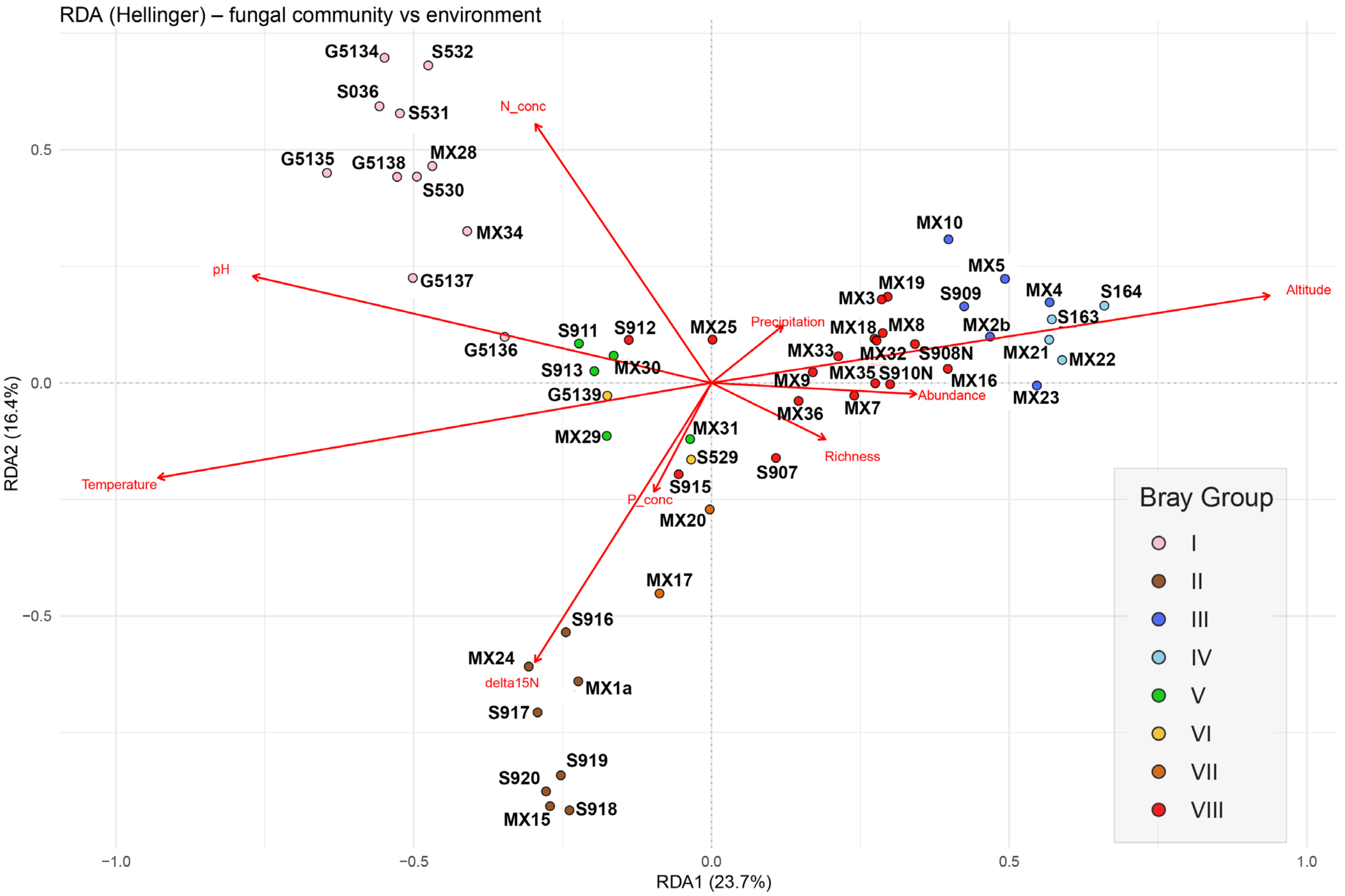


**FIGURE 6** | Redundancy analysis (RDA) of fungal community composition (Hellinger-transformed OTU data) across 55 sites in central and southern Mexico (the northern Neotropics) constrained by environmental and physicochemical variables. Samples are colored according to their Bray Groups (I–VIII). Red arrows represent environmental vectors, with their length and direction indicating the strength and orientation of correlations with community turnover.

sustain reduced richness. By framing vegetation and geography as the first hierarchical filter, our study lays a foundation for predictive ecology of soil fungi in Mexico.

Although Group VIII did not exhibit a consistent taxonomic pattern, which likely reflects its biogeographic position at the interface between Neotropical and Nearctic regions. This transitional zone, composed of cloud forests and oak-dominated forests, harbors a mixture of lineages from both realms, explaining its lack of indicator species. From a predictive perspective, this heterogeneity highlights the vulnerability of transitional ecosystems under climate change. Global models suggest that tropical vegetation is expected to expand northwards and upslope, while temperate conifer and oak forests may retract (Pérez-García and Meave 2006; Mair et al. 2012; Ramírez-Barahona et al. 2025; Desprez-Loustau et al. 2007). As a result, the distinct biogeographic signal of Group VIII may diminish further, leading to homogenization towards Neotropical assemblages. Recognizing the uniqueness and fragility of this transition zone is therefore critical for anticipating future shifts in fungal diversity and for conservation planning. A limitation of the CONABIO vegetation layers is that they assign a single dominant type per site, overlooking the mixed composition present in many Mexican forests. Direct observation of the sampled sites allowed us to identify cases of mixed vegetation, which was essential for properly interpreting the Bray–Curtis clustering. However, for Group VIII, additional effort may be needed to achieve a more accurate characterization of vegetation composition.

## 4.2 | Alpha Diversity and Functional Balance Under Contrasting Conditions

Rainforests exhibited the greatest observed richness and Shannon diversity, reflecting balanced coexistence among functional guilds and diverse plant–fungal interactions (Rillig and Mummey 2006; Mangan et al. 2010; Tedersoo et al. 2014). In contrast, conifer forests reached similar richness but lower evenness due to the dominance of ectomycorrhizal fungi. Interestingly, xeric shrublands (Group VII), although species-poor, showed some of the highest evenness values. This finding highlights that under stressful, resource-limited conditions, competitive exclusion may be relaxed, allowing multiple taxa to persist at relatively similar abundances (Zuo et al. 2021). We report observed richness but interpret it with caution and emphasize Shannon and Simpson diversity indices as more robust descriptors of alpha diversity in this dataset. Similar concerns have been raised in fungal metagenomics, where species abundance distributions and richness estimates can be biased by sequencing depth and methodological constraints, highlighting the importance of combining classical community ecology concepts with high-throughput sequencing data (Unterseher et al. 2011).

The functional annotation of xeric shrublands also requires caution. Many lineages were classified as plant pathogens, but this likely reflects database-level bias: genus-level assignments often assume pathogenicity even when fungi occur in dormant, saprotrophic, or endophytic states (Weiss et al. 2011; Zanne et al. 2020). This suggests that these fungi may not be actively pathogenic but instead survive in latent phases, contributing to the surprising evenness observed in such harsh systems. Together, these findings support our second prediction, that host mycorrhizal status and environmental harshness influence not only richness but also guild balance and dominance patterns.

## 4.3 | Prevalence and Indicator Taxa: Generalist Versus Specialist Soil Fungi

Our prevalence analysis revealed a set of generalist fungi such as *Fusarium solani*, *Saitozyma podzolica*, and *Trichoderma spirale*, which occurred broadly across habitats. These taxa are functionally versatile, acting as saprotrophs, pathogens, or mycoparasites depending on environmental context (Torbati et al. 2021; Das et al. 2023; Ye et al. 2023). Their ubiquity suggests they contribute broadly to nutrient cycling and stress tolerance across ecosystems (Wang et al. 2021). In contrast, indicator species analysis identified habitat specialists tightly associated with vegetation types: *Geastrum* and *Scleroderma* in tropical dry forests, *Russula* and *Gymnopus* in temperate conifer forests, *Umbelopsis* in *Pinus–Quercus* subtropical forests, and *Tomentella* in coastal dunes. No indicators were detected for Group VIII, reflecting its ecological heterogeneity.

These complementary approaches highlight two levels of assembly: generalists that underpin ecosystem resilience across gradients, and specialists that reflect local vegetation and soil conditions. This duality further corroborates our second prediction, showing how mycorrhizal hosts and vegetation types filter fungal specialists while allowing generalists to persist widely.

## 4.4 | Environmental and Climatic Gradients as Multiscale Drivers of Soil Fungal Communities

Multivariate RDA confirmed that pH and precipitation were the strongest independent predictors of fungal community turnover (Ramírez-Barahona et al. 2025), while elevation, nutrient concentrations (N and P), $\delta^{15}$N, and richness contributed significantly at secondary scales (Zhao et al. 2020). Sequential tests initially identified elevation and pH as the most influential predictors, but marginal tests—accounting for collinearity—highlighted pH and precipitation as the primary independent drivers of community composition. Despite this reduction in its marginal effect, the long elevational vector in the RDA ordination indicates that elevation remains a dominant integrative gradient influencing fungal turnover.

Richness increased with elevation but decreased with hotter temperature and pH, echoing findings from global syntheses (Steidinger et al. 2020; Bahram et al. 2021; Geml et al. 2022). However, unlike global meta-analyses where elevation is often a weak predictor due to signal dilution (when broad-scale datasets average out regional climatic and edaphic variability) (Tedersoo et al. 2014, 2021), in Mexico elevation still exerts a strong indirect influence through its correlation with pH, precipitation, and temperature. This difference underscores the role of Mexico's extreme topographic heterogeneity, which compresses sharp climatic gradients into small spatial scales, magnifying the effect of elevation (Rico et al. 2021). Part of this environmental signal may also arise from vegetation–soil feedbacks, although the high fungal richness observed in coniferous forests despite comparatively low plant diversity suggests a partial uncoupling between plant and fungal responses.

Nutrient patterns further refined this picture. In Yucatán dry forests, $\delta^{15}$N depletion suggested low nitrogen bioavailability despite high total nitrogen concentrations in karstic soils (Escalante et al. 2018). In such calcareous environments, much of the nitrogen pool is chemically immobilized by high pH and carbonate complexation, which limits its availability to plants and microbes (Alghamdi et al. 2023). Mycorrhizal associations likely mitigate this nutrient limitation by enhancing nitrogen uptake and recycling efficiency—a mechanism also documented in seasonally dry tropical forests of the northern Yucatán Peninsula (Hasselquist et al. 2010; Ceccon et al. 2003; He et al. 2017). Moreover, arbuscular mycorrhizal fungi often cooperate with diazotrophs to sustain nitrogen and phosphorus fluxes under conditions of low nutrient availability (Xiao et al. 2022). This functional buffering may foster local endemism by allowing fungal taxa to persist in nutrient-poor or chemically restrictive soils (Tedersoo et al. 2022).

In xeric shrublands, high phosphorus concentrations reflect limited leaching in arid soils (Xie et al. 2023), which may explain the prevalence of saprotrophs and pathogens adapted to exploit phosphorus-rich, nitrogen-poor conditions.

These results confirm our third prediction: that broad climatic and elevational gradients structure beta diversity while local nutrient conditions modulate turnover within vegetation types (Leff et al. 2015).

## 4.5 | Methodological Insights and Novelty

By applying PacBio HiFi metabarcoding at a national scale, we provide one of the first high-resolution baselines of soil fungal community composition in Mexico. The combination of clustering, diversity metrics, prevalence and indicator analyses, and multivariate modeling illustrates how a predictive framework can be explicitly tested across hierarchical ecological filters.

The high proportion of unclassified fungi—particularly in tropical forests—underscores both the uniqueness of Neotropical fungal diversity and the urgent need for expanded reference databases. Methodological transparency is also critical: while PacBio increases taxonomic resolution, its shallow depth yields many singletons, requiring cautious interpretation of observed richness. By focusing on Shannon, Simpson, and Pielou indices alongside richness, we balanced sensitivity to abundant taxa with robustness against noise from rare OTUs.

The novelty of this study lies in linking soil fungal ecology in Mexico to a multiscale predictive framework, showing that: (1) Habitat climatic and soil variables set upper limits to diversity. (2) Host mycorrhizal status filters community composition. (3) Climatic and edaphic gradients refine turnover at regional and local scales. This hierarchical approach positions our work as a cornerstone for the upcoming Soil Biodiversity Atlas of Mexico, providing both methodological guidance and ecological insights for future metabarcoding efforts.

## 5 | Conclusion and Perspectives

This study provides the first large-scale assessment of soil fungal diversity across the northern Neotropics using long-read PacBio HiFi metabarcoding. Our results highlight three main insights: (i) structurally complex habitats such as rainforests and conifer forests sustain richer and more balanced fungal communities than environmentally harsh systems like dunes or xeric shrublands; (ii) host mycorrhizal status filters community composition, with ectomycorrhizal forests enriched in ECM fungi and tropical systems showing more diverse functional assemblages; and (iii) broad climatic and edaphic gradients, particularly pH, precipitation, and elevation, are the strongest independent predictors of fungal turnover, while nutrients refine variation at local scales.

We also found that generalist taxa (e.g., *Fusarium solani*, *Saitozyma podzolica*, *Trichoderma spirale*) coexist with habitat-specific indicator species, revealing both widespread and specialized ecological strategies. Transitional Group VIII forests lacked indicator taxa, reflecting their mixed Nearctic–Neotropical composition. Our findings also reinforce the relevance of temperate forests, tropical rainforests, and xeric shrublands as reservoirs of unique fungal taxa, emphasizing the need for conserving these ecosystems under increasing anthropogenic pressures and climate change. By identifying the environmental filters that structure fungal diversity (notably elevation, pH, and temperature), this study provides a framework for anticipating potential shifts in fungal communities under ongoing climate and land-use change. While our results are not predictive models per se, they highlight the key drivers most likely to determine future trajectories of fungal community turnover in the northern Neotropics.

Considering the need for comprehensive biodiversity assessments, our research group is leading the national initiative "Soil Biodiversity Atlas of Mexico", which integrates bacteria, fungi, and soil fauna across ecosystems and agroecosystems. By combining broad-scale sampling with state-of-the-art sequencing approaches, the Atlas seeks to close critical knowledge gaps and provide a predictive framework for soil biodiversity conservation under climate change.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The datasets generated and analyzed during this study are publicly available in the Zenodo repository at https://doi.org/10.5281/zenodo.18716370. The archived materials include processed OTU tables, taxonomic assignments, fungal trait classifications, sample metadata, visualization outputs, and the complete analysis scripts required to reproduce the results. The full analysis workflow and additional supporting resources are also available at: https://github.com/Burn121212/FungiMX.git.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figures S1-S6. Table S1:** Metadata of vegetation and ecogeographic characteristics for the 55 sites in central and southern Mexico (the northern Neotropics). Each site is annotated with its vegetation type, dominant plant species, and associated environmental descriptors used for community clustering and ordination analyses. This information was used to contextualize Bray Groups I–VIII and to interpret fungal community turnover in relation to vegetation and habitat type. **Table S2:** Alpha diversity metrics (Observed richness, Shannon, Simpson, and Pielou's evenness) calculated for each sampling site in central and southern Mexico (the northern Neotropics) across Bray Groups I–VIII. Values are based on PacBio HiFi reads without rarefaction; observed richness is reported with caution due to the presence of many singletons. **Table S3:** Results of the indicator species analysis (IndVal) across Bray Groups I–VIII in central and southern Mexico (the northern Neotropics). Significant associations were determined at FDR $\leq 0.05$. The analysis identified: 19 OTUs as indicators for Group I, 14 OTUs for Group II, 5 OTUs for Group III, 6 OTUs for Group IV, 24 OTU for Group V, 3 OTUs for Group VI, and 12 OTUs for Group VII. No significant indicator OTUs were detected for Group VIII, reflecting its heterogeneous composition. **Table S4:** Physicochemical and environmental variables across 55 sites in central and southern Mexico (the northern Neotropics) used in this study. **Table S5:** Permutation tests and diagnostic statistics for environmental predictors in the Hellinger-based redundancy analysis (RDA) of fungal community composition in central and southern Mexico (the northern Neotropics).