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Do shared traits create the same fates? Examining the link between morphological type and the biogeography of fungal and bacterial communities

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ABSTRACT

Although it has been commonly observed that fungi and bacteria differ in their regional biogeographic patterns, it is not well understood what traits contribute to these different distributions. Here, we evaluate how morphological type (i.e. unicellular or filamentous growth form) influences the biogeography of soil fungal and bacterial communities across not only Euclidean (i.e. geographic) distances, but also across gradients of climate and edaphic factors and plant community composition. Specifically, we assessed the decay in community similarity over distance (distance-decay relationship) for microbes with unicellular and filamentous morphology in both fungi and bacteria across 40 ecologically diverse sampling sites in Minnesota, USA. Overall, we found that while distance-decay relationships were similar in fungal and bacterial communities over Euclidean distances, there were important differences among morphological groups of fungi and bacteria across gradients of environmental and plant community similarity. Specifically, the distance-decay relationship of unicellular fungi and unicellular bacteria were indistinguishable across environmental similarity. However, as plant community similarity decreased, only filamentous fungi and unicellular bacteria differed significantly in the strength of their distance-decay relationships. Like analyses of other study systems, we also found that pH explained much of the variance in community composition across microbial domains and morphological types and that plant community diversity was more closely correlated with fungal diversity than with bacterial diversity. Collectively, our results suggest that specific ecological traits such as morphological type along with microbial domain are key factors shaping the biogeography of microbial communities.

1. Introduction

The decline in community similarity over Euclidean distance, also known as distance-decay, is one of the most commonly observed patterns in the diversity of life on Earth (Soininen and Hillebrand, 2007). A foundational review by Martiny et al. (2006) formalized the analysis of distance-decay relationships for microorganisms to assess the relative importance of historical influence and the contemporary environment on microbial community similarity. Since that framework was proposed, our ecological understanding of the factors governing microbial biogeography has increased rapidly, with many studies finding strong evidence for contemporary environmental selection (Glassman et al., 2015; Urbanová et al., 2015; Chen et al., 2017; Guerrero-Ramírez et al., 2017; Waldrop et al., 2017; Wang et al., 2017) and others demonstrating a combined effect of environmental selection and historical dispersal limitation (Astorga et al., 2012; Peay et al., 2012; Bahram et al., 2014; Talbot et al., 2014; Wang et al., 2015; O'Brien et al.,

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2016; Choudoir et al., 2017; Fierer, 2017; Glassman et al., 2017; Ma et al., 2017; Zhang et al., 2018).

Although biogeographic patterns of microbial diversity are often considered to be similar for all microorganisms, there is growing evidence that the abiotic factors structuring the diversity of prokaryotic and eukaryotic microbial communities differ, particularly in soils (Hanson et al., 2012; Chemidlin Prévost-Bouré et al., 2014; Urbanová et al., 2015; Peay et al., 2016; Ma et al., 2017; Bahram et al., 2018). For example, at global scales, pH appears to be the key abiotic variable driving the structure of prokaryotic soil communities, while water availability appears to be more important for eukaryotic microorganisms such as fungi (Bååth and Anderson, 2003; Bahram et al., 2018). To date, however, it remains largely unclear which traits or factors are responsible for such differences. To make generalizable predictions about landscape-level distribution patterns in microbial diversity across multiple domains of life, a better understanding of how specific traits common to both prokaryotes and eukaryotes is needed.

Similar to broad-scale morphological groups of larger organisms (e.g. trees, shrubs, and forbs for plants or bipeds, quadrupeds, winged for animals), microorganisms can be classified into distinct groups based on morphological characteristics. For instance, while most bacteria are unicellular, it is common for bacteria in the phylum Actinobacteria to have a filamentous growth form (McCarthy and Williams, 1992). Among fungi, this morphological pattern is reversed; most species have a filamentous growth form, but some species are unicellular some or all of the time (e.g. yeasts). Unicellular or filamentous morphologies in microorganisms likely have a variety of important adaptive tradeoffs. In particular, unicellular organisms may require fewer resources and respond to rapid shifts in environmental conditions (Treseder and Lennon, 2015), while filamentous morphologies promote the movement of water or resources across highly heterogeneous environments and over relatively large distances (Griffin, 1985; Boswell et al., 2002). Here, we use the terms morphological type and morphology to describe the filamentous or unicellular nature of the most common morphology for a given taxon across its life history.

To assess how variation in a common microbial trait – morphological type (i.e. unicellular versus filamentous growth form) – influences microbial distance-decay relationships, we analyzed fungal and bacterial communities across a heterogeneous regional-scale gradient. Microorganisms are most commonly dispersed as spores, and their dispersal kernel (i.e. the distribution of dispersal distances) for a single point source varies widely due to differences in the number of spores produced, spore size and surface structure, vulnerability to desiccation and UV damage, mode of dispersal (e.g. wind, animal-mediated, water, etc.), and landscape configuration (James and Vilgalys, 2001; Golan and Pringle, 2017). At larger scales (i.e. thousands of kilometers), dispersal events are more rare (although see Golan and Pringle, 2017), increasing the likelihood of historical effects on local microbial community composition (Hanson, 2017). By contrast, at more local scales (i.e. centimeters to meters to kilometers), highly heterogeneous environmental conditions and local dispersal limitation are likely to overwhelm the effects of historical events (Green and Bohannan, 2006; Martiny et al., 2011; Peay and Bruns, 2014). Given these differences, we expect to see evidence of both dispersal limitation and environmental selection at the regional scale (i.e., hundreds of kilometers) (Cline and Zak, 2014).

Specifically, we compare the distance-decay relationships among four groups of microbes (unicellular fungi, filamentous fungi, unicellular bacteria, and filamentous bacteria) across sites at the confluence of multiple North American biomes. Although we clearly recognize that microbes have many growth forms and complex physical traits, here, we use unicellular and filamentous morphology as a generalizable trait reflecting differences in properties such as cell size, architecture, and surface:volume ratio. We predicted that although distance-decay relationships would be significant for all four microbial groups, the similarity of unicellular microbial communities would change less quickly in response to Euclidean distance or environmental gradients due to enhanced stress tolerance. Furthermore, we predicted that bacterial communities would be more similar than fungal communities across the same distance because of differences in the dispersal capability across the two domains, bacteria and fungi. Here, we use the term domain as a proxy for evolutionary phylogenetic divergence between fungi and bacteria.

2. Materials and methods

2.1. Study system

Field sites were located at 52 Scientific and Natural Areas in the state of Minnesota (USA), spanning the entire range of the state (600 km north-south and 500 km east-west, Fig. 1). The sites spanned five dominant vegetation habitats, including *Pinus*-coniferous forests, *Acer*-dominated deciduous forests, *Quercus*-dominated savannahs, prairies, and wetlands. At each site, the presence and absence of individual high-cover plant species was determined using the ecosystem level classification scheme in the Field Guide to the Native Plant Communities of Minnesota ((Field guide to the native plant communities of Minnesota, n.d.); Supplement 1).

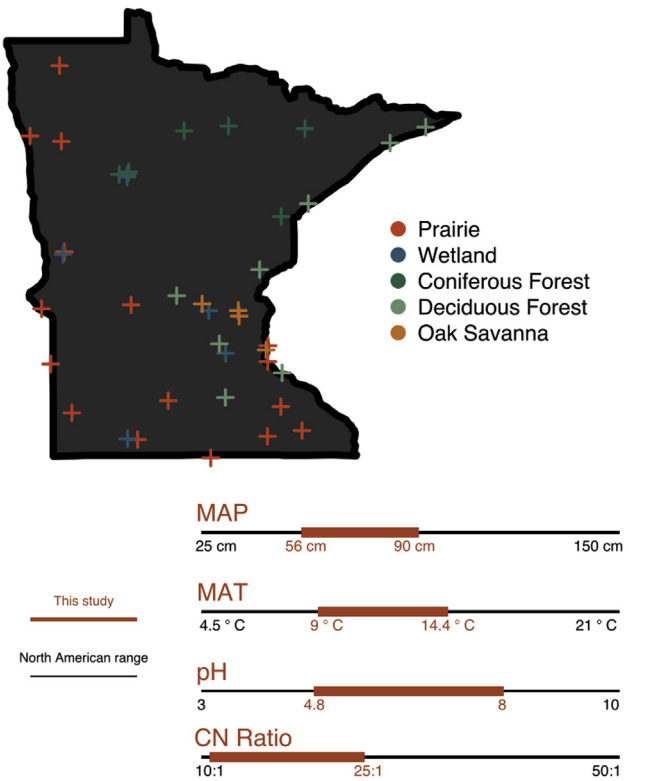

Fig. 1. Map of the sampling sites across the state of Minnesota USA. Symbols representing each of the five ecosystem types are indicated by different colors on the map. The average range of abiotic environmental factors considered in this study (shown in orange), including mean annual precipitation (MAP), mean annual daily maximum temperature (MAMT), pH, and carbon to nitrogen ratio (C:N Ratio), shown in the approximate distribution of the continental North American range of the same factors (shown in black).

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Sites representing habitats with fewer than 6 sample replicates, as well as those locations that had been burned in the last year were excluded due to significant influence of fire on microbial community structure (Supplement 1, Final N = 40).

Climatic conditions at each site were characterized from National Oceanic and Atmospheric Administration data repositories describing daily mean maximum and minimum temperatures, and their distribution across season, annual and seasonal precipitation, and snow accumulation and seasonality from 1981 to 2010 (fftp://ftp.ncdc.noaa.gov/pub/data/normals/1981-2010/). The geographic sampling captured several regional patterns of climate, including latitudinal and longitudinal gradients of precipitation and temperature. Specifically, sites in the northeast corner of the state are the coldest and driest and get progressively warmer and wetter towards the southeast. These gradients represent wide ranges of precipitation and temperature given their geographic proximity.

2.2. Soil sampling

In May and June 2014, soils were collected from each site. After removing vegetation from the soil surface, one soil core (2 cm wide × 10 cm deep) was collected for sequencing analysis, and three cores, located within 1 m of each other, were pooled for chemical analyses. The cores were taken from a randomly selected location within each site but were >100 m away from any road. Cores were kept on ice in the field, then frozen at and stored at −20 °C at the University of Minnesota. In the laboratory, all soil samples were individually homogenized, sieved, and stored at −20 °C ahead of soil chemistry and molecular microbial community characterization. Soils were characterized for soil nitrogen and soil organic carbon by high temperature combustion. Prior to organic carbon (C) and nitrogen (N) analysis, carbonates were removed from soil samples via HCl fumigation (Harris et al., 2001). A known mass of sample was weighed for elemental analysis of C and N via high-temperature combustion on a VarioMAX elemental analyzer (Elementar Americas, Ronkonkoma, NY) calibrated to glutamic acid standards. Elemental analyzer runs were interspersed with blanks and glutamic acid standards to measure accuracy over the course of the run. Mean accuracy of check standards was within 0.18 and 0.073% of expected values for N and soil organic carbon, respectively. The absolute mean deviation of duplicate samples was 0.010 and 0.049 mg/g for N and soil organic carbon, respectively. Soil pH was measured in a 2:1 slurry of soil and water after homogenization and sieving through 2 mm mesh.

2.3. Molecular analyses

2.3.1. Amplicon library preparation

Total genomic DNA was extracted from a 0.25 g subsample of each core collected for sequencing using the DNeasy PowerSoil DNA extraction kit following manufacturer's protocols (QIAGEN, Hilden, Germany). Bacterial DNA from the V4 region of the 16S rRNA gene was amplified using the primer pair 515f-806R and fungal rDNA was amplified from the ITS1 gene region using primer pair ITS1F-ITS2. Initial amplifications for both bacteria and fungi (total number of samples = 104) were followed by second shorter PCRs to add unique sample barcodes and Illumina MiSeq adaptors (Gohl et al., 2016). Successfully amplified samples were cleaned with AmPure magnetic bead kits and then pooled (Agencourt, Beverly, MA). The bacterial library was sequenced on two lanes of a 2 × 150 bp Illumina HiSeq run, while the fungal library was sequenced on one lane of a 2 × 250 bp Illumina MiSeq run at the University of Minnesota Genomics Center (UMGC, St. Paul, MN, USA).

2.3.2. Sequence processing and microbial identification

Initial quality filtering of the 16S sequence data was conducted in MOTHUR (Schloss et al., 2009) using standard operating protocols (https://www.mothur.org/wiki/MiSeq_SOP, see Staley et al. (2017) for additional details). Bacterial sequences passing quality filtering were *de novo* clustered into operational taxonomic units (OTUs) at 97% sequence similarity and taxonomy was assigned to the genus level using the SILVA database version 123 (Quast et al., 2013). Based on heterogeneity in total read depth, the bacterial OTU × sample matrix was rarefied to 31,427 reads per sample. ITS sequences were processed with the FAST pipeline (https://github.com/ZeweiSong/FAST/) using methods described in Fernandez and Kennedy (2018). Briefly, quality filtered ITS sequences were *de novo* clustered at 97% similarity using VSEARCH, and OTUs with less than 70% match length and 75% similarity to members of the Kingdom Fungi were removed. Fungal taxonomy was assigned using the UNITE database using best match (v7, Koljalg et al., 2014) and growth morphology information was assigned using FUNGuild (Nguyen et al., 2016a). Of the 100 most abundant fungal OTUs, 27 were not assigned due to low taxonomic resolution. Using individual BLAST searches, 21 of these 27 unassigned OTUs were manually assigned morphology information based on genus- or species-level similarities. To account for sequence read depth heterogeneity across all samples, the fungal OTU × sample matrix was rarefied to 3200 reads. Raw sequence data and associated metadata were uploaded to the NCBI Sequence Read Archive (https://www.ncbi.nlm.nih.gov/sra) under accession SRP 142068.

2.3.3. Data processing

To evaluate the effects of Euclidean distance, abiotic environmental conditions, and plant community similarity on fungal and bacterial distance-decay patterns, three separate distance matrices were created (hereafter collectively referred to as Euclidean distance, environmental similarity, and plant community similarity metrics, respectively). The Euclidean distance matrix was constructed from GPS coordinates of each site and the cosine function *distm* (R package '*geosphere*' (Hijmans et al., 2017)). Based on *a priori* predictions about the importance of climate and edaphic factors in structuring microbial communities (Fierer and Jackson, 2006), mean annual max temperature (MAMT), mean annual precipitation (MAP), soil pH, and soil carbon:nitrogen ratio (C:N) were selected as the input variables to calculate the environmental similarity matrix (Supplement 2). We use the term plant community similarity to describe the turnover of plant communities between sites. Although this approach does not include other biotic ecosystem players including soil fauna or megafauna, we use plant community similarity as a proxy for biotic composition at each site because the vegetative differences between sites are sufficient to discern ecosystem types. Both the Euclidean distance and environmental similarity matrices were calculated from Bray-Curtis dissimilarities, while the plant community similarity matrix was based on Jaccard dissimilarities (due to only having access to presence-absence plant community data). Comparisons of the distance-decay relationships across different metrics of distance in a multiple regression framework was done by using z-scored (centered and scaled) values for each distance metric.

The bacterial and fungal datasets were sorted into two morphological types, unicellular or filamentous, for a total of four groups. We consulted Bergey's Manual of Determinative Bacteriology to classify filamentous and unicellular bacteria by conducting a systematic search using the words "filamentous" and "myceli*" (Brown, 1939). Taxa with any reference to these terms were considered filamentous, except those that were listed as filamentous on only one growth medium or were listed as only sometimes forming filaments. Of the 29,218 bacterial OTUs assigned, 12% were

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considered filamentous according to Bergey's Manual of Determinative Bacteriology (N = 3623). These OTUs all belonged to the phylum Actinobacteria and the order Actinomycetales. [According to Bergey's Manual of Determinative Bacteriology, filamentous bacteria are also found in the family Beggiatoaceae, the order Chlamydobacteriales, and the genus *Chlorochromatium*, however these taxa were not present in our dataset (Brown, 1939)]. We considered all the remaining bacterial OTUs as unicellular. Of the 1174 fungal OTUs with functional assignments from FUNGuild, 10% were morphologically designated as yeasts (N = 116), included OTUs in both the Ascomycota and Basidiomycota. We considered all OTUs without a yeast designation as filamentous.

2.4. Statistical analyses

Distance-decay relationships of community similarity across Euclidean distance, environmental similarity, and plant community similarity were compared among the four microbial groups using analysis of covariance (ANCOVA). We used post-hoc general linear hypothesis tests to assess the differences in the model estimates of slope and intercept coefficients for the four microbial groups (R packages '*emmeans*', Russell, 2018, and '*multcomp*' Hothorn et al., 2008).

To explore how variance in Euclidean distance, environmental similarity, or plant community similarity explained microbial community composition, we constructed generalized dissimilarity models (GDM) for each of the four microbial groups (R package '*gdm*', Manion et al., 2018). A major advantage of GDM models is accounting for non-linearity in the ecological similarity response to environmental factors uniquely for each variable, and to partition variance across both tabular and matrix predictors in a single model. We included Euclidean distance, pH, carbon to nitrogen ratio (C:N ratio), mean annual max daily temperature (MAMT), mean annual precipitation (MAP), and plant community similarity in these GDM models and partitioned variance among these variables using the permutational variance importance tool. I-spline relationships between ecological similarity and each of these variables were calculated, as well as the total variance explained by the model and the partial variance explained by each predictor.

Because Euclidean distance and abiotic environmental similarity are geographically autocorrelated ($R^2 = 0.484$, $p < 0.001$), we verified the MLR results using multivariate variance partitioning models, performing Mantel tests to quantify the relative effects of geographic distance, abiotic environment, and biotic plant community on microbial community composition (Martiny et al., 2006). To account for Euclidean autocorrelation of abiotic and biotic environmental gradients individually, we also conducted two partial Mantel tests to test whether Euclidean effects on microbial beta diversity were independent of environment.

3. Results

There were significant distance-decay relationships for fungi and bacteria across Euclidean distance (fungi: $P_{1,778} < 0.001$, $R = 0.071$; bacteria: $P_{1,778} < 0.001$, $R = 0.064$; Fig. 2A), environmental similarity (fungi: $P_{1,778} < 0.001$, $R = 0.233$; bacteria: $P_{1,778} < 0.001$, $R = 0.300$; Fig. 2B), and plant community similarity (bacteria: $P_{1,778} < 0.001$, $R = 0.143$; fungi: $P_{1,778} < 0.001$, $R = 0.272$; Fig. 2C). While the slopes of these relationships were not significantly different by morphology across Euclidean distance (Fig. 2D), rates of decay did vary by morphology across environmental similarity (Fig. 2E). Specifically, unicellular fungi and unicellular bacteria had significantly lower turnover than filamentous fungi, which had a steeper distance-decay relationship slope, while filamentous bacteria exhibited an intermediate distance-decay slope. When compared across plant community similarity, filamentous fungi had a significantly stronger distance-decay relationship slope than unicellular bacteria. However, the distance-decay pattern for filamentous bacteria was similar to both unicellular fungi and unicellular bacteria, and the distance-decay pattern for unicellular fungi was similar to both filamentous fungi and filamentous bacteria (Fig. 2F). Notably, across all distance metrics, there were important differences in the intercepts of four groups, with filamentous fungal communities being substantially less similar on average than unicellular fungi or bacteria with either morphology (Fig. 2G, H, I).

In the GDM models including Euclidean distance, environmental variables, and plant community dissimilarity, we observed nonlinear relationships between community similarity and each of the predictor factors that varied according to both microbial domain and morphological type (Fig. 3). In total, each of the four GDM models explained a substantial amount of the model deviance for each of the microbial groups (unicellular fungi = 19%; multicellular fungi = 59.1%; unicellular bacteria = 64.9%; multicellular bacteria = 26.5%). Euclidean distance was only a significant predictor of ecological community distance for unicellular fungi and unicellular bacteria, but it accounted for a small proportion of the total model variance (Fig. 4). In contrast, pH was consistently a strong driver of community composition for all four of the microbial groups (unicellular fungi = 13%; filamentous fungi = 25%; unicellular bacteria = 60%; filamentous bacteria = 60%). Climate and edaphic factors also affected fungal and bacterial communities differently. Specifically, precipitation was only significant in structuring unicellular fungal communities, but pH was a strong predictor across all microbial groups. We found that the proportion of filamentous microbes changed significantly across a gradient of soil pH, but that this relationship differed between domains. In fungi, the proportion of microbes with filamentous morphology increased with pH, while for bacteria, filamentous bacteria decreased (fungi: $P_{1,38} = 0.024$, $R^2 = 0.103$; bacteria: $P_{1,38} = 0.005$, $R = 0.1665$ Fig. S1). However, C:N ratio did not account for variation between domains or morphological types. Additionally, precipitation was only significantly important for unicellular fungal communities, explaining 27% of the variation. With regard to plant community similarity, this variable was a strong predictor for both groups of fungi (unicellular fungi = 21% and filamentous fungi = 26%), but for neither group of bacteria (unicellular bacteria = 2.3% and filamentous bacteria = 2.4%). Euclidean distance accounted for 16–27% of the total variance in microbial community composition (Euclidean distance: unicellular bacteria = 27%; filamentous bacteria = 14%; filamentous fungi = 20%, unicellular fungi = 16%, Fig. S2A). When comparing the independent effects of abiotic and biotic environment on microbial community composition, more than half of the variation in bacterial communities was explained by abiotic environmental characteristics (Environmental similarity: unicellular bacteria = 54%; filamentous bacteria = 34%; filamentous fungi = 39%; unicellular fungi = 24%); while more than half of the variation in fungal community composition was correlated with plant community composition (plant community similarity: unicellular bacteria = 40%; filamentous bacteria = 23%; filamentous fungi = 58%; unicellular fungi = 30%; Fig. S2A). After controlling for co-variation between abiotic environment and Euclidean distance, however, Euclidean distance was no longer a significant predictor of microbial community composition in either bacteria or fungi (Fig. S2B). By contrast, when partitioning variance between biotic environment and Euclidean distance, the latter remained significantly correlated with unicellular bacterial, filamentous bacteria, and filamentous fungal communities, though it accounted for only 21%, 9%, and 11% of the community variation, respectively (Fig. S2B).

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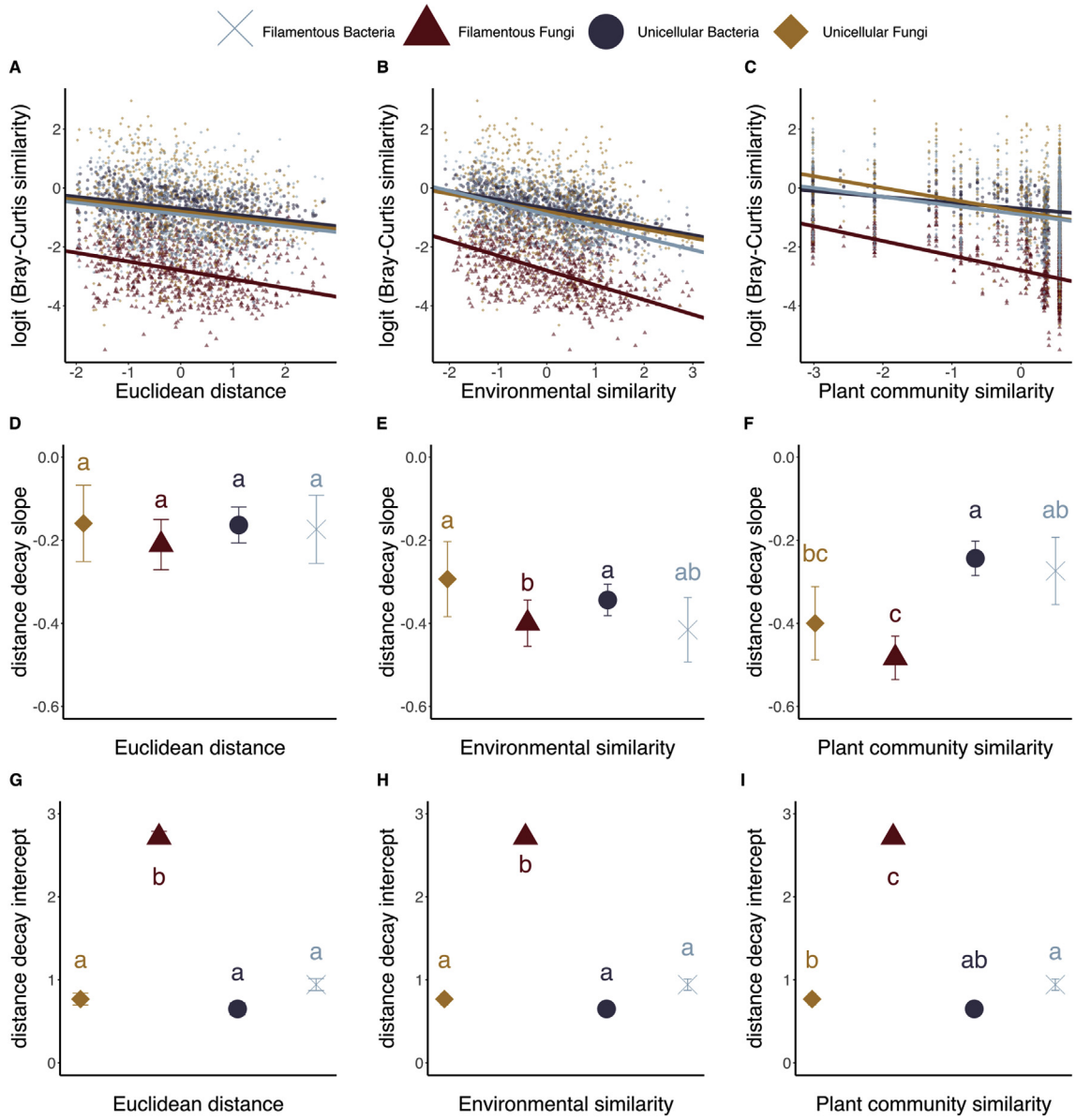

Fig. 2. A, B, and C. Multiple regressions analysis of community distance-decay relationships across Euclidean distance (A), environmental similarity (B), and plant community similarity (C). The corresponding slopes (D,E,F) and intercepts (G,H,I) of each partial regression, with different letters representing significant differences based on *post-hoc* Tukey tests. Error bars for slope and intercept estimates represent confidence intervals.

4. Discussion

To our knowledge, this is the first demonstration that distance-decay relationships of different microbial domains, which have been shown in many systems, can be significantly predicted by a common trait – morphological type. Specifically, we found that unicellular fungal communities (i.e. yeasts) exhibited patterns of distance-decay nearly indistinguishable from those of unicellular bacterial communities, suggesting that morphological type may be an important factor or proxy for traits related to community diversity among environments. Because a filamentous morphological form is also typically associated with a larger body size, these findings also suggest that the community composition of larger microorganisms likely turns over more quickly than that of smaller microorganisms. Indeed, here we find that across plant community similarity, distance-decay relationships are strongest for filamentous fungi, but decline with estimated size, where unicellular fungi and filamentous bacterial distance-decay relationships are intermediate to filamentous fungi and unicellular bacteria.

Our results align with previous work demonstrating that body size is an important trait both for dispersal capability and stress tolerance for both macro- and microorganisms (Schimel et al., 2007; De Bie et al., 2012; Treseder et al., 2014). For example, in a study of marine organisms ranging in size from bacterial cells to large fish, it was shown that bacteria (treated as a single morphological group) dispersed more easily than fungi (treated as a single morphological group) (De Bie et al., 2012). Other work has also shown that dispersal capability is closely related to biogeography (Nemergut et al., 2013; Chen et al., 2017; Ma et al., 2017; Albright and Martiny, 2018), and that the amount of environmental control on an organism's range is variable according to its dispersal capability (Astorga et al., 2012). The high stress tolerance in unicellular fungal forms such as yeasts and endospore-forming bacteria also promotes the idea that such stress tolerance may widen

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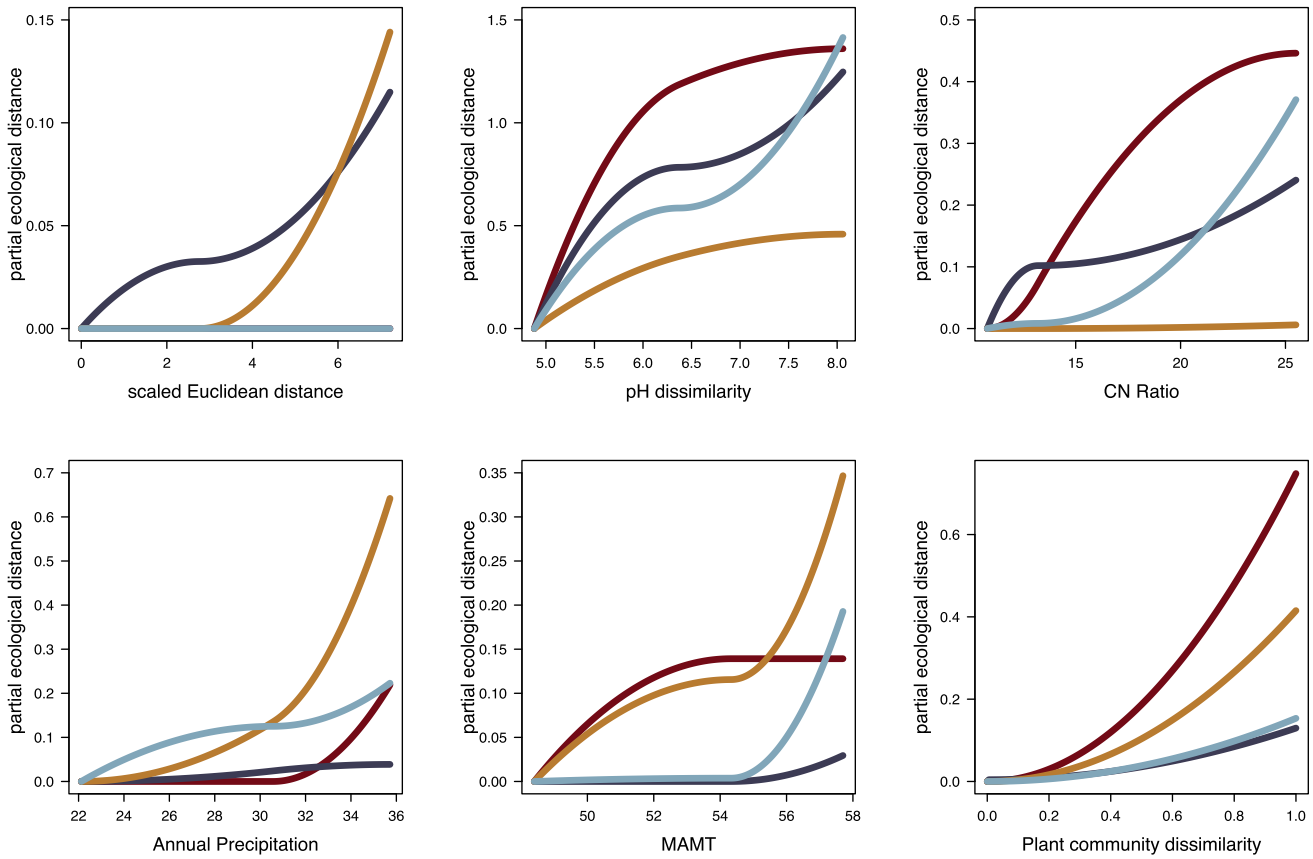

Fig. 3. GDM-fitted I-splines (or partial regression fits) for variables that were significantly associated with community composition across the four microbial groups.

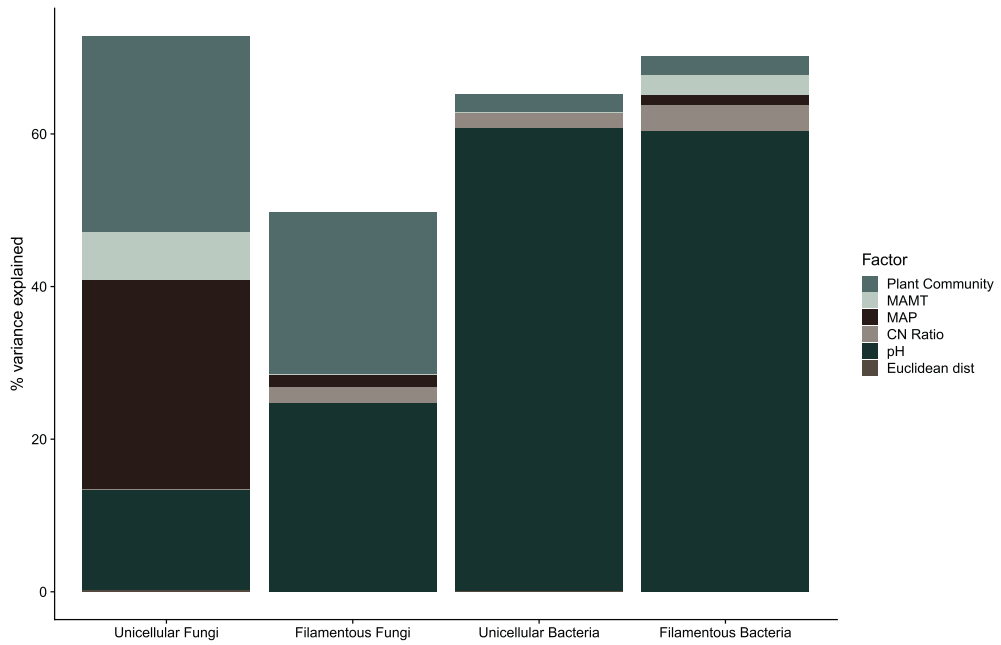

Fig. 4. Partitioning of variance (via permutation) among GDM predictor variables for the four GDM models corresponding to each microbial group.

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an organism's geographical range (Treseder et al., 2014). Unicellular organisms in the soil are affected by soil conditions in a small area (10–100 μm). It has been hypothesized that this limited range constitutes a stressful environment, including frequent wetting and drying cycles in individual soil pores and highly variable nutrient availability, which may select for high levels of stress tolerance (Vos et al., 2013; Claessen et al., 2014; Dunthorn et al., 2017). By contrast, filamentous microbes may be able to better buffer themselves against these cycles by foraging for water and nutrients throughout more of the soil profile (Klein and Paschke, 2004; Singh et al., 2008; Brown and Jumpponen, 2014; Raynaud and Nunan, 2014). While our results support this possibility for unicellular versus multicellular microorganisms, we were not able to test this assertion for endospore-forming bacterial communities, as they represented only 3 out of 29,218 OTUs (<0.01%) in our dataset.

We also observed some notable differences in the correlation of microbial domain and morphological type in the environmental similarity and plant community similarity analyses. Only fungal communities were predicted strongly by plant community similarity. These results are consistent with other studies showing a stronger correlation of plant community similarity and fungal community composition than for bacteria (Urbanová et al., 2015; Chen et al., 2017). From previous work, we expected to see effects of both Euclidean distance and environmental heterogeneity at the regional scale sampled in this study (Hanson et al., 2012; Chen et al., 2017). In particular, it has been suggested that environmental selection is the prevailing process shaping local diversity at small scales (<10 km), whereas dispersal limitation plays a more significant role at global scales (>3000 km; Martiny et al., 2006; Waldrop et al., 2017). Instead, we found that Euclidean distance alone accounted for less variation in microbial communities than expected, which we believe was due to the relatively high environmental and plant community heterogeneity of the region we sampled.

An important potential caveat to our findings of a link between microbial biogeography and morphological growth type is the potential for phylogenetic conservation across multiple non-related traits. In our bacterial analyses, all of the filamentous bacteria belonged to the order Actinomycetales. Therefore, it is possible that our findings regarding morphological growth type are confounded with other traits present within this lineage. For example, the presence of rigid cell walls with muramic acid and/or the production of a diverse array of secondary metabolites (Brown, 1939) might also influence the regional biogeography of members of the Actinomycetales by making them more formidable competitors. In fact, phylogenetic conservation of traits have been shown to result in phylogenetic patchiness in microbial communities across landscapes through tradeoffs between stress tolerance and competitive ability (Goberna et al., 2014). Additionally, variation in plant community composition can also result in phylogenetic microbial community patchiness due to patterns of microbe-plant host specificity that are often phylogenetically constrained (Porter and Rice, 2013; Goberna et al., 2014; Nguyen et al., 2016b). While still limited in distribution across the entire fungal phylogeny (Golan and Pringle, 2017), unicellular fungi (i.e., yeasts) were independently present in both phyla Ascomycota and Basidiomycota in our dataset (Fig. S6; Tedersoo et al., 2018). Given that the results we obtained for fungi were consistent across these distantly related groups, that suggests our trait of interest, morphological growth type, rather other phylogenetic conserved traits was responsible for the differential biogeography of unicellular fungi. However, we advocate that future tests of this relationship, particularly for bacteria, carefully consider the possibility of phylogenetic conservatism of stress tolerance, competitive ability, of microbe-plant host specificity on distance-decay relationships.

A second consideration regarding the interpretation of our findings is the fact that they were major differences in the sizes of our unicellular versus filamentous groups for both bacteria and fungi (i.e. ~10x more filamentous fungal OTUs than unicellular OTUs and, conversely, ~10x more unicellular bacterial OTUs than filamentous OTUs). Given these discrepancies, is also possible that the patterns we observed may be an artifact of differential sample size. To assess this possibility, we tested whether subsampling from the larger group (i.e., including fewer OTUs from the group with 10x more OTUs) altered the observed distance-decay relationships. We did this by comparing the same distance-decay relationships on similarly-sized sets of OTUs for other bacterial and fungal clades. Specifically, for fungi, we compared unicellular fungi to the subset of OTUs classified as Mortierellales, an order of filamentous non-mushroom forming fungi. For bacteria, we compared our filamentous bacterial group to the r-selected, single-celled bacterial phylum Bacteroidetes. Both of these tests revealed the same patterns between unicellular and filamentous growth morphologies as we found in the larger OTU datasets (Supplement 3), indicating our results are not likely due to artifacts of differential sample size.

A final factor to consider is how reproductive traits such as the size and morphology of reproductive structures influence microbial distance-decay relationships. It is possible that structures that facilitate spore dispersal may result in greater community homogeneity because spores may be transported over long distances or withstand stressful environmental conditions in a spore or dormant state (Checinska et al., 2015). In our dataset, however, the distance-decay relationships we observed for filamentous fungi do not appear to be the direct result of mushroom formation, as filamentous non-mushroom forming fungi in the order Mortierellales had similar distance-decay relationships (Supplement 3). Since large aboveground spore-bearing structures are functionally absent in bacteria, this also suggests that the differences we observed are not driven by the morphology of microbial reproductive structures. That said, more studies characterizing differences between non-reproductive body morphology and propagule morphology are needed to provide an integrated understanding of how microbes respond to dispersal limitation and environmental selection in both reproductive and non-reproductive structures. Similarly, further study of other common microbial traits, such as metabolic habit (i.e. saprotrophs vs. symbionts) and host associations (specialist vs. generalists), will aid in determining which traits are most important for structuring microbial diversity in soil systems (Schimel et al., 2007; Lennon, 2012; Crowther et al., 2014; Talbot et al., 2014; Aguilar-Trigueros et al., 2015; Calhim et al., 2018; Krah et al., 2018).

In summary, this study is the first to explicitly investigate the role of morphological type, a trait present in multiple microbial domains, in shaping the distance-decay relationships of both fungi and bacteria. Our results suggest that morphology is particularly relevant in determining how microorganisms respond to their abiotic environment, while domain is a stronger predictor of microbial community response to plant community similarity. Collectively, these findings suggest that direct consideration of ecological traits will aid in improving models of microbial biogeography and enable deeper understanding of the link between microbial diversity and functioning across ecosystems.

Declaration of competing interest

The authors declare no competing interests.

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Supplementary data

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