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Abstract

The tropical dry forest is a tropical biome characterized by prolonged dry seasons, and harbors an exceptionally rich floristic biodiversity. Yet it is among the most threatened biomes and its belowground diversity remains poorly documented. Here, we analyzed the soil environmental DNA with metabarcoding to quantify the belowground diversity and composition of 11 tropical dry forest sites across four biogeographic regions in Colombia, and we provide a comparative analysis of the biogeographic drivers of soil biodiversity, including soil properties, climate, and spatial factors. We found that the soil microbial communities of tropical dry forests had high proportions of taxa associated with dry conditions, such as Actinomycetota, Glomeromycetes, and Amoebozoa, compared to other tropical forests. Soil mesofauna consisted mainly of ants, termites, and earthworms, with few enchytraeids. The soil microbial alpha and beta diversity were primarily driven by soil physicochemical and climatic drivers, bacteria being more sensitive to aridity than fungi. Macroorganisms exhibited patterns of diversity that were less well explained by the tested predictors. Rather, most of their variation was associated with the sampled region, reflecting a marked biogeographic structure and suggesting that macroorganisms are more prone to isolation-by-distance than microorganisms. Overall, the prevalence of drought-associated microbial taxa and the specific composition of soil mesofauna indicate that tropical dry forests harbour a distinctive belowground biota. These findings provide an important baseline for understanding soil biodiversity in tropical dry forests and support conservation and restoration efforts at the biome scale.

Key words : community assembly, DNA metabarcoding, eDNA, mesofauna, microbes, soil biodiversity, tropical America.

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Highlights

- Using soil environmental DNA, we provide the first trans-kingdom description of soil biodiversity in tropical dry forest soils across Colombia.

- Tropical dry forest soil communities are composed of taxa associated with dry environments.

- The main drivers of soil diversity and community composition are taxon-dependent: microorganisms are primarily structured by local climate and soil properties, whereas macroorganisms are mainly structured by geographic locality.

Introduction

The tropical dry forest biome is characterized by prolonged periods of dry months, and it is found throughout the tropics, notably in the Americas (Dexter et al. 2015), which represent about 54% of the biome's area (Miles et al. 2006) and host a remarkably high biological richness (Allen et al. 2017; González-M et al. 2018). Because tropical dry forests grow on typically fertile soils, they are among the most threatened tropical biomes (Pennington et al. 2006) and have historically attracted human exploitation, primarily for agriculture (Hocquenghem 1998; García et al. 2014). This threat is particularly acute in the Americas, where 66% of the original cover of tropical dry forests has been lost (Portillo-Quintero and Sánchez-Azofeifa 2010), with deforestation rates six times higher than in Asia and Africa (Miles et al. 2006), highlighting the disproportionate pressure on tropical dry forests of the Americas. In addition, the remaining fragments of tropical dry forests suffer from widespread degradation and limited protection (Stan et al. 2024). Developing management strategies to protect tropical dry forests is essential, but this is predicated on an improved understanding of the drivers of their biodiversity (Portillo-Quintero et al. 2015). Yet, compared to tropical rainforests, ecological knowledge remains limited in tropical dry forests (Siyum 2020; Moonlight et al. 2021; Stan et al. 2024).

Tree diversity of tropical dry forests in the Americas is characterized by high levels of floristic turnover and endemism that reflect a strong biogeographic imprint within the biome (Banda-R et al. 2016; Allen et al. 2017). Large-scale dispersal barriers, such as the uplift of the Andes, have resulted in dispersal limitation, generating isolated biogeographic regions (Särkinen et al. 2012). Tropical dry forests are also marked by seasonality (Lehmann et al. 2011; Méndez-Alonzo et al. 2012), steep elevation

gradients, and vary dramatically in bedrock type (Townsend et al. 2008; Waring et al. 2021) or soil conditions (Rundel and Boonpragob 1995; Sampaio 1995; González-M et al. 2018; Rivero-Villar et al. 2022). These abiotic factors result in distinctive sets of tree communities in the Americas (González-M et al. 2018), with up to twelve floristically distinct groups of contrasting composition (Banda-R et al. 2016). However, there is limited knowledge about tropical dry forest beyond plant communities.

Here we focus on the belowground compartment which contains around 59% of global terrestrial biodiversity (Anthony et al. 2023) and includes bacteria, fungi, protists, micro- and mesofauna (invertebrates) besides plants. These organisms play an essential role in litter decomposition, nutrient cycling, soil structure and stability, carbon storage, and, ultimately, in forest resilience and restoration potential (Bardgett and van der Putten 2014). Soil biogeography has been reported to be governed by a variety of abiotic factors, including climate, soil pH, texture, C/N ratio, including floristic composition and dispersal limitation (Fierer and Jackson 2006; Tedersoo et al. 2014; Prober et al. 2015; Bahram et al. 2018; Delgado-Baquerizo et al. 2018; Phillips et al. 2019; Luan et al. 2020). The drivers of soil community assembly are expected to be taxon-dependent, because soil biota spans a broad range of body sizes, evolutionary histories, life-history strategies, and dispersal capacities. Indeed, dispersal ability often correlates with the organism body or propagule size either positively in the case of active dispersal (Auger et al. 2024), or negatively for passive dispersal (Martiny et al. 2006), and it modulates the importance of drift, selection and speciation locally and globally (Zinger et al. 2019; Luan et al. 2020). Therefore, documenting community assembly in tropical American dry forests requires a multi-taxa perspective.

A multi-taxa analysis of biological diversity is now attainable with environmental DNA to an unprecedented detail. Environmental DNA refers to DNA fragments that can be retrieved from an environmental sample (*sensu* Pawlowski et al. 2020), which can be then sequenced to document the biological communities within or living nearby the sample. In particular, eDNA metabarcoding, which is the amplification and sequencing of taxonomically informative DNA regions from environmental samples, now allows to simultaneously identify numerous taxonomic across the tree of life (Taberlet et al. 2018). This method holds great potential to explore biodiversity patterns even in poorly documented geographical areas such as the seasonally dry tropics (Zinger et al. 2020). For instance, eDNA metabarcoding has already been used to analyze soil biodiversity in boreal (Tedersoo et al. 2016; Calderón-Sanou et al. 2021), temperate (Drummond et al. 2015; Calderón-Sanou et al. 2020) or tropical rainforests (Ritter et al. 2019; Zinger et al. 2019).

Here, we used environmental DNA metabarcoding of soil samples to comprehensively describe soil biodiversity across the tropical dry forests of Colombia, encompassing a high heterogeneity in soils, climates, geological landscapes (Banda-R et al. 2016; Kattan et al. 2019) and vegetation (González-M et al. 2018). Specifically, we ask: (i) what is the diversity and overall composition of soil communities in tropical dry forests across the tree of life? and (ii) to what extent are these soil communities shaped by soil properties, climate, or isolation-by-distance (i.e. differ between biogeographic regions)? We expect that, similarly to vegetation, soil biodiversity in tropical dry forests also exhibits a high diversity and spatial turnover, but that these patterns differ among organisms, and depend on their dispersal ability.

Methods

Study sites, soil and climate characteristics

Study sites

The study was conducted at 11 sites across remnant fragments of tropical dry forests (TDF) in Colombia (Fig. 1A). Sampling sites spanned the geographic range of this biome in the country, from the northern Caribbean region through the inter-Andean valleys of the Magdalena (eastern) and Cauca (western) rivers, to the Patía valley in southern Colombia. At the scale of the Americas, based on plant cover, the northern plots fall within the floristic Caribbean node, whereas the others belong to a distinct inter-Andean node (both defined in Banda-R et al. 2016). Within these floristic nodes, plant species assemblages differ among regions (Kattan et al. 2019). For the purpose of biogeographic analysis, the sampled TDF fragments were grouped into four distinct regional units (Guajira, Magdalena, Cauca, and Patía). These names correspond to distinct and widely recognized WWF Ecoregions (Olson et al. 2001), thus providing a validated biogeographic framework for our study. At each site, a 1-ha plot was previously established and is now part of a continuous observation network of TDFs in Colombia (González-M. et al. 2019; Norden et al. 2021).

Soil sampling and processing

Field sampling was carried out during the dry season between November 2018 and February 2019. Within each 1-ha plot, soils were sampled at 16 points following a 20 × 20 m grid. The grid was subdivided into four subplots of four neighbouring points each. At each sampling point, leaf litter was removed and five 0-10 cm soil cores (four

corners plus center of a 1 m quadrat) were taken with a soil auger, pooled into a point-level composite, and homogenized. An aliquot of 15g each point-level composite was transferred the same day into sterile 250 mL Nalgene bottles containing ~40 g of silica gel for desiccation, for storage for DNA analyses. The rest of each point-level composite was pooled by subplot for physicochemical analyses, using equal masses from four points. Therefore, for physicochemical analysis, we had four composite soils within each 1-ha plot (n = 44 in total across the 11 plots).

Climatic and soil physicochemical properties

To characterize climate and biophysical conditions at each site, we retrieved nine climatic variables from González-M. et al. (2019) : total annual precipitation (TAP, mm), potential evapotranspiration (PET, mm), aridity index (Aridity, PET/TAP), annual number of rainy days (ARD), total precipitation during the three driest months (TPDriest, mm), isothermality (Isoth, %), water vapor pressure (WVP, kPa), wind speed (Wind, m/s) and solar radiation (SRad, MJ/m²). In addition, we extracted remote-sensing variables aggregated over 2018-2019 and summarized over each 1-ha plot: NDVI (Landsat Collection 2, Level-2, 8-day composites, Google Earth Engine), mean annual soil temperature at depths of 0-5 cm and 5-15 cm (Lembrechts et al. 2022), and a proxy for topo-climatic diversity (capturing local variability in temperature/humidity) derived from slope position and insolation (Theobald et al. 2015).

Soil physicochemical analyses were performed at the Soil Health Laboratory of Universidad de Bogotá Jorge Tadeo Lozano (UTADEO). The following properties were determined: pH, granulometry (clay <2 µm, silt 2-63 µm, sand 63-2000 µm; g per 100

g dry soil), electrical conductivity (EC, dS/m), base saturation (sat, %), soil organic carbon (Corg, %), the percentage of water (Pw, %), cation exchange capacity (CEC, cmol+/kg), and finally exchangeable ions (K, Ca, Mg, Na, P, B) and micronutrients (Fe, Mn, Cu, Zn) expressed in mg/kg.

The average and range values of all parameters across the study sites are provided in Table S1.

In order to summarize the environmental variability of the studied sites for downstream analyses, we ran two separate principal component analyses (PCA) for climatic and soil variables respectively, using centered and scaled variables. The climatic PCA (Fig. 1B) yielded PC1 (PCcont, 51.8%), reflecting rainfall frequency and thermal amplitude, and PC2 (PChum, 23%), reflecting water balance. The soil PCA (Fig. 1C) yielded PC1 (hereafter PCsrich, 46.4%), capturing a fertility–texture gradient (sandy, nutrient-poor soils at negative scores vs. clay-rich, more fertile soils at positive scores), and PC2 (PCpH, 15.2%), capturing a soil acidity gradient. In these two ordination spaces, the different regions exhibited distinct climatic and soil conditions (Fig. 1).

Molecular analyses

Back in the lab at the Humboldt Institute, DNA was extracted from the 16 point-level composite samples collected in each plot. In addition, one extraction blank (negative control) was included per plot, so that a total of 17 DNA extractions were processed for each plot. DNA extractions were performed as previously described (Taberlet et al., 2012, Zinger et al. 2016; Zinger, et al. 2019). PCR targeted six markers (Table S2): chloroplast trnL (Viridiplantae, hereafter referred to as “Plantae”), mitochondrial 16S rRNA (Insecta), mitochondrial 12S rRNA (Oligochaeta), ITS1 (Fungi), 18S rRNA

(Eukaryota), and 16S rRNA (Bacteria). Details on these markers are provided in Table S2.

For PCR amplification, each PCR reaction was carried out in a total volume of 20 µl and comprised 10 µl of AmpliTaq Gold Master Mix (Life Technologies, Carlsbad, CA, USA), 5.84 µl of Nuclease-Free Ambion Water (Thermo Fisher Scientific, Massachusetts, USA), 0.25 µM of each primer, 3.2 µg of BSA (Roche Diagnostic, Basel, Switzerland), and 2 µl of DNA template that was previously 10-fold diluted to reduce the amounts of PCR inhibitors. Thermocycling conditions for each primer pair are indicated in Table S2. All controls (extraction blanks, PCR negative controls and positive controls) were amplified and sequenced in parallel with the regular samples. These were used to guide choices in our data curation process. Two PCR replicates were performed for each sample and control. Amplification was conducted using a double indexing strategy (Binladen et al. 2007) using a system of 32 by 36 octamers with at least five differences between them located at the 5' end of each primer (Coissac 2012). In doing so, each PCR product had a unique combination of tags for both forward and reverse primers, allowing for the retrieval of sequence data for each sample. Ten wells per PCR plate were left empty to act as sequencing controls (unused tag combinations) for downstream data curation (see below). PCR products were pooled and sequencing libraries were constructed using the Illumina TruSeq Nano DNA kit following the supplier's instructions (Illumina Inc., San Diego, California, USA), except that we omitted the final PCR amplification step of the ligated libraries in order to limit tag-jump biases (Taberlet et al. 2018). The libraries were then sequenced on Hiseq and Miseq Illumina platforms (San Diego, CA, USA) depending on the marker considered, using the paired-end technology.

Bioinformatics analyses

Bioinformatic analyses were performed on the GenoToul bioinformatics platform (Toulouse, France), with the OBITOOLS package (Boyer et al. 2016) organized into a snakemake workflow (Benoiston 2022). Briefly, paired-end sequencing reads were assembled, assigned to their respective samples allowing two mismatches for each of the two primers and no mismatch for the tags. Following this, sequencing reads were dereplicated and sequences of low quality removed (outside the expected length, containing Ns or with paired-end alignment scores below 50 or being singletons; Table S2). We then built MOTUs (Molecular Operational Taxonomic Units) using the 'sumaclust' clustering algorithm (Mercier et al. 2013) at a sequence similarity threshold of 97% for all markers, except for the plant data, for which we used a threshold of 95% since the eDNA target region is shorter (typically around 50 base pairs). Taxonomic assignment of insect, oligochaete, and plant MOTUs, was conducted using the ecoPCR program (Ficetola et al. 2010) and their specific markers on the European Molecular Biology Laboratory (EMBL; release 261). MOTUs were then assigned a taxonomy, using the ecotag program of the OBITOOLS (Boyer et al. 2016). For taxonomic assignment of fungi, we used DNAbarcoder (Vu et al. 2022). For bacteria and eukaryote MOTUs, the SILVA taxonomic database r138.2 was used (version 1.9; (Quast et al. 2012).

Datasets were subsequently filtered to remove contaminants and artifacts such as PCR chimeras and remaining sequencing errors, using routines in the metabaR package (Zinger et al. 2021), in R version 4.4.2 (R Development Core Team 2013). The filtering process consisted of four steps: (i) a negative control-based filtering, where MOTUs whose maximum abundance was found in extraction/PCR negative

controls were removed from the dataset. These are more likely to be reagent/aerosol contaminants, better amplified in the absence of competing DNA fragments in biological samples; (ii) a reference-based filtering, where MOTUs that were too dissimilar from sequences available (< 80%) in reference databases were identified as potential chimeras generated during sequencing and amplification and removed. In addition, we removed all taxa that were not targeted by the primer used. (iii) An abundance-based filtering, consisting of identifying and correcting tag-jumps (Schnell et al. 2015) which are incorrect assignments of a few numbers of sequences corresponding to true MOTUs occurring to the wrong sample. For this, MOTUs with <0.01% of the total OTU abundance in the entire dataset were set to zero. And, finally (iv) we applied a PCR-based filter, discarding any PCR reaction that yielded fewer than 1,000 reads for the respective marker. A summary on the parameters and thresholds used in these filters is provided in Table S2.

Statistical analyses

All statistical analyses were conducted with R version 4.4.2 (R Development Core Team 2013) using the vegan package (version 2.8-0, Oksanen et al. 2001). To evaluate changes in diversity and composition of TDF belowground communities across sites, we first aggregated read counts from the four point-level samples within each subplot to obtain subplot-level MOTU abundance tables for each marker. To this end, we applied the Hill number framework on the relative abundance (*subplot x MOTUs*) matrices of each marker. The Hill numbers framework provides measures of both alpha and beta diversity that modulate the weight given to rare MOTUs through the order q, the lower it is, the more rare species have equal weight to more abundant ones (Chao et al., 2014).

For alpha diversity indices, we computed diversity indices at q=0 and q=1, which respectively correspond to MOTU richness at q=0, and tend towards the exponential of Shannon's entropy at q=1. For these two indices, we provide accumulation curves across all sampled forests in Colombia using a subplot-order randomization repeated 999 times, computing the diversity after each additional subplot. For the rest of the analyses we only consider diversity measures at q=1 because this diversity measure is less sensitive to uneven sequencing depth (Fig. S1) and because it downweights rare MOTUs, which often correspond to remaining artifacts (Haegeman et al. 2013; Calderón-Sanou et al. 2020). In order to remove the outliers of the data, we used the Iglewicz and Hoaglin outlier test (Iglewicz and Hoaglin, 1993), which is based on the modified Z-Score. This method is particularly suited to skewed ecological data because it relies on robust statistics and is less sensitive to extreme values (Legendre & Legendre, 2012). Following Iglewicz and Hoaglin, values with a modified Z-score higher than 3.5 were excluded. Thus, five alpha diversity values were removed for Oligochaetes and one value for Eukaryotes.

For beta diversity, we evaluated changes in community composition across sites. We computed this using diversity indices that correspond to the Jaccard-type turnover measure based on Hill numbers (q = 1; Chao et al 2014). Briefly, this index consists of decomposing beta diversity as the fraction of gamma diversity over alpha diversity. This yields a pairwise site dissimilarity matrix. Specifically, for pairwise comparisons, the denominator is a geometric mean of the alpha diversities of order q=1 of the two compared sites. This allows us to obtain a beta diversity measure that represents the effective turnover rate between two communities, expressed as the effective number of distinct communities, normalized to range between 0 and 1.

Next we conducted exploratory analyses to describe how soil alpha and beta diversity co-varied with the potential predictors. We compared alpha diversity indices of each taxonomic group between biogeographic regions using a Kruskal-Wallis test, followed by a post-hoc analysis with a Dunn-test with Holm correction if the test was significant. We also measured the correlation between local diversity and different environmental variables (PC_{cont}, PC_{hum}, PC_{srich}, PC_{pH}) using Spearman correlation tests. Furthermore, to assess how these same variables explained the community composition (beta diversity), we fitted a distance-based redundancy analysis (dbRDA), an extension of standard RDA to dissimilarity data which accommodates non-Euclidean distances (Legendre & Anderson, 1999), such as the ones we used here. By relating community dissimilarities to explanatory variables, this method produces a constrained ordination that visually depicts the influence of the environmental variables on beta diversity.

Finally, to quantify the relative contribution of soil and climatic abiotic drivers and isolation-by-distance processes, we conducted a variation partitioning analysis (Legendre and Legendre 2012). This approach decomposes the total variation into unique fractions, i.e. the part of the variation attributable exclusively to one set of variables, and into shared fractions, i.e. the part of the variation explained jointly by several sets. The models included one set of climatic variables (consisting of PC_{cont} and PC_{hum}), one set of soil variables (PC_{srich}, PC_{pH}), and one spatial variable (i.e. the region identity), which we used here as a proxy for isolation-by-distance processes. We built these models for both alpha and beta diversity, and the significance of the unique fractions was assessed with permutation tests (999 permutations, Legendre et al. 2011).

Results

Diversity and composition of TDF belowground communities

We obtained a total of 94,015 molecular operational taxonomic units (MOTUs) and 99,815,363 reads across all markers and all sites. Of these, we detected 46,351 MOTUs (5,436,421 reads) for bacteria; 36,490 MOTUs (79,933,683 reads) for eukaryotes; 7,446 MOTUs (2,027,066 reads) for fungi; 1,325 MOTUs (695,887 reads) for insects; 1,739 MOTUs (8,804,374 reads) for oligochaetes, and 664 MOTUs (2,917,932 reads) for plants. On average across markers, we successfully assigned 95.3% ± 6.2% of MOTUs at the class level, 87.2% ± 10.5% at the order, 61.7% ± 19.7% at the family, and 38.2% ± 14.9% at the genus (Fig. S2).

For Bacteria, the most abundant clades were Actinomycetota, Alphaproteobacteria, and Acidobacteriota (Fig. 2A). Data from the Eukaryota marker were dominated by microorganisms, prominently Fungi, but also contained Viridiplantae and Metazoa reads (Fig. 2b), the latter being mainly composed of earthworms (Clitellata), Insecta and Arachnida (Fig. S3A). Within the Eukaryota marker, protists accounted for only 4.6% of the reads, and corresponded mainly to Rhizaria, Amoebozoa and Alveolata (Fig. S3B). Nematodes accounted for a small proportion of metazoan reads (6%). With the fungi-specific marker, we found that fungi were dominated by Eurotiomycetes, Sordariomycetes, and Agaricomycetes (Fig. 2C). The insects' marker data were dominated by Blattodea, Coleoptera, and Hymenoptera (Fig. 2D). The oligochaetes marker data were dominated by Crassiclitellata, Tubificida and Enchytraeida (Fig. 2E). Finally, plant marker data were dominated by Fabaceae, Euphorbiaceae, and

Nyctaginaceae (Fig. 2F, see also Fig. S4 for a description of plant composition across regions and Fig. S5 for a description of each marker composition across regions).

The accumulation curves describing belowground diversity in Colombian TDFs did not reach an asymptote for any marker when diversity was measured as MOTU richness (Hill number q = 0; Fig. 3A,B), but reached when measured as Shannon diversity (Hill number q = 1; Fig. 3C,D). The same pattern was observed at the plot level, where sequencing coverage was too low to describe marker diversity at q=0, but allowed to describe the diversity at q=1 for most markers (Fig. S1).

Drivers of soil alpha and beta diversity

We found that TDF soil alpha diversity differed across regions, with bacterial diversity being the lowest in Patía, our southernmost site, and fungal diversity the highest in Guajira, a Caribbean region at the northern tip of Colombia (Fig. 4A). We also found that Oligochaeta diversity was the highest in Patía. However, since this result is supported only by two subplots (after filtering process), we prefer to consider it as preliminary and requiring further investigation with a broader sampling effort in Patía. Bacterial alpha diversity correlated positively with humidity (PChum) and negatively with soil fertility (PCsrich). Fungal, eukaryotic, and oligochaete alpha diversities negatively correlated with climatic predictors (PChum for fungi; PCcont for both eukaryotes and oligochaetes; Fig. 4B). Variation partitioning analyses explained ~50% of the total alpha diversity variation across taxonomic groups, when all predictor classes were included. The contribution of each class of predictor is shown in Fig. 4C and Fig. S6.

Considering beta diversity, communities of microorganisms showed moderate compositional differences among regions. Their turnover appeared mostly driven by climatic parameters, with bacteria also driven by soil pH and fungi also driven by soil fertility (Fig. 5A,C). By contrast, macroorganisms (plants, insects, and oligochaetes) displayed marked compositional differences among regions that were driven by climatic and soil fertility variables (Fig. 5D-F). The proportion of explained variation by all tested predictors decreased with organism size, from 71% in Bacteria to 11% in Insecta. The respective contribution of each set of variables is shown in Fig. 5G and Fig. S6.

For both alpha and beta diversity analyses, the contribution of the unique fraction explained by the region to the total explained variation was higher in macro- than in microorganisms. Conversely, soil conditions explained much of the variation in community composition in microbes; either as a unique or shared fraction; particularly for beta diversity (Fig. 5G).

Discussion

In this study, we provide for the first time a description of soil communities in Colombian tropical dry forests across kingdoms of life, leveraging the power of eDNA-based approaches. We also describe the main drivers of soil biodiversity variation in this biome.

The soil taxonomic composition of TDFs tends to differ from that of other biomes, including tropical ones. For example, most tropical forest soils are dominated by Acidobacteriota (Fierer et al. 2009), whereas bacterial communities of TDFs studied

here were dominated by Actinomycetota, a group previously reported as being associated with dry environments (Delgado-Baquerizo et al. 2018), such as deserts (Fierer et al. 2009). Eukaryotes were dominated by fungi, and, through the lens of the fungal-specific marker, we found a relatively lower abundance of Agaricomycetes and a high proportion of arbuscular mycorrhizal fungi (i.e. Glomeromycetes) compared to what is generally reported in TDF soils (Öpik et al. 2010; Tedersoo et al. 2014). Our findings are consistent with previous observations in tropical America, where arbuscular mycorrhizal fungi have been reported to be highly diverse (Tedersoo et al. 2014; Van Nuland et al. 2025), and with the fact that arbuscular mycorrhizal fungi often have higher richness in dry ecosystems than in tropical humid forests (Pagano et al. 2019).

The protist community was dominated by Cercozoa and Ciliophora, as expected from global soil patterns (Oliverio et al. 2020). Although this dominance was also indicative of arid environmental conditions, the protist community deviated from other tropical ecosystems in two aspects. First, protists accounted for a much lower proportion of eukaryotic reads than typically reported (De Araujo et al. 2018). Second, the relative abundance of Amoebozoa was higher than in previous observations (Mahé et al. 2016; De Araujo et al. 2018). This finding was consistent with the well-known drought resistance of Amoebozoa compared to other protists (Geisen et al. 2018). Our results are thus in line with the drier conditions typical of tropical dry forests, which could in our case be further exacerbated by the fact that our sampling campaign was carried out during the dry season.

The metazoan communities of the eukaryotic marker mainly consisted of arthropods (mainly arachnids and insects) and earthworms (Clitellata), a composition that largely

differs from tropical rainforests or desert soils, which are dominated by earthworms and nematodes, respectively (Fierer et al., 2009). Here, nematodes were relatively rare, consistent with previous observations that tropical soils are depauperate in nematodes (Van Den Hoogen et al. 2019). The insect-specific marker harbored mainly ants, beetles and termites. This composition aligns with the large contribution of ants and termites to soil-arthropod biomass in tropical forests (Rosenberg et al. 2023) and in TDFs in particular (Casalla and Korb 2019; Bautista-Giraldo et al. 2025). Concerning the oligochaete-specific marker, communities were mainly dominated by earthworms, but we also detected a non-negligible proportion of Tubificida. Although this group is mainly found in aquatic ecosystems, some Tubificida species are known to colonize soils where they can form drought-resistant cysts that can persist near the surface (Montalto and Marchese 2005), while most other oligochaetes migrate deeper into the soil (Jiménez and Decaëns 2000). Conversely, enchytraeids were less abundant, consistent with the observation that they are sensitive to drought (Maraldo and Holmstrup 2010; Holmstrup et al. 2012). Hence soil animals also exhibited a composition that is consistent with the drier conditions occurring in TDFs compared to other tropical forest types.

Finally, for the plant-specific marker, Fabaceae and Euphorbiaceae were among the most represented families, consistent with the floristic inventories of Colombian tropical dry forests (Allen et al. 2017; González-M et al. 2018). Conversely, Rubiaceae, a family abundant in botanical surveys, accounted for only 1% of the plant sequences. That molecular plant inventories from soil samples exhibit some inconsistencies with traditional botanical survey is a repeated observation (reviewed in Zinger et al. 2020) and may arise from biases originating from both molecular (primer biases, in-adapted

sampling design of the environmental matrix) and botanical surveys (recording of trees of a certain age/size). In addition, shallow coring (0-10 cm), given root architecture, can bias soil eDNA detections relative to tree inventories, favoring, for example, shallow-rooted taxa and underrepresenting deep-rooted taxa.

By sampling eleven sites across Colombia, we were able to cover various TDF environmental conditions and effectively capture the diversity of abundant members of the soil biota, across the molecular markers studied here, as suggested by the saturation of the accumulation curves at q=1. However, when considering MOTU richness (q=0), the accumulation curves did not reach saturation, suggesting that more sampling remains necessary to fully capture the rare tail of soil biodiversity in TDFs.

We found that microbial alpha diversity was more explained by a combination of soil and climate than by the biogeographic regions, whereas it was the contrary for macroorganisms. Notably, across the four regions studied here, soil alpha diversity tended to be lower for bacteria, insects, and plants in the Patía region. This result is again in agreement with the drier conditions occurring in this location, together with the higher human footprint and low extent of forest fragments found in this area (González-M et al. 2018).

Not all taxa had an alpha diversity that responded similarly to abiotic and biogeographic variables. Bacterial alpha diversity increased with climatic humidity, which is consistent with the stress exerted by aridity on bacterial activity (Maestre et al. 2015). However, bacterial alpha diversity also decreased with the increasing soil fertility, which could result from a dominance of few copiotrophs in nutrient-rich soils (Leff et al. 2015; Dai et al. 2018). Soil pH, a well-known driver of soil bacterial diversity

447 at the global scale (Fierer and Jackson 2006; Delgado-Baquerizo et al. 2018), did not
448 emerge as a significant predictor. We explain this difference by the pH levels covered
449 here (pH >6), which is narrower and excludes lower pH values where the diversity-pH
450 relationship is actually reported in large-scale studies (Fierer and Jackson 2006;
451 Delgado-Baquerizo et al. 2018).

452 For the eukaryote marker, alpha diversity was higher under wetter climates and low
453 climatic variability (i.e., smaller daily and seasonal temperature ranges), consistent
454 with the major influence of climatic factors on fungi, protists and plants (Linares-
455 Palomino et al. 2010, Oliverio et al. 2020; Tedersoo et al. 2022). Fungal alpha diversity
456 correlated negatively with humidity, contrasting with global-scale patterns (Tedersoo
457 et al. 2014; 2022). In TDF soils, our results therefore suggest that wetter sites harbor
458 higher bacterial diversity, whereas drier conditions can support higher fungal diversity,
459 consistent with reports that bacterial communities are less resistant to drought than
460 fungal communities (De Vries et al. 2018; Chacon et al. 2023).

461 By contrast with microorganisms, the alpha diversity of macroorganisms did not
462 correlate significantly with the individual abiotic factors. However, when considering
463 climate, soil, and region as variable sets, both plants and insects were mostly
464 influenced by the region and, to a lesser extent, by climate. Soil properties also exerted
465 a significant influence on insects. These results suggest that the diversity of plants and
466 insects in TDFs of Colombia is shaped by the interplay between geographic context
467 and abiotic factors, consistent with previous observations made on insects (Marques
468 and Schoereder 2014; Marques et al. 2017; Silva et al. 2017; Liu et al. 2022; Dantas
469 and Fonseca 2023; Camargo-Vanegas et al. 2024) and plants (Banda-R et al. 2016).
470 Moreover, other important factors that we did not consider here could be better

471 predictors for earthworms, such as plant community composition (which we could not
472 fully capture with the plant marker) or litter availability (Delgado-Baquerizo et al. 2018;
473 Phillips et al. 2019; Tedersoo et al. 2022). To conclude, given the variability in the main
474 environmental drivers across taxa, the response of soil TDF diversity to environmental
475 changes cannot be simply inferred from a single taxonomic group — typically using
476 plants as “umbrella” species — unlike previous reports for tropical rainforest
477 arthropods (Basset et al. 2012).

478 Considering the drivers of soil beta diversity, we observed marked compositional
479 differences among regions. For bacteria, compositional variation was partly driven by
480 soil pH, in agreement with previous observations (Delgado-Baquerizo et al. 2018). For
481 the five remaining biotic groups, compositional variation was driven to a lesser extent
482 by the other climatic and edaphic variables, a result likewise consistent with large-
483 scale studies (Delgado-Baquerizo et al. 2018; Phillips et al. 2019; Tedersoo et al.
484 2022). The contribution of the pure effect of the region relative to that of abiotic (i.e.,
485 structured across regions or not) was greater for soil mesofauna and plants than for
486 soil microorganisms. This suggests that the soil mesofauna and plants exhibit a
487 pronounced biogeographic differentiation among regions, consistent with local
488 diversification and limited dispersal (Kattan et al. 2004; González-M et al. 2018, Kattan
489 et al. 2019). In contrast, the biogeographic signature of microorganisms is observed
490 to be less driven by dispersal limitation, in line with the initial expectation that they
491 have greater passive dispersal potential (Martiny et al. 2006; Hanson et al. 2012;
492 Nemergut et al. 2013; Barberán 2014).

493 We also observed that the total explained variation in community composition was
494 greater in microorganisms than in macroorganisms communities. This mirrors

495 previous observations (Zinger et al. 2019) and likely results from a difference in spatial
496 scaling across the taxonomic groups (Prosser et al. 2007). Typically our sampling is
497 likely to be far less complete for larger organisms (insects, oligochaetes and plants),
498 leading to the observation of apparently random patterns (Chase and Myers 2011;
499 Chase 2014; Vellend 2016). Further analyses including additional edaphic (e.g.,
500 bioavailable rather than total metals/nutrients), climatic (e.g., number of dry days within
501 the wet season), biotic (e.g., prey or predators) and human-related parameters (e.g.,
502 human footprint) will help improve understanding of the biogeography of the soil multi-
503 taxon biota in TDFs.

504 Conclusion

505 Our analysis delivers a first multi-taxon, cross-kingdom description of soil tropical dry
506 forest communities and of their variation in alpha and beta diversity. Given that tropical
507 dry forests are among the most threatened and least documented tropical biomes,
508 improving our knowledge of their belowground biota is crucial for conservation and
509 restoration planning. We show that the influence of environmental and spatial drivers
510 on diversity and composition differs across soil taxonomic groups. This finding
511 suggests that a single taxonomic group cannot be used as a proxy to anticipate the
512 distribution of the rest of the soil community. Moreover, our results indicate that tropical
513 dry forests harbour a distinctive belowground biota. This work also illustrates the utility
514 of eDNA for describing the soil biological component, and its potential to shed light on
515 the ecology and taxonomy of soil biota. Deploying our approach in combination with
516 additional contextual parameters at larger spatial and temporal scales should help to
517 fully capture the diversity of these highly dynamic tropical ecosystems and refine our
518 understanding of their underlying ecological and evolutionary drivers. While much

519 remains to be done to complete this picture, this present work establishes a critical
520 baseline for assessing the conservation status of these forests and the effects of land-
521 use change or restoration actions in these fragile environments.

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531 Conceptualization : I.C.S., M.G., J.C., N.N., L.Z. Data curation : J.R. Formal analysis
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534 Resources : M.G., A.I., N.N., U.S.-D., RG-M. Software : J.R. Supervision : I.C.S., L.Z.
535 Validation : J.R., I.C.S., L.Z. Visualization : J.R. Writing – original draft : J.R. Writing –
536 review & editing : All authors.

537 Data accessibility

538 All data and codes used for the paper are available on InDoRES national portal hosted
539 under the joint supervision of the CNRS Ecology and Environment Institute (INEE) and

the Muséum National d'Histoire Naturelle (MNHN). (a definite link will be provided upon manuscript acceptance, in the meantime, we provide a link for referees: https://data.indores.fr).

Figures

Figure 1 : Distribution of TDFs across Colombia and associated climatic and soil physico-chemical conditions. (A) Topography (grey tones) and the localisation of remaining TDFs forest fragments (colored areas) across Colombia are shown in background. Purple and yellow forest fragments correspond to the Nor-Andina and Orinoquía regions, respectively, where no plots were sampled in this study (B) Principal component analysis summarizing the climatic conditions of the studied sites. (C) PCA summarizing the soil physico-chemical conditions of the studied TDFs. Data for (A) and (B) was obtained from Gonzalez M. *et al*. (2019).

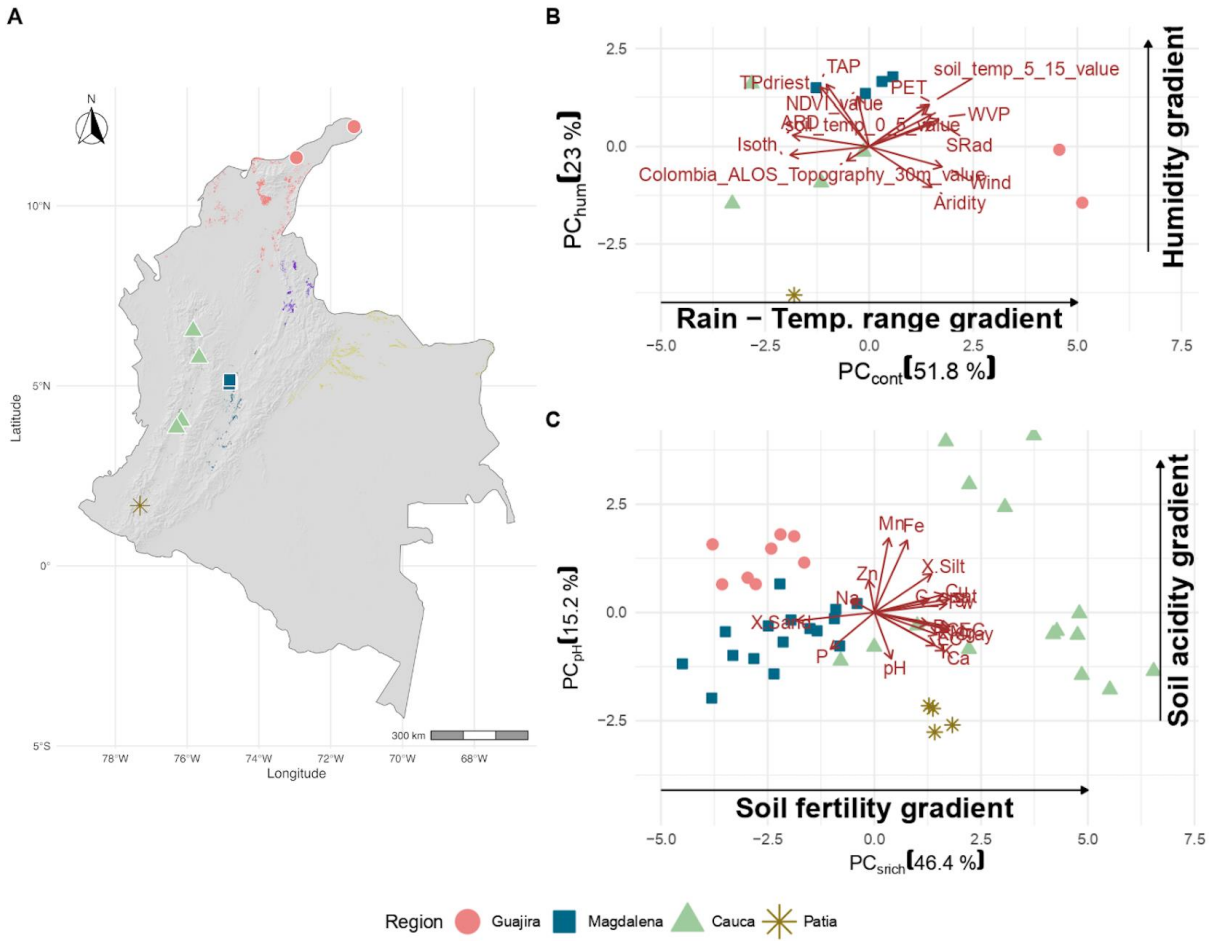


Figure 2 : Taxonomic composition across each taxonomic group in Colombian TDFs soils. Percentage values correspond to the percentage read abundance following taxonomic assignment. (A) and (B) show the composition for generalist markers for Bacteria and Eukaryota, while the remaining panels (C,D,E,F) refer to clade-specific markers.

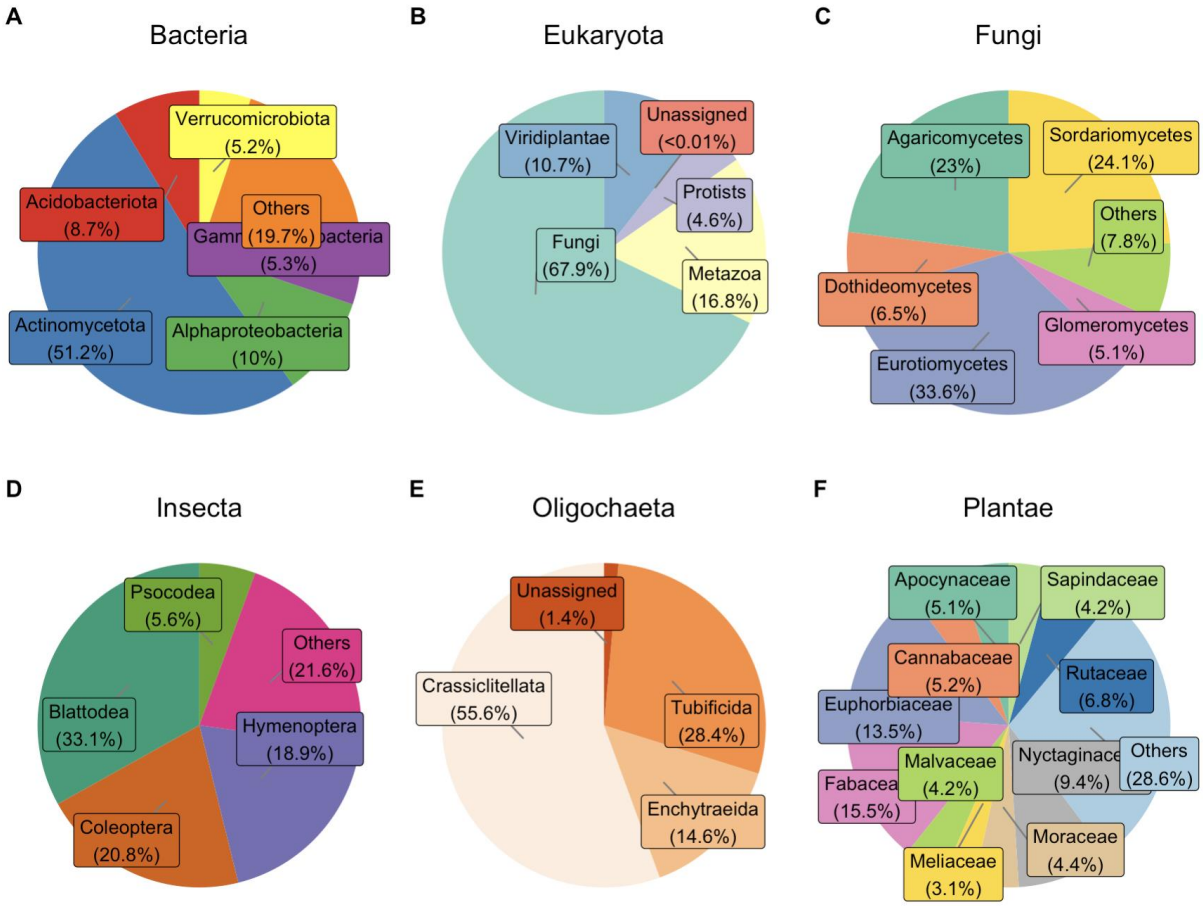


Figure 3 : Accumulation curves of Colombian TDFs soil diversity across taxonomic groups. (A) and (B) represent species richness (diversity order q=0), while panels (C) and (D) show Shannon diversity (order q=1). (A) and (B) compare generalist markers (Bacteria and Eukaryota), while (C) and (D) detail the diversity for specific markers within Eukaryota (Fungi, Plantae, Insecta, Oligochaeta). Lines correspond to the average diversity values obtained for each sampling effort over 999 random permutations of subplot order while transparent ribbons correspond to the corresponding 95% confidence interval.

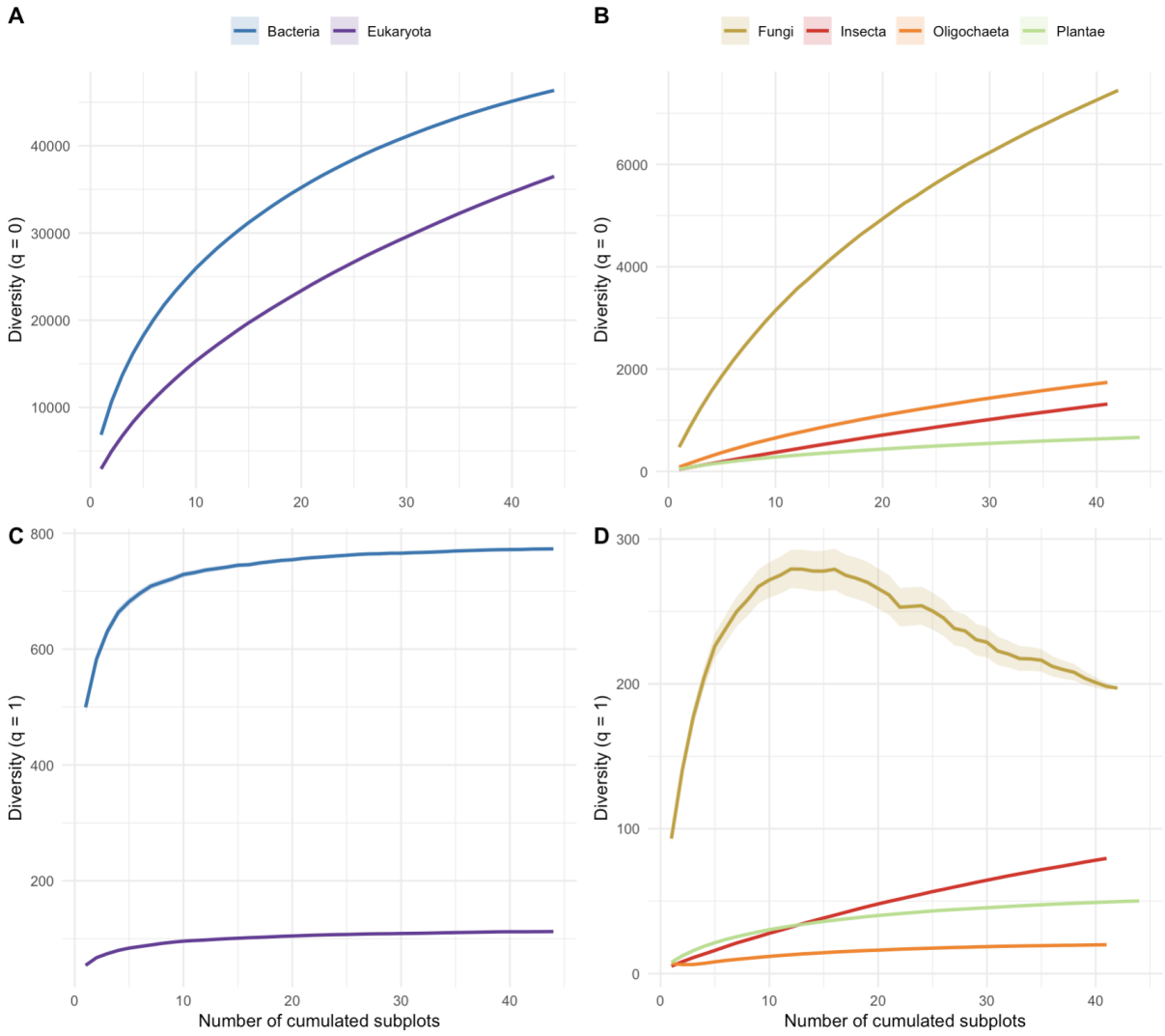


Figure 4 : Environmental and geographical drivers of soil alpha diversity. (A) alpha diversity (order q=1) across regions. P-values of the Kruskal-Wallis and following Dunn's post-hoc tests (Holm adjustment) are shown. (B) Spearman correlations between alpha diversity and environmental predictors (climate and soil). Only significant correlations are shown. (C) Variation partitioning of alpha diversity explained by region, soil, and climate variables. Significance of unique effects is shown in Fig. S4a.

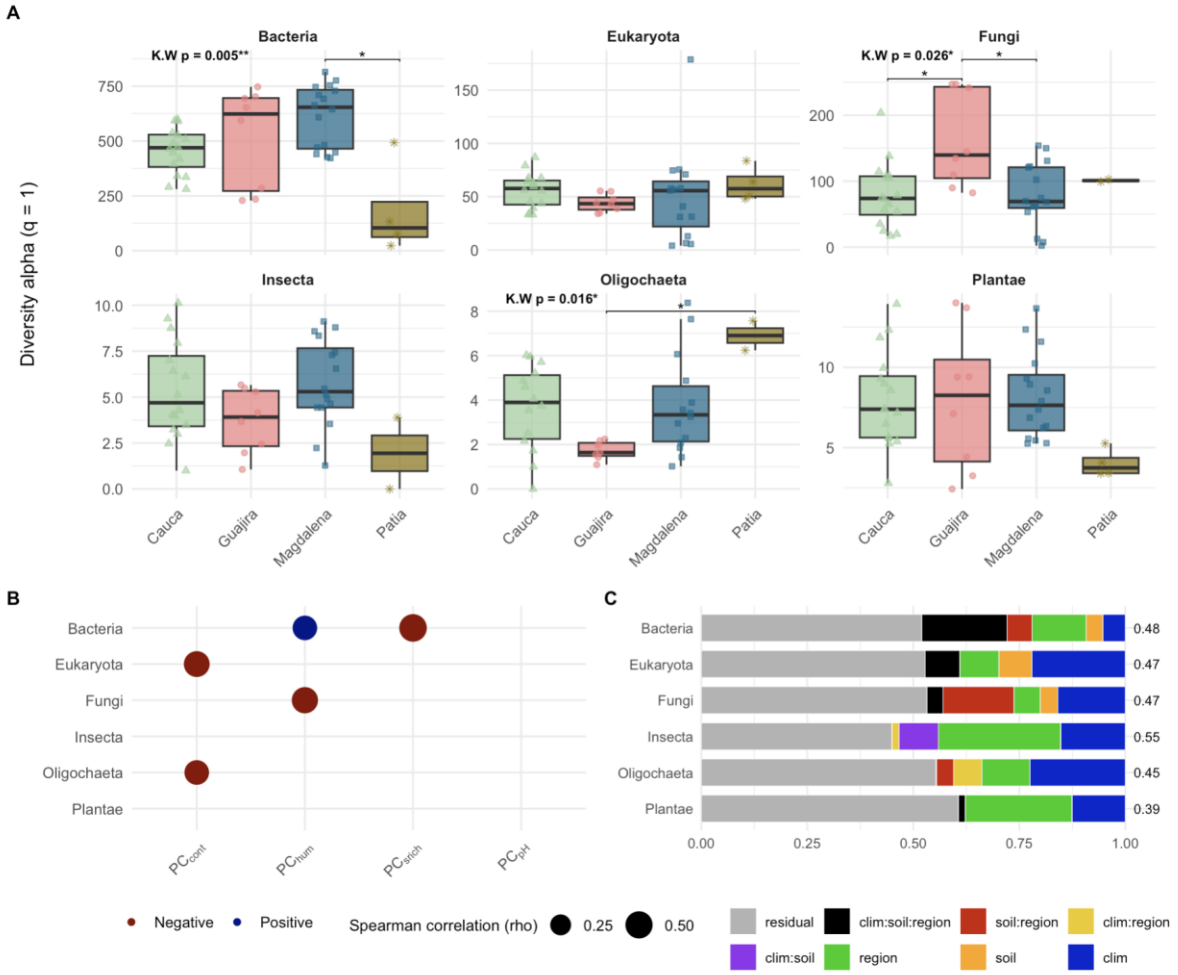
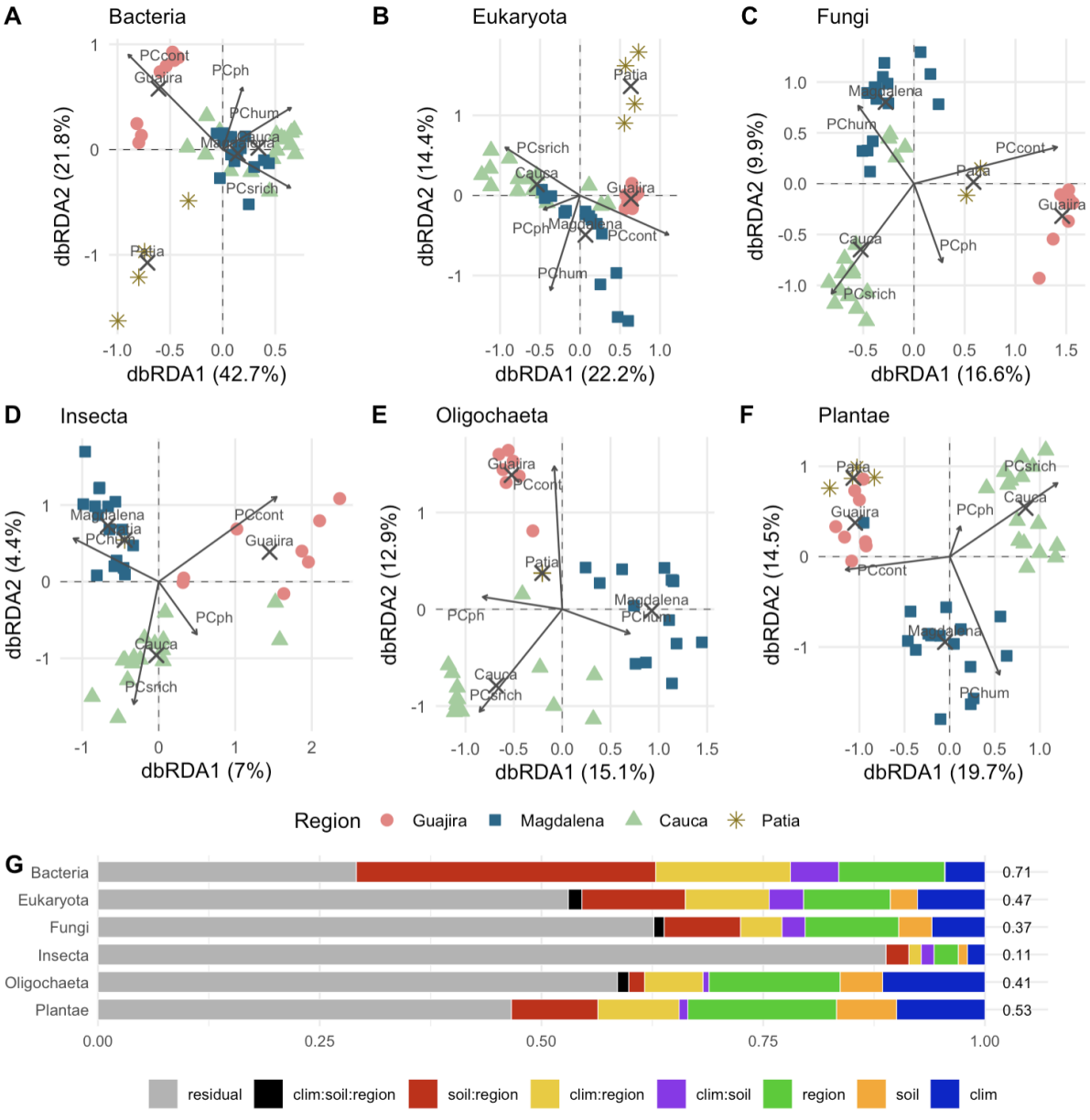


Figure 5 : Drivers of soil biota beta diversity across Colombian TDF types. (A-F) dbRDA ordinations of community beta diversity by biogeographical predictors ; (A) and (B) correspond to generalist markers and (C) (D) (E) and (F) to specific markers. (G) Variation partitioning of diversity explained by region, soil, and climate



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