Increasing aridity reduces soil microbial diversity and abundance in global drylands

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Soil bacteria and fungi play key roles in the functioning of terrestrial ecosystems, yet our understanding of their responses to climate change lags significantly behind that of other organisms. This gap in our understanding is particularly true for drylands, which occupy ∼41% of Earth´s surface, because no global, systematic assessments of the joint diversity of soil bacteria and fungi have been conducted in these environments to date. Here we present results from a study conducted across 80 dryland sites from all continents, except Antarctica, to assess how changes in aridity affect the composition, abundance, and diversity of soil bacteria and fungi. The diversity and abundance of soil bacteria and fungi was reduced as aridity increased. These results were largely driven by the negative impacts of aridity on soil organic carbon content, which positively affected the abundance and diversity of both bacteria and fungi. Aridity promoted shifts in the composition of soil bacteria, with increases in the relative abundance of *Chloroflexi* and α-*Proteobacteria* and decreases in *Acidobacteria* and *Verrucomicrobia*. Contrary to what has been reported by previous continental and global-scale studies, soil pH was not a major driver of bacterial diversity, and fungal communities were dominated by *Ascomycota*. Our results fill a critical gap in our understanding of soil microbial communities in terrestrial ecosystems. They suggest that changes in aridity, such as those predicted by climate-change models, may reduce microbial abundance and diversity, a response that will likely impact the provision of key ecosystem services by global drylands.

bacteria | fungi | climate change | arid | semiarid

Climate change is a major driver of biodiversity loss from local to global scales, in both terrestrial and aquatic ecosystems (1, 2). Given the dependence of crucial ecosystem processes and services on biodiversity (3–5), climate-change-driven biodiversity losses will dramatically alter the functioning of natural ecosystems (4, 6). Key ecosystem processes—such as nutrient cycling, carbon (C) sequestration, and organic matter decomposition—depend on soil bacteria and fungi (7–9). However, we have limited knowledge of the role of climatic factors as drivers of their abundance and diversity at regional and global scales (10–12). This gap in our understanding is particularly true for drylands, areas with an aridity index (precipitation/potential evapotranspiration ratio) below 0.65 (13), which are among the most sensitive ecosystems to climate change (14). Drylands are expected to expand in global area by 11–23% by 2100 (15), experiencing increased aridity and reduced soil moisture (16). Land degradation and desertification already affect ∼250 million people in the developing world (17). Altered climate and the growth of human populations will almost inevitably exacerbate these problems in drylands (14, 17). Because the provisioning of ecosystem services essential for human development (e.g., soil fertility, food, and biomass production) heavily relies on the abundance, composition, and diversity of soil fungi and bacteria (18, 19), it is

Significance

Climate change is increasing the degree of aridity in drylands, which occupy 41% of Earth's surface and support 38% of its population. Soil bacteria and fungi are largely responsible for key ecosystem services, including soil fertility and climate regulation, yet their responses to changes in aridity are poorly understood. Using a field survey conducted in drylands worldwide and DNA-sequencing approaches, we found that increases in aridity reduce the diversity and abundance of soil bacteria and fungi. This study represents an important advancement in our understanding of soil microbial communities and their likely responses to ongoing climate change.

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crucial to understand how changes in aridity affect soil microbial communities. Drylands, however, are poorly represented in global soil bacteria and fungi databases (10–12, 20), and no field study has simultaneously examined how the abundance, composition, and diversity of these organisms vary along aridity gradients in drylands worldwide.

Here, we present a global field study conducted across 80 dryland sites from all continents, except Antarctica (Fig. S1), to assess how changes in aridity, as defined by the aridity index, affect the total abundance and diversity of soil bacteria and fungi and the relative abundance of major bacterial and fungal taxa. The studied ecosystems encompass a wide variety of the climatic, edaphic, and vegetation conditions found in drylands worldwide (*Materials and Methods*). We predict that increases in aridity should reduce the abundance and diversity of soil bacteria and fungi due to the negative relationships typically found between aridity and the availability of resources such as water and C (21), which largely drive soil microbial abundance and activity in drylands (22–24). To test this hypothesis, we characterized bacterial and fungal communities in the soil surface (top 7.5 cm) along natural aridity gradients by using Illumina Miseq profiling of ribosomal genes and internal transcribed spacer (ITS) markers, quantified bacterial and fungal abundances with quantitative PCR (qPCR), and gathered information on multiple biotic and abiotic factors known to influence soil microbes (Fig. S2).

Results and Discussion

Bacterial communities were dominated by *Actinobacteria*, *Proteobacteria*, *Acidobacteria*, and *Planctomycetes* (Fig. S3*A*), which are common bacterial phyla in soils worldwide (8, 11). The most abundant soil fungi were those from the phylum *Ascomycota*, followed by *Basidiomycota*, *Chytridiomycota*, and Zygomycetous fungi (Fig. S3*B*). Our findings contrast with a recent global survey of soil fungi (12) reporting a greater dominance of *Basidiomycota* than we observed (56% vs. 22%). These discrepancies probably relate to the low proportion of drylands surveyed in that study (<1% of 350 sites) and underscore our limited understanding of fungal communities inhabiting dryland soils. Minor differences in the dominant bacterial and fungal phyla were observed when assessing differences among major vegetation types, because variation in their relative abundance was <5% when comparing grasslands and woodlands (Fig. S3 *A* and *B*).

We evaluated the direct relationship between the diversity and abundance of soil bacteria and fungi and aridity using ordinary least-squares (OLS) regression models (*Materials and Methods*). In addition—and to account for possible large-scale spatial nonindependence of the sites surveyed (25)—we included the dominant eigenvector of the Euclidean distance matrix of sites as an additional predictor into these models (spatial models; refs. 26 and 27). Increases in aridity were linearly associated with reductions in fungal and bacterial diversity and abundance (Fig. 1). The diversity of several bacterial and fungal taxa also followed this pattern (Figs. S4 and S5), although nonlinear (e.g., *Acidobacteria* and *Proteobacteria*; Fig. S4 *B* and *E*) and nonsignificant (e.g., *Chloroflexi*; Fig. S4*D*; and Zygomycetous fungi; Fig. S5*E*) relationships were also found. Aridity also affected the dominance of major bacterial phyla. The relative abundance of *Acidobacteria* declined linearly as aridity increased (Fig. 2*A*), whereas that of *Chloroflexi* followed the opposite pattern (Fig. 2*C*). Other bacterial phyla and classes were nonlinearly related to aridity, with peaks in their relative abundance at either low (e.g., *Verrumicrobia*) or high (e.g., α-*Proteobacteria*) aridity levels (Fig. 2 *B* and *D*–*F*). These results can be explained by the different life strategies of bacterial taxa. *Chloroflexi* are known to have multiple adaptations to environmental

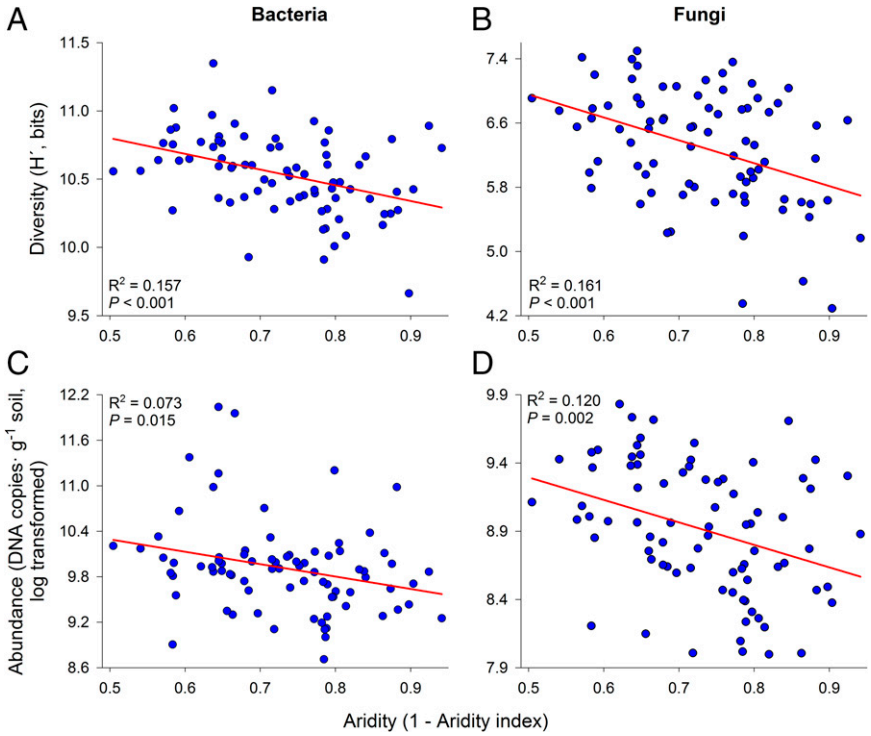

Fig. 1. Relationships between aridity and the diversity and abundance of soil bacteria and fungi. The solid lines represent the fitted OLS model. The proportion of variance explained (R^2) of regressions including the dominant eigenvector of the Euclidean distance matrix of sites (for spatial models, see *SI Materials and Methods*), and the differences in the second-order Akaike Information Criterion [ΔAICc] between these models and those shown in the figure, are as follows: $R^2 = 0.197$, ΔAICc = −1.501 (*A*); $R^2 = 0.169$, ΔAICc = 1.399 (*B*); $R^2 = 0.193$, ΔAICc = −8.879 (*C*); and $R^2 = 0.298$, ΔAICc = −15.86 (*D*). A negative ΔAICc value indicates that the AICc of the spatial model is lower than that of the nonspatial model.

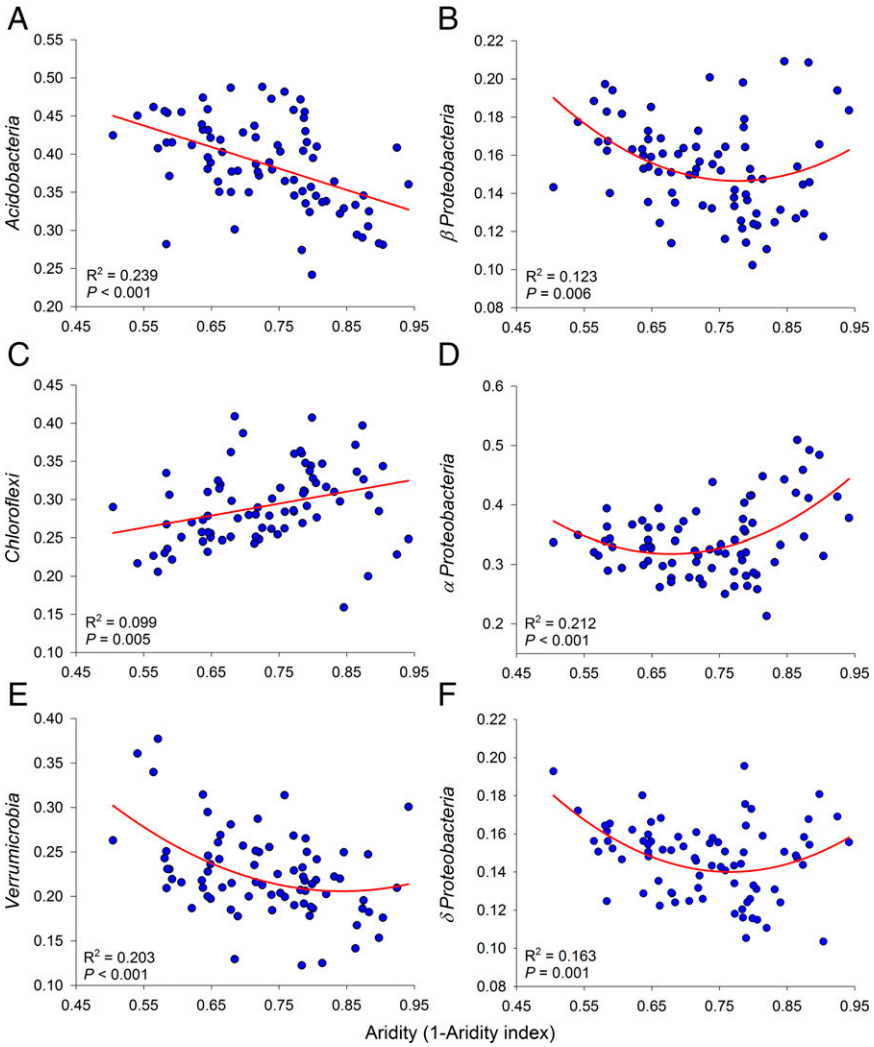

Fig. 2. Relationships between aridity and the relative abundance (arcsine-transformed proportions) of dominant soil bacterial phyla and classes. The solid lines represent the fitted linear or quadratic OLS model. The proportion of variance explained (R^2) of regressions including the dominant eigenvector of the Euclidean distance matrix of sites, and the differences in the ΔAICc between these models and those shown in the figure are as follows: $R^2 = 0.319$, ΔAICc = −6.288 (*A*); $R^2 = 0.164$, ΔAICc = −0.173 (*B*); $R^2 = 0.112$, ΔAICc = 1.047 (*C*); $R^2 = 0.245$, ΔAICc = −1.376 (*D*); $R^2 = 0.341$, ΔAICc = −12.93 (*E*); and $R^2 = 0.250$, ΔAICc = −6.234 (*F*). The rest of the legend is as in Fig. 1.

harshness (28), whereas *Acidobacteria* and *Verrucomicrobia* typically show opportunistic responses to short-term changes in water availability, with rapid declines and increases in ribosomal synthesis during drought and after soil rewetting, respectively (24). The relative abundance of major fungal phyla did not change with aridity (R^2 of linear/logarithmic/quadratic regression < 0.07, $P >$ 0.08 in all cases). These findings are consistent with those from studies showing that the relative abundance of fungal phyla remained largely unchanged with soil desiccation during a summer drought (24). Spatial models that included aridity were superior predictors of changes in the abundance of fungi and bacteria (Fig. 1), in the diversity of *Actinobacteria* and *Acidobacteria* (Fig. S4), and in the relative abundance of *Acidobacteria*, *Verrumicrobia*, and δ-*Proteobacteria* (Fig. 2). These results are likely to be driven by the strong relationships between aridity and latitude/longitude found in our database (Fig. 3*A*).

To further investigate the direct and indirect effects of aridity on soil bacteria and fungi, we generated structural equation models (SEMs) based on the known effects and relationships among aridity and other key drivers of the diversity and abundance of these microorganisms (mean diurnal temperature range, plant cover, soil pH, and organic C content; Fig. S2). Latitude and longitude were also included in our models, given their effects on microbial abundance (Fig. 2 *C* and *D*) and on the rest of biotic and abiotic variables evaluated (Fig. 3 *A* and *B*). Our models explained between 34% and 49% of the variance found in microbial diversity and abundance among the sites surveyed (Fig. 3 *A* and *B*). Aridity indirectly impacted the diversity and abundance of soil bacteria and fungi by strongly affecting soil pH, soil organic C content, and total plant cover (Fig. 3 *C* and *D*). Organic C content had a direct positive effect on the diversity and abundance of both bacteria and fungi (Fig. 3 *A* and *B* and Fig. S6) and was the strongest predictor of such community attributes in the case of bacteria (Fig. 3*C*). These results suggest that soil microbial communities are limited by C in dryland soils (22, 23) and align with studies from polar regions, indicating that soil C content is a major driver of the diversity of soil bacteria and fungi (29). Our findings also mimic observed global patterns in microbial biomass C, which have been found to increase in tandem with soil C contents from southern to northern latitudes (30, 31). The negative effect of mean diurnal temperature range (MDR) on bacterial and fungal abundance is likely due to (*i*) increases in physiological stress

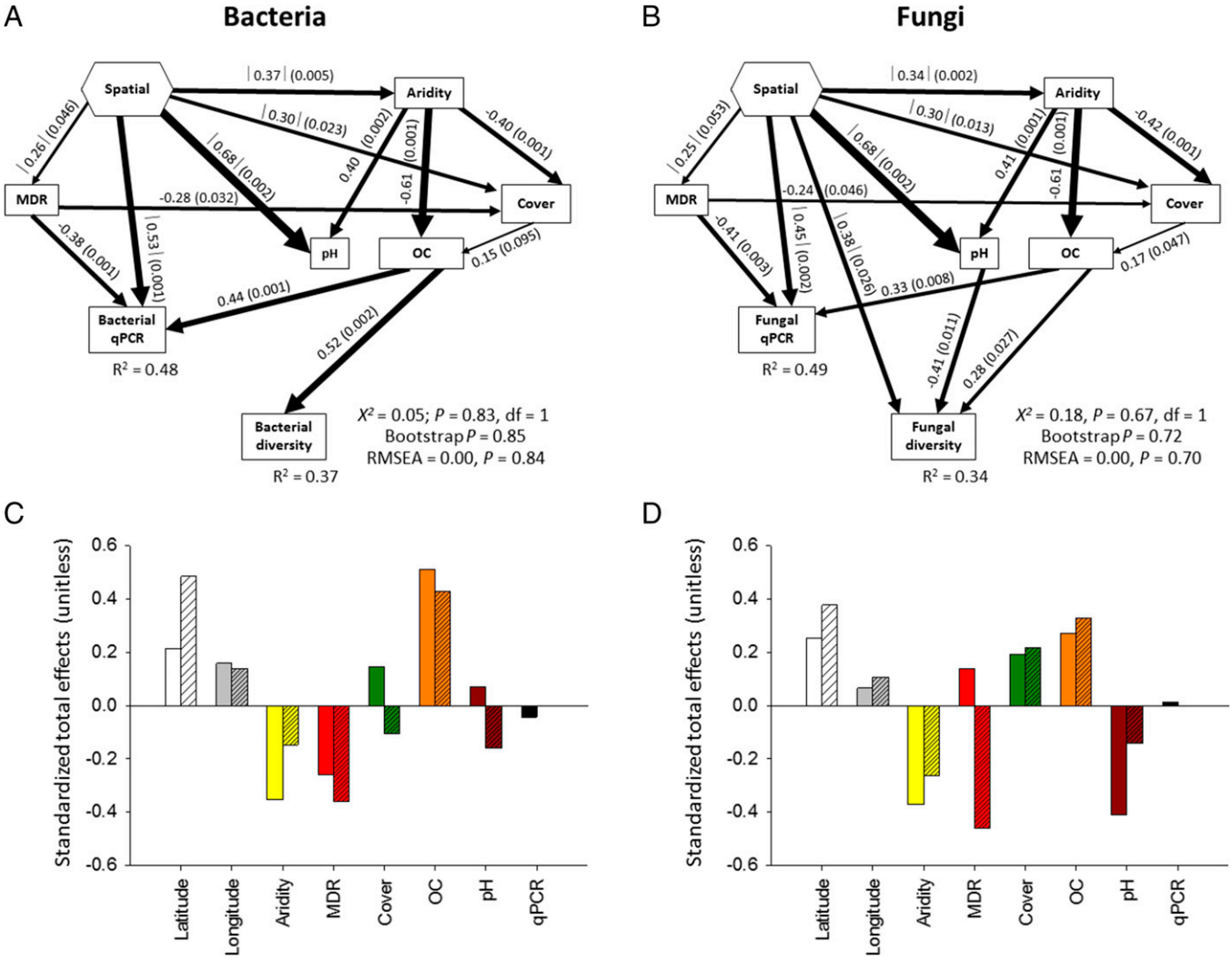

Fig. 3. SEMs fitted to the diversity and abundance of soil bacteria (*A*) and fungi (*B*) and standardized total effects (direct plus indirect effects) derived from them (*C* and *D*). Numbers adjacent to arrows are path coefficients (*P* values) and indicative of the effect size of the relationship. The sign of the spatial composite is not interpretable; thus, absolute values are presented. Filled and dashed bars in *C* and *D* denote the standardized effects on diversity and abundance, respectively. Cover, total plant cover; OC, soil organic C content; qPCR, abundance measured using real-time PCR; R^2, the proportion of variance explained; spatial, composite variable including latitude and longitude.

associated with rapid temperature changes (32); and (*ii*) negative effects of MDR on total plant cover, which reduced organic C inputs into the soil (Fig. 3 *A* and *B*). Soil pH was uncorrelated with bacterial diversity and abundance, in contrast to previous findings highlighting soil pH as a major predictor of bacterial richness across a wide range of ecosystem types (20, 33). These discrepancies are likely linked to the high (and relative narrow range of) pH values found at our study sites (6.2–8.9), because linear increases in bacterial diversity with pH have been found mainly in soils with pH values of 3.5–6.5 (20, 33). Our findings thus indicate that the importance of soil pH as a driver of bacterial diversity patterns reported by previous large-scale studies (20, 33) does not hold in drylands, where soil pH values are generally >6.5 (34). However, both soil pH and organic C content were strongly correlated with the relative abundance of major bacterial phyla and classes (Figs. S7 and S8). Despite these results, the relationships (positive or negative) between soil pH and the relative abundance of bacterial phyla and classes remained significant, even after controlling for the effects of both aridity and organic C (partial correlation analysis; $r_{Acidobacteria} = -0.240$, $P = 0.037$; $r_{Actinobacteria} = 0.363$, $P = 0.001$; $r_{Chloroflexi} = 0.236$, $P = 0.040$; $r_{Verrumicrobia} = -0.626$, $P < 0.001$; $r_{\beta\text{-}Proteobacteria} = -0.446$, $P < 0.001$; $r_{\delta\text{-}Proteobacteria} = -0.263$, $P = 0.022$; $r_{\gamma\text{-}Proteobacteria} = 0.272$, $P = 0.017$; df = 74 in all cases). These results support the notion that soil pH drives changes in bacterial composition in terrestrial ecosystems (20, 33, 35). Soil pH was negatively related to fungal diversity (Fig. 3 *B* and *D*), consistent with a global study showing a negative correlation between soil pH and fungal richness after accounting for the effects of other environmental drivers (12). The relative abundance of *Glomeromycota* increased concomitantly with soil pH, but that of other fungal phyla was not affected by this soil variable (Fig. S9). These results may have been associated with the wide pH optimum of many fungal taxa (35). The relative abundance of *Chytridiomycota* declined, but that of *Glomeromycota* increased, as soil organic C increased. Other fungal groups were not related to soil organic C (Fig. S9).

Our results indicate that increases in aridity—such as those forecasted for the second half of this century (15)—will likely reduce the abundance and diversity of soil bacteria and fungi in drylands globally and may promote shifts in the composition of soil bacterial communities. These predictions, however, have a degree of uncertainty given the observational nature of our survey,

which does not account for the different effects of human activities and other climate-change drivers that may change with aridity. For example, if the introduction of exotic, invasive species by humans in ecosystems occurs along with increasing aridity, some of the observed links between aridity, soil organic C content, and microbial diversity could break down (36). Increases in water use efficiency (WUE) due to elevated [CO_2] may enhance overall plant growth and soil C fixation in drylands (37), which could mitigate the reduction of microbial abundance and diversity expected as aridity increases. Whether this enhancement of WUE can compensate for the detrimental effects of increased aridity on water availability and plant growth is largely unknown. A recent study showed that increased aridity over the last four decades was responsible for a sustained decline in plant productivity, regardless of CO_2-induced increases in WUE during this period (38).

Conclusions

Here we show that increases in aridity, such as those predicted by climate-change models (15, 16), reduce the diversity and abundance of soil bacteria and fungi in drylands, the largest biome on Earth (39). These responses are mainly driven by reductions in soil organic C content associated with increases in aridity and, in the case of microbial abundance, with increases in diurnal temperature variations. Soil pH affected both the abundance of fungi and the relative abundance of major bacterial phyla and classes, but had no effect on the diversity of soil bacteria. Unlike reports of previous global surveys from terrestrial ecosystems (12), fungal communities in dryland soils were dominated by *Ascomycota*. These findings highlight the unique features of soil microbial communities in drylands. Both the community structure and relative importance of environmental factors driving variation in microbial communities in global drylands differ from previous records from other terrestrial ecosystems. Our results fill a critical gap in our understanding of microbial community structure in global drylands and provide additional insights into how soil microbial communities may respond to climate change. Ecosystem models are beginning to incorporate information on microbial abundance, composition, and diversity, which is needed to improve predictions of soil C stocks and their dynamics (31), and the links between aridity, soil organic C content, and these microbial community attributes shown here can be used to refine and validate them.

Materials and Methods

Complete documentation of the study sites, field survey, sample collection, and laboratory procedures, as well as additional details on the statistical analyses are provided in *SI Materials and Methods*.

Field data were collected from 80 dryland sites selected to represent a wide range of the environmental and biotic characteristics of global drylands (Fig. S1; figshare DOI 10.6084/m9.figshare.1487693). At each site, the cover of perennial vegetation was measured by using the line-intercept method along four 30-m-long transects (5). Replicated soil samples (0- to 7.5-cm depth) were randomly taken under the canopy of the dominant perennial plant species and in open areas devoid of perennial vegetation (10–15 samples per site). After field collection, a fraction of the soil samples was immediately frozen at −20 °C for microbial analyses. These analyses were conducted on composite samples of each microsite (open and vegetated areas) and site. Soil DNA was extracted from 0.5 g of defrosted soil samples by using the Powersoil DNA Isolation Kit (Mo Bio Laboratories). qPCR reactions were performed in triplicate by using 96-well plates on an ABI 7300 Real-Time PCR (Applied Biosystems). The bacterial 16S-rRNA genes and fungal ITS were amplified with the Eub 338-Eub 518 and ITS 1-5.8S primer sets (40). After qPCR analyses, the extracted DNA samples were frozen and shipped to the Next Generation Genome Sequencing Facility of Western Sydney University, where they were defrosted and analyzed by using the Illumina MiSeq platform (41) and the 341F/805R (bacteria) and FITS7/ITS4 (fungi) primer sets (42, 43). Initial sequence processing and diversity analyses for both bacterial 16S rDNA and fungal ITS genes were conducted as described in *SI Materials and Methods*.

Before numerical and statistical analyses, all soil and microbial variables used in this study were averaged to obtain site-level estimates by using the mean values observed in bare ground and vegetated areas, weighted by their respective cover at each site (5). We first modeled the relationships between aridity and the abundance and diversity of bacteria and fungi using either linear or curvilinear (quadratic) regressions. The aridity [1 − aridity index (AI), where AI is precipitation/potential evapotranspiration] of each site was obtained by using data from ref. 44. Similarly, we explored the relationships between aridity and the abundance and diversity of main bacterial and fungal phyla and classes, as well as between soil organic C content/pH and these taxa using regression and partial correlation analyses as described in *SI Materials and Methods*. To determine the mechanisms underlying the observed effects of aridity on microbial abundance and diversity, we used SEM (45). This approach tests the plausibility of a causal model encompassing a set of a priori hypotheses (Fig. S2). Our a priori model included spatial structure (latitude and longitude), aridity, mean diurnal temperature range (obtained from ref. 46), soil pH, organic C, and total plant cover as predictors of the total amount (as measured with qPCR) and diversity (Shannon index) of both bacteria and fungi. SEM analyses were conducted as described in *SI Materials and Methods* by using AMOS (Version 18.0; Amos Development). All of the data used in the primary analyses are available from figshare (DOI 10.6084/m9.figshare.1487693).

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