Ecology, 93(8), 2012, pp. 1867–1879

Mapping the niche space of soil microorganisms using taxonomy and traits

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Abstract. The biodiversity of microbial communities has important implications for the stability and functioning of ecosystem processes. Yet, very little is known about the environmental factors that define the microbial niche and how this influences the composition and activity of microbial communities. In this study, we derived niche parameters from physiological response curves that quantified microbial respiration for a diverse collection of soil bacteria and fungi along a soil moisture gradient. On average, soil microorganisms had relatively dry optima (0.3 MPa) and were capable of respiring under low water potentials (−2.0 MPa). Within their limits of activity, microorganisms exhibited a wide range of responses, suggesting that some taxa may be able to coexist by partitioning the moisture niche axis. For example, we identified dry-adapted generalists that tolerated a broad range of water potentials, along with wet-adapted specialists with metabolism restricted to less-negative water potentials. These contrasting ecological strategies had a phylogenetic signal at a coarse taxonomic level (phylum), suggesting that the moisture niche of soil microorganisms is highly conserved. In addition, variation in microbial responses along the moisture gradient was linked to the distribution of several functional traits. In particular, strains that were capable of producing biofilms had drier moisture optima and wider niche breadths. However, biofilm production appeared to come at a cost that was reflected in a prolonged lag time prior to exponential growth, suggesting that there is a trade-off associated with traits that allow microorganisms to contend with moisture stress. Together, we have identified functional groups of microorganisms that will help predict the structure and functioning of microbial communities under contrasting soil moisture regimes.

Key words: *bacteria; biodiversity; cultivation; desiccation; environmental filtering; fungi; neutral theory of biodiversity; phylogeny; respiration; soil; sorting; traits-based ecology.*

Introduction

The niche concept is one of the cornerstones of ecology and evolutionary biology. By describing the performance of a species in relation to environmental conditions, niche theory can provide insight into the outcome of species interactions (Levine and Hille-RisLambers 2009), estimate the biogeographic range limits of species distributions (Kearney and Porter 2004), and generate predictions about how species will respond to future climate scenarios (Post et al. 2009). Although the niche concept is not without criticism, it has proven to be a powerful framework for understanding the distribution and abundance of plant and animal species (see Chase and Leibold 2003).

Niche theory also holds promise for understanding the tremendous amount of microbial diversity that has been discovered over the past few decades. Although microorganisms are the most abundant and diverse taxa on Earth (cf. Whitman et al. 1998, Curtis et al. 2002) and play an important role in the stability and functioning of managed and natural ecosystems (Hashsham et al. 2000, Bell et al. 2005), ecologists are only beginning to understand how abiotic and biotic factors influence microbial diversity. Several lines of evidence suggest that niche-based processes may contribute to the structure of microbial communities. First, the biogeographic distributions of microbial taxa are often correlated with environmental features that capture important niche axes (Fierer and Jackson 2006, Bryant et al. 2008). Second, some bacterial taxa exhibit nonrandom co-occurrence patterns with other bacterial taxa, a situation that can arise when species have nonoverlapping niches (Horner-Devine et al. 2007). Third, closely related microbial taxa are sometimes found in similar habitats more often than would be expected by chance (Horner-Devine and Bohannan 2006); this pattern can reflect

Manuscript received 24 September 2011; revised 5 March 2012, accepted 13 March 2012. Corresponding Editor: D. A. Wardle.

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niche conservatism, whereby species retain traits that allow them to contend with certain environmental conditions (Wiens and Graham 2005). Alternatively, microbial communities are sometimes overdispersed, such that distantly related taxa are found together more often than would be expected by chance (Horner-Devine and Bohannan 2006); this phylogenetic pattern is often attributed to niche differentiation resulting from competitive interactions (Webb et al. 2002, but see Losos 2008).

Recently, it has been proposed that a traits-based approach may provide valuable insight into the biogeography, assembly, and functioning of microbial communities (Green et al. 2008, Wallenstein and Hall 2011). This approach focuses on functional traits, which refer to physiological, morphological, or genomic characteristics that influence the performance or fitness of organisms under a set of environmental conditions. Compared to studies of plants and animals, however, there are a number of obstacles that need to be overcome when considering traits of microorganisms. Many microbial taxa appear identical, making it infeasible to distinguish traits based on morphological features. In addition, because most microorganisms cannot yet be cultivated, it has been difficult to establish functional groups or to make generalizations about the phylogenetic distribution of functional traits. Some of these challenges are being addressed through advances in molecular techniques and the development of novel cultivation strategies. For example, the combination of ecophysiological and genomic approaches has been used to identify microbial survival strategies (Yoder-Himes et al. 2009) and resource-based trade-offs that underlie niche differentiation (Coleman and Chisholm 2010, Treseder et al. 2011).

Soils represent one of the largest reservoirs of microbial diversity. It is typical to retrieve hundreds to thousands of fungal and bacterial taxa from a single gram of soil (Rousk et al. 2010, Fierer and Lennon 2011). Although microorganisms are influenced by a suite of biotic and abiotic factors, there is good reason to believe that the activity and diversity of soil microbial communities is strongly influenced by soil moisture availability. Moisture determines the physical connectivity of the soil matrix, which has important implications for resource availability, dispersal, and the strength of species interactions (Treves et al. 2003). In addition, moisture directly affects the physiology of soil microorganisms. For example, in saturated soils, the metabolism of microorganisms can become limited by the rates of oxygen diffusion into pore water (Pett-Ridge and Firestone 2005). In contrast, microorganisms experience desiccation stress in unsaturated soils, which reduces population growth rates and can ultimately lead to cell death (Potts 1994). It is commonly assumed that microbial taxa vary in their response to moisture availability (Paul and Clark 1996), yet surprisingly few studies have characterized the moisture niche for a diverse collection of soil microorganisms. Although early attempts were made to classify certain groups of microorganisms as moisture specialists or moisture generalists (Griffin 1981), it is unclear whether this dichotomy accurately depicts the ecological strategies of diverse microbial communities. It has been suggested that microbial adaptation to moisture stress may be phylogenetically conserved (Schimel et al. 2007), but in general, there is uncertainty about the taxonomic scale at which microorganisms share common responses to environmental variables (see Philippot et al. 2010). Furthermore, the functional traits that confer adaptation to soil moisture variability have not been confirmed, and it remains to be determined if there are trade-offs that constrain microbial responses to this environmental driver.

In this study, we considered the niche space and functional traits of soil microorganisms in the context of soil moisture variability. We estimated niche parameters for the respiration rates of individual strains of soil bacteria and fungi by constructing physiological response curves along a water potential gradient. We used the niche parameters to identify generalist and specialist taxa, tested for trade-offs between these ecological strategies, and made linkages to functional traits at different taxonomic scales. Results from our study generated niche-based predictions that can be used for understanding the biogeographic distributions of soil microorganisms, while also identifying traits that may allow microorganisms to adapt to altered moisture and precipitation regimes.

Methods

Microbial strains

Many of the microorganisms used in this study were recovered from soils at the Kellogg Biological Station (KBS) Long-Term Ecological Research (LTER) site (Hickory Corners, Michigan, USA; see Plate 1) using a combination of isolation strategies that included low-nutrient agar, quorum-sensing compounds, and altered atmospheric gas composition (see Stevenson et al. 2004). Additional strains came from surface soils (0–10 cm depth) collected at various times of the year in five KBS-LTER land use treatments: agricultural crop rotation (T1), successional fields (T7), never-tilled grasslands (T8), deciduous forests (DF), and coniferous forests (CF). For bacteria, 1 g of soil was extracted in 10 mL of 1% sodium pyrophosphate before suspensions were plated onto R2 agar or *Pseudomonas* isolation agar (BD Difco, Sparks, Maryland, USA). For fungi, 1 g of soil was incubated in medium on a shaker table (150 rpm) before plating dilutions onto R2 agar or 1% maltose agar containing antibiotics (50 ng/mL of both tetracycline and streptomycin). Enrichments were incubated at a range of temperatures (4°–25°C), in some cases for periods of up to one year. We supplemented our culture collection with fungal strains from the USDA Forest Products Laboratory (Madi-

son, Wisconsin, USA) and a few well-characterized bacterial strains from other laboratories. All populations were purified via multiple transfers of single colonies or hyphal strands, and then cryogenically preserved in 20% glycerol at −80°C for later use in microcosm experiments. Additional information concerning the strains, including accession numbers, can be found in Appendix A.

We identified each microbial strain by direct sequencing of its DNA. We obtained nucleic acids from log phase cultures using phenol:chloroform extraction. We used 5 ng of the this DNA as a template in a polymerase chain reaction (PCR) with primers that targeted the 16S rRNA gene for bacteria (8F and 1492R) or the internal transcribed spacer (ITS) region of the rRNA gene for fungi (ITS1 and ITS4). The resulting PCR products were sequenced at the Research Technology Support Facility (RTSF) at Michigan State University (East Lansing, Michigan, USA). We determined the taxonomy of each bacterial isolate using the classifier tool in the Ribosomal Database Project (Wang et al. 2007). For fungi, we determined the taxonomic identity of each isolate by matching our sequences to the most closely related cultured representative using the BLAST database (*available online*).[6] To visualize the diversity and phylogenetic relationships among isolates in our collection, we constructed neighbor-joining trees from aligned sequences in ClustalW (*available online*).[7]

Physiological response curves

We developed a microcosm system to quantify the physiological response of each isolate to a controlled soil moisture gradient. To eliminate contamination, we used an artificial soil matrix comprised of 70% quartz sand, 20% kaolinite clay, and 10% bentonite clay (all from Sigma-Aldrich, St. Louis, Missouri, USA). We washed the sand with 1% HCl followed by three rinses of distilled H_2O. We ensured that the clays were homoionic by washing them three times in 0.1 mol/L $CaCl_2$ (pH 7). The sand and clays were dried at 100°C for 24 h prior to being mixed and dispensed (10 g) into 25-mL glass scintillation vials. After autoclaving the vials, we aseptically mixed 300 mg of R2B medium (BD Difco, Sparks, Maryland, USA) into each microcosm as the sole resource. We then established a moisture gradient by manipulating the water potential of the soil microcosms. Water potential refers to the energy status of water, which is strongly influenced by its adherence to particles in the soil matrix. Because soil organisms directly experience these physical forces, water potential is the preferred way to express the effects of moisture on microbial physiology (Or et al. 2007). We manipulated water potential in each microcosm using a water-retention curve that equated volumetric water content (cm^3 H_2O/cm^3 soil) with water potential (MPa) for the artificial soil matrix. We measured soil water potential with a WP4-T Dewpoint Meter for values ranging from −0.25 to −4.15 MPa, and a T5 Mini Tensiometer attached to an Infield 7 Datalogger for values ranging from −0.0005 to −0.25 MPa (Decagon Devices, Pullman, Washington, USA).

We inoculated each microbial strain (100 μL of log phase culture) into a set of microcosms that captured a broad moisture gradient. The moisture gradient had 11 water potential levels ranging from −0.0005 MPa (wettest) to −4.15 MPa (driest). The microcosms were sealed with a septum cap and incubated at 25°C for 48–96 h. There was no measurable loss of water from the microcosms over the incubation period. We quantified microbial respiration as the amount of CO_2 that evolved in the headspace during the incubation using a LI-820 infrared gas analyzer (LI-COR, Lincoln, Nebraska, USA). Although soil respiration can be decoupled from anabolic processes, our results revealed that respiration and growth (measured using quantitative PCR and plate counting techniques) were positively correlated (Appendix B). Thus, we interpret respiration not only as a functional process (i.e., the mineralization of organic carbon), but also as an indicator of microbial fitness or performance. We constructed physiological response curves for 45 microbial isolates. On average, each response curve was comprised of 18 respiration measurements along the moisture gradient.

Niche parameters

We used maximum likelihood estimation to characterize the physiological response curve of each microbial strain along the experimental moisture gradient. As expected, preliminary data revealed that microbial respiration generally declined with decreasing water potential. However, soil microbial activity is not always maximized under the wettest conditions (Paul and Clark 1996), and we often observed peaks of respiration at intermediate water potentials. Therefore, we used the following function, which provided flexibility and produced ecologically meaningful niche parameters:

$$R = R_{\max}\left(\exp\left[-\left|\frac{W - W_{\text{opt}}}{\sigma}\right|^{\tau}\right]\right). \quad (1)$$

In this model, R is the respiration rate; $R_{\max}$ is the maximum respiration rate; W is soil water potential; W_{opt} is the soil water potential corresponding to the maximum respiration rate (i.e., the optimum); σ describes the rate that respiration declines as a strain moves away from W_{opt}, which is used to estimate niche breadth; and τ is the kernel that defines the general shape of the physiological response curve. For example, when $\tau = 2$, the function is Gaussian, and when $\tau = 1$, the function is negative exponential (Pigolotti et al. 2010). With these parameters, we then defined niche breadth (b) as:

$$b = \sigma(-\log_{10} x)^{1/\tau} \quad (2)$$

[6] http://blast.ncbi.nlm.nih.gov
[7] www.clustal.org

where x defines a range of water potential based on a proportion of R_{max}. We assigned a value of 0.5 to x so that niche breadth describes water potential where the respiration rate of a microbial strain is $\geq$50% of its maximum R_{max}. Because water potential could not be >0 in our system, we constrained the statistical optimization so that W_{opt} was always within the range of manipulated moisture levels. We used the maximum likelihood package (bblme) in R (R Core Development Team 2009) to estimate the niche parameters for the physiological response curve associated with each of the microbial strains.

Functional traits

For each strain, we measured a number of traits that we hypothesized would help explain variability in the physiological response of microbial populations to the experimental moisture gradient. First, we performed growth curve experiments to estimate the maximum specific growth rate (μ_{max}) and lag time of each strain (Lennon et al. 2007) as these traits could potentially reflect a moisture stress-competition trade-off (Grime 1979). Briefly, we fitted parameters to the change in biomass (measured as the optical density at 600 nm [OD600]) over time (48–96 h) in test tubes ($n = 3$) containing 5 mL of R2B media after being inoculated with a small volume (50 mL) of log phase culture. Second, soil moisture content is often negatively correlated with oxygen availability. As such, microorganisms that are tolerant of low oxygen concentrations may perform well under moist soil conditions. To assess this metabolic flexibility, we estimated the microaerotolerance of each strain as the ratio of biomass under hypoxic (2% O_2) and aerobic (21.5% O_2) conditions after 48 h of incubation in R2B medium. For the hypoxic conditions, we adjusted the O_2 concentrations in septum-sealed incubation vials by displacing a fraction of the headspace with 0.1-μm-filtered N_2 gas. Third, moisture content controls microbial motility in the soil matrix, which in turn may influence an organism's ability to access resources required for growth and respiration. Therefore, we estimated motility by spotting 5 mL of a log phase culture on the middle of a semi-solid agar plate (Niu et al. 2005). We then quantified motility as the diameter of microbial growth on the plate over 96 h. Last, it has been hypothesized that production of exopolymeric substances (EPS), which are used in the production of biofilms, can help microorganisms tolerate desiccation stress (Roberson and Firestone 1992, Or et al. 2007). We estimated biofilm production using the Crystal Violet assay (O'Toole et al. 1999) after incubating each isolate in 96 well plates for 48 h. All of the incubations used to quantify physiological traits were conducted at 25°C.

Phylogenetic signal

Phylogenetic signal is a pattern that arises when closely related taxa are more ecologically similar to one another than distantly related taxa. In addition to testing for the presence vs. absence of this pattern, we identified the taxonomic scale at which niche parameters and functional traits exhibited phylogenetic signal. To do this, we partitioned the variance of each niche parameter and functional trait at seven taxonomic levels (i.e., domain, phylum, class, order, family, genus, and strain) using a hierarchical linear model (lmer in the lme4 package) for R (Bates and Maechler 2009). We randomly permuted the observed values among all microbial strains ($n = 10\,000$) and recalculated the variance explained at each taxonomic level. We rejected the null hypothesis (i.e., no signal) if the observed level of explained variance at a given taxonomic level fell outside the 95% confidence intervals of explained variance that were generated from our randomizations.

Results

Microbial strains

Our culture collection of soil microorganisms contained 23 strains of bacteria and 22 strains of fungi. For all but two strains, we were able to assign bacteria to the genus level using the Ribosomal Database Project (RDP) classifier with bootstrap support exceeding an 80% confidence threshold. Taxonomic assignments for bacterial strains KBS0721 and KBS0717 were ambiguous at the genus level using the RDP classifier, so we identified their most closely related cultured representatives using BLAST (*Cloacibacterium* [Bacteroidetes] and *Bacillus* [Firmicutes], respectively). The bacterial collection contained representatives from 5 phyla (Acidobacteria, Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria), 7 classes, 9 orders, 15 families, and 19 genera (Fig. 1). We defined Gram-positive bacteria as isolates belonging to Actinobacteria and Firmicutes ($n = 9$) and Gram-negative bacteria as isolates belonging to the remaining bacterial phyla. For the fungal strains, BLAST results yielded high query coverage, high maximum identity, and extremely low E values (a parameter describing the probability of obtaining a sequence from BLAST database by chance), providing confidence in our taxonomic assignments. The fungal collection contained representatives from 3 phyla (Basidiomycota, Ascomycota, and Zygomycota), 8 classes, 10 orders, 14 families, and 17 genera (Fig. 1). More detail on the taxonomy of the culture collection can be found in Appendix A.

Physiological response curves

Our statistical model (Eqs. 1 and 2) was effective at capturing diverse physiological responses of our microbial strains to the experimental moisture gradient (Fig. 2). In general, respiration declined with decreasing water potential. However, there was substantial variability in the three parameters that described a given strain's moisture niche. The optimal water potential (W_{opt}) for some strains occurred under the wettest conditions (Fig. 2b), but other taxa performed best in drier soils (Fig.

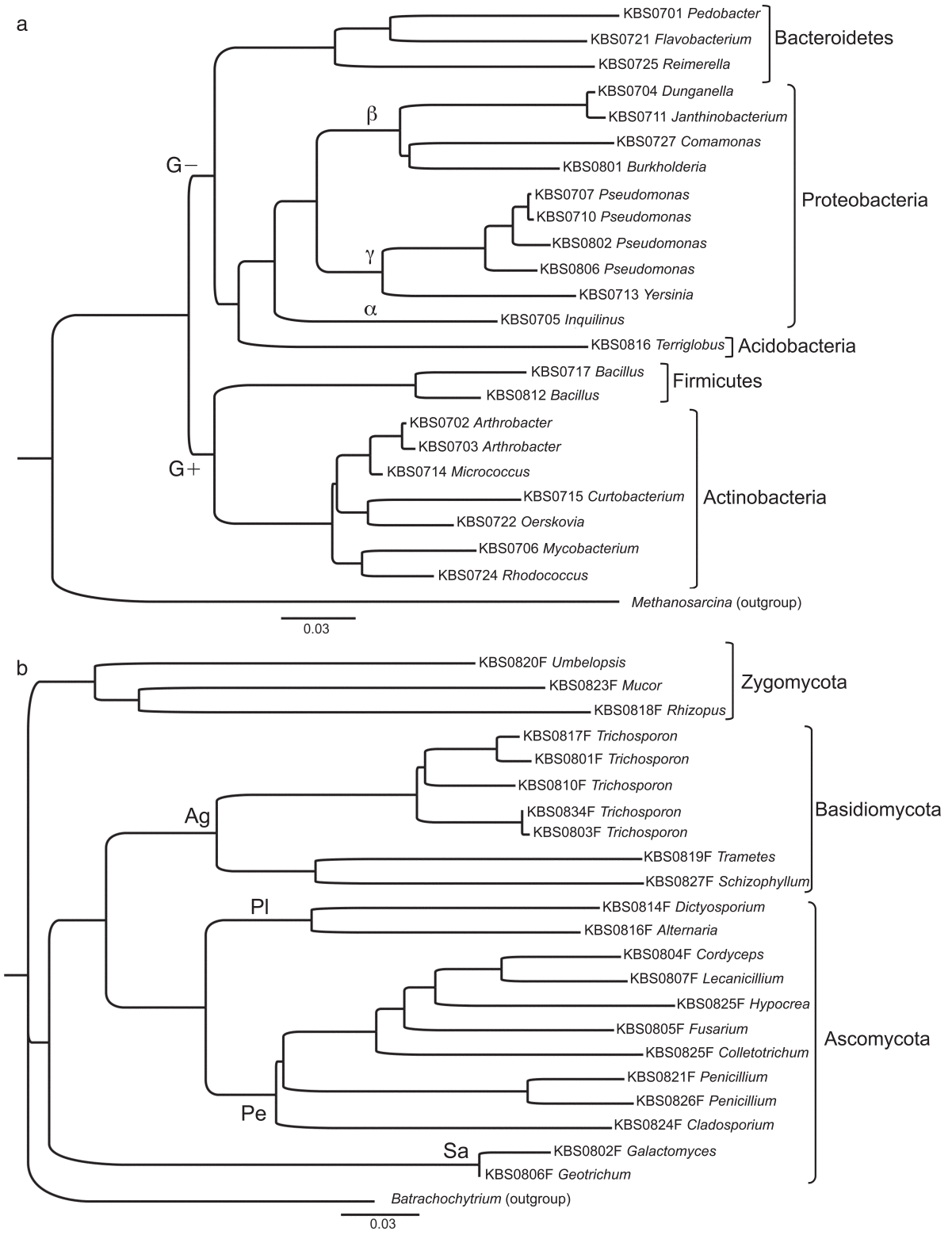

FIG. 1. Phylogenetic trees representing the diversity of (a) bacteria and (b) fungi in the culture collection used to map the niches of microorganisms along a soil moisture gradient. Trees were constructed from aligned sequences (16S rRNA for bacteria; ITS for fungi) using neighbor-joining methods. Brackets to the right of the branches include strains that fall within a given phylum. The following symbols designate groupings of isolates in the bacterial tree: G+, Gram positive; G–, Gram negative; β, Betaproteobacteria; γ, Gammaproteobacteria; and α, Alphaproteobacteria. The following aabreviations designate groupings of isolates in the fungal tree: Ag, Agaricomycotina; Pl, Pleosporales; Pe, Pezizomycotina; and Sa, Saccharomycotina.

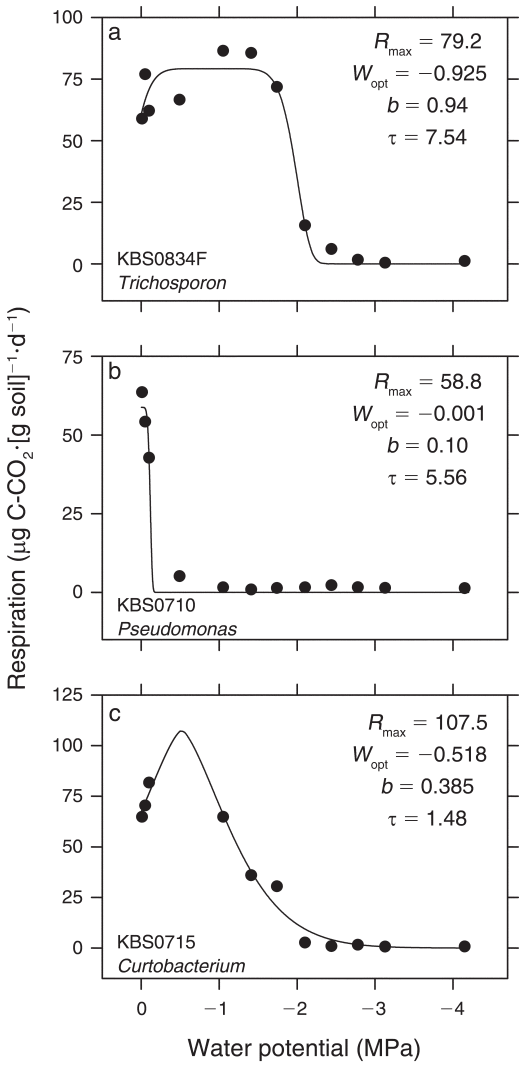

FIG. 2. Physiological response curves for three microbial isolates representing some of the variability in respiration rates along the soil moisture gradient established in our experimental microcosms. The values in the top right of each panel represent niche parameter values that were fit to the data using Eqs. 1 and 2. Key to abbreviations: R_{max}, maximum respiration rate; W_{opt}, optimum water potential; b, niche breadth; and τ, kernel that defines the general shape of the physiological response curve. The strain code and corresponding genus name are located in the bottom-left corner of each panel. *Trichosporon* is a Basidiomycete yeast fungus, *Pseudomonas* is a type of Gram-negative bacteria belonging to the Gammaproteobacteria, and *Curtobacterium* is a type of Gram-positive bacteria in the Actinobacteria phylum.

2a, c). Across all strains, the optimum water potential was −3.2 ± 0.046 MPa (mean ± SEM); a value that is significantly more negative (one-sample t test, $t_{44} = 6.78$, $P < 0.001$) than the soil microbial W_{opt} suggested elsewhere (–0.01 MPa; Paul and Clark 1996). There was also a large amount of variability in niche breadth (b), the parameter that describes the tolerance of a microbial strain to variation in water potential. Some strains were highly specialized and their respiration rate was restricted to a narrow range of soil moisture (minimum b = 0.0001 MPa), while other taxa could tolerate a much broader range of water potentials (maximum $b = 1.135$ MPa). We estimated the lower limits of moisture on microbial respiration by changing x in Eq. 2 from 0.5 to 0.05. This defined a range of water potentials where the respiration rates of each strain were ≥95% of R_{max}. With the exception of one bacterial strain (KBS0812, *Bacillus* sp.) and two fungal strains (KBS0805F, *Trichosporon* sp.), respiration rates of our microbial strains were restricted to water potentials that were >−2.0 MPa. The maximum respiration rate (R_{max}) ranged from 10.8 to 140.3 mg C-CO_2·[g soil]$^{-1}$·d^{-1}.

We detected significant correlations among all of the niche parameters generated from the physiological response curves (Fig. 3, Table 1). Most striking was the strong positive relationship between niche breadth (b) and optimum water potential (W_{opt}):

$$b = 0.02 - 1.01(W_{opt}) \qquad (r^2 = 0.90,\ P < 0.0001). \quad (3)$$

Although a much weaker relationship, the maximum respiration (R_{max}) rate increased linearly with increasing niche breadth:

$$R_{max} = 52.4 + 31.2(b) \qquad (r^2 = 0.10,\ P = 0.03). \quad (4)$$

Last, we observed a humped-shaped relationship between the maximum respiration rate and optimum water potential:

$$R_{max} = 40.5 + 136.9(W_{opt}) - 108.7(W_{opt})^2 \qquad (5)$$
$$(r^2 = 0.28,\ P = 0.009).$$

Using Akaike's information criterion (AIC), we determined that the statistical model including a quadratic term (Eq. 5) was superior to the simpler linear model (ΔAIC = 35.2) when describing the relationship between R_{max} and W_{opt}.

Phylogenetic signal of niche parameters and functional traits

A significant fraction of variation for all three niche parameters (W_{opt}, b, and R_{max}) could be explained at relatively coarse taxonomic scales (Fig. 4). Based on our randomizations, we expected that 58–65% of the variability in our niche parameters would occur at the strain level. However, the amount of variation explained at the strain level (21–29%) was significantly less than what was expected by chance. Instead, the hierarchical analysis partitioned 58% of the variation in niche breadth (b) and 52% of the variation in optimum (W_{opt}) at the phylum level. Strains belonging to the Firmicutes phylum (i.e., *Bacillus* isolates) had the driest optimum (–0.97 ± 0.100 MPa) and the widest niche breadth (1.0 ± 0.133 MPa), while Actinobacteria, the other phylum containing Gram-positive bacteria, had substantially wetter optima (–0.16 ± 0.073 MPa) and narrower niche breadths (0.15 ± 0.073 MPa). With the exception of the

single Acidobacteria strain, we found that the Gram-negative bacteria (Bacteroidetes and Proteobacteria phyla) had the wettest optima (−0.007 to −0.08 MPa) and narrowest niche breadth (0.01–0.06 MPa). Although 57% of the variation in R_{max} could be explained at the genus level, 22% of the variation in this niche parameter could be accounted for at the domain level, with fungi having an R_{max} that was double that of bacteria (Figs. 4 and 5).

In addition, there was a phylogenetic signal associated with some of the functional traits measured on our microbial strains (Fig. 6). For example, 30% of the variation in biofilm production could be partitioned at the phylum level. Biofilm production was the only functional trait that was significantly correlated with any of the niche parameters describing the microbial responses to the moisture gradient (Table 1). Specifically, biofilm production was positively correlated with both W_{opt} ($r = 0.42$, $P = 0.005$) and niche breadth ($r = 0.39$, $P = 0.009$). We calculated partial correlations to evaluate the independent effects of biofilm production on niche breadth and W_{opt}. Although there was a stronger partial correlation between W_{opt} and biofilm production when holding niche breadth constant ($r = 0.16$, $P = 0.284$) than there was between niche breadth and biofilm production when holding W_{opt} constant ($r = -0.02$, $P = 0.897$), neither of these relationships was significant on their own. Also, biofilm production was negatively correlated with lag time ($r = -0.27$, $P = 0.098$) and microaerotolerance ($r = -0.31$, $P = 0.053$). Last, a significant fraction of the variation in lag time could be explained at the domain (17%), class (28%), and strain (4%) level, while approximately one-third of the variability in motility could be accounted for at the class level.

Discussion

Moisture controls the distribution, abundance, and activity of nearly all life forms, including microorganisms (Potts 1994). Despite this, very few studies have compared the moisture niche for different groups of microorganisms. Furthermore, it is unclear whether or not there are common microbial traits or adaptations that have evolved to contend with moisture stress. To address these issues, we derived niche parameters from physiological response curves for a collection of bacteria and fungi along an experimental soil moisture gradient. Our soil microbial isolates exhibited a wide range of responses to the moisture gradient and suggest that some taxa may be able to coexist by partitioning the moisture niche axis. For example, we identified dry-adapted generalists that tolerated a broad range of water potentials, along with wet-adapted specialists whose metabolism was restricted to high water potentials. These contrasting ecological strategies had a phylogenetic signal that could be linked to the distribution of functional traits. In particular, our results suggest that the allocation of resources towards biofilm production

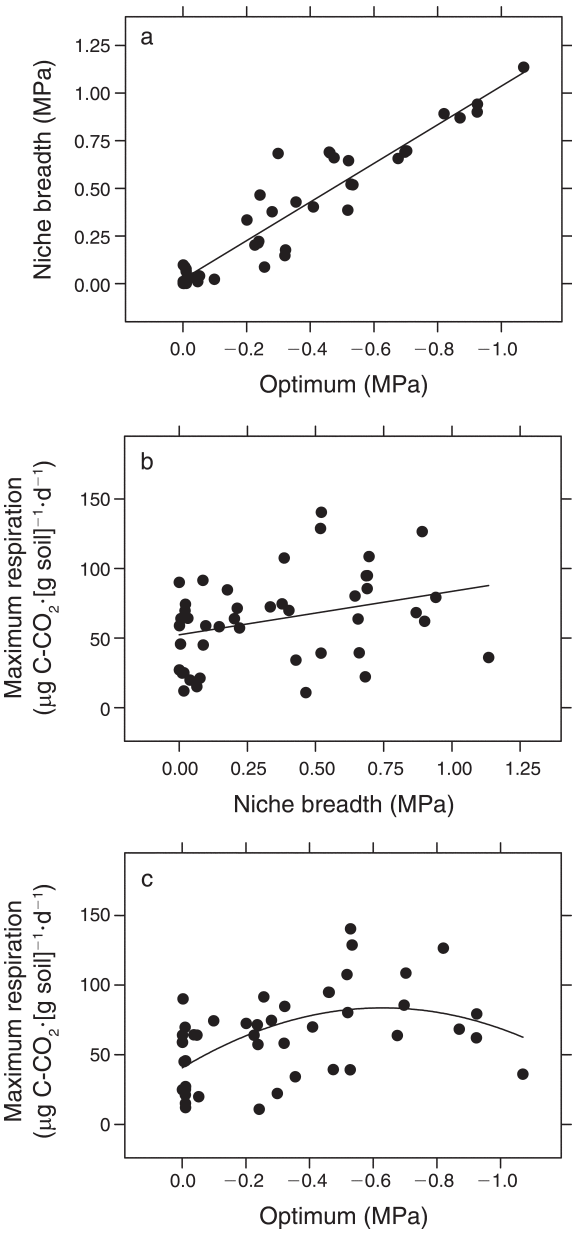

Fig. 3. Correlations between the niche parameters generated for the physiological response curves for the fungal and bacterial isolates used in this study. Niche parameters were generated using Eqs. 1 and 2 after measuring respiration rates of each isolate along a soil moisture gradient.

(a trait that appears to be conserved at a coarse taxonomic scale) may help soil microorganisms contend with desiccation stress. Together, our results help define functional groups of microorganisms that are likely to respond to changing soil moisture regimes.

Physiological limits to soil moisture

Physiological response curves were extremely variable among strains of soil microorganisms, but in general, microbial metabolism declined nonlinearly with decreas-

TABLE 1. Pairwise Pearson correlation coefficients (r) between niche parameters and functional traits measured on a collection of soil microbial isolates.

Trait	R_{max}	W_{opt}	b	O_2-Tol	μ_{max}	Lag	Biofilm	Motility
R_{max}	1	−0.43**	0.32*	0.03	0.19	−0.28†	−0.05	0.15
W_{opt}		1	−0.95***	−0.06	0.02	0.12	0.42**	0.10
b			1	0.02	−0.04	−0.01	0.39**	0.06
O_2-Tol				1	0.21	0.25†	−0.31†	0.14
μ_{max}					1	0.48**	−0.24	−0.03
Lag						1	−0.27†	−0.37*
Biofilm							1	0.23
Motility								1

Notes: Niche parameter abbreviations are: R_{max}, maximum respiration; W_{opt}, optimum water potential; and b, niche breadth. Functional trait abbreviations are: O_2-Tol, microaerotolerance; μ_{max}, maximum specific growth rate; Lag, lag time; Biofilm, biofilm production; and Motility, motility.

† $P = 0.1$–0.05; * $P = 0.05$–0.01; ** $P = 0.01$–0.001; *** $P < 0.001$.

ing water potential (Fig. 2). It has been suggested that soil microbial activity is inhibited at water potentials below −0.5 MPa owing in part to physical constraints associated with substrate transport and cell motility (Fenchel et al. 1998). However, we detected respiration for many of our isolates in much drier soils (−2.0 MPa). It is important to note that, even though they may not respire at detectable levels, many microorganisms can survive under much lower water potentials. For example, *Arthrobacter crystallopoietes*, a soil bacterium (Actinobacterium) that is closely related to strains used in our study (KBS0702 and KBS0703), tolerated extreme desiccation for at least six months with minimal loss of viability (Boylen 1973). Similarly, a number of the strains used in our study could be resuscitated after being exposed to air-dried conditions for six weeks (J. T. Lennon, *unpublished data*). On the opposite end of the moisture gradient, we found that most strains performed suboptimally under the wettest soil conditions. It has been hypothesized that the optimal water potential for soil microbial activity is approximately −0.01 MPa (Paul and Clark 1996). However, across all strains, we observed that the optimum water potential (W_{opt}) for our soil isolates was significantly drier (−0.3 MPa).

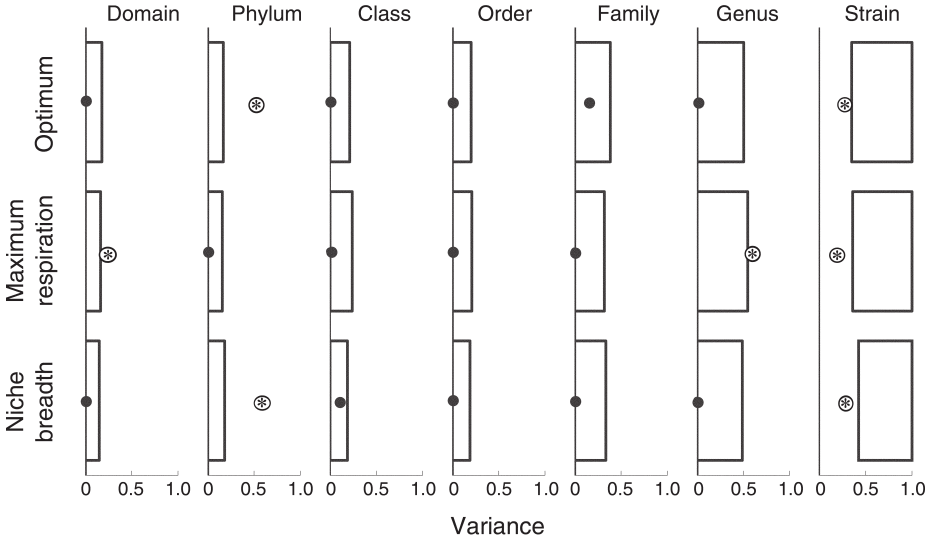

FIG. 4. Phylogenetic signal associated with the moisture niche parameters (W_{opt}, optimum water potential; R_{max}, maximum respiration rate; b, niche breadth) extracted from physiological response curves that were generated using a diverse collection of soil bacterial and fungal isolates. Boxes represent the ranges of expected variation based on randomization of niche parameters given the phylogenetic structure of our isolates. Symbols represent the observed amount of variation explained at each taxonomic scale. Solid symbols correspond to observations that fell within the 95% confidence intervals generated from our randomizations (i.e., not significant); open symbols with asterisks correspond to observations that fell outside the 95% confidence intervals generated from our randomizations (i.e., significant). When observed variance is significantly greater than what is expected by chance, results suggest that there has been diversification of the moisture niche at a given taxonomic level. When observed variance is significantly less than what is expected by chance, results suggest that the moisture niche has been conserved at a given taxonomic level.

These findings suggest that the activity of soil microorganisms is inhibited by high water potentials, possibly owing to the limited diffusion of oxygen that occurs when soils periodically experience saturated conditions (Pett-Ridge and Firestone 2005).

Niche distributions: evidence for generalists and specialists

Our statistical model captured variability among strains and allowed us to estimate parameters that characterized the microbial moisture niche. First, the optimal water potential (W_{opt}) spanned a wide range of values (−0.0005 to −1.0 MPa), providing evidence that soil microorganisms are adapted to different soil water potentials. These differences in W_{opt} suggest that some microbial taxa may be able to coexist through the partitioning of the soil moisture niche-axis in either space or time. Second, we observed a strong correlation between W_{opt} and niche breadth across our strains (Fig. 3a). Very few isolates deviated from this relationship. The relationship between these two niche parameters suggests dry-adapted populations are generalists (i.e., wide niche breadth), while wet-adapted populations are specialists (narrow niche breadth). However, this finding is inconsistent with previous classification schemes for soil microorganisms. It has been hypothesized that niche breadth and moisture optimum of microbial taxa can be decoupled (Griffin 1981), but we found no evidence for dry-adapted specialists or wet-adapted generalists. It is possible that soil microorganisms with different moisture niches could be isolated using alternate enrichment conditions or by sampling different ecosystems. Alternatively, the strong coupling between W_{opt} and niche breadth may reflect the fact that microorganisms living in dry soil environments must contend with more dynamic soil moisture regimes, whereas microorganisms from mesic environments tend to experience more stable soil moisture conditions (see Prentice et al. 1992).

Contrary to our expectations, generalist taxa performed better than specialist taxa. Although the relationship was somewhat weak, we found that the maximum respiration rate (R_{max}) was positively correlated with niche breadth (Fig. 3b). If we treat respiration as a proxy for growth or fitness, our results suggest that generalist taxa should outperform specialist taxa. This finding is at odds with ecological and evolutionary theory, which predicts that there should be a cost associated with generalist strategies (e.g., Wilson and Yoshimura 1994). One explanation for this pattern may be reflected in the hump-shaped relationship between W_{opt} and R_{max} (Fig. 3c), which suggests that the performance of soil microorganisms is maximized for taxa with intermediate water potential optima. Alternatively, other important environmental variables (e.g., temperature, resources, pH) tend to covary with water potential, which may place constraints on the shape of the moisture niche and help explain the lack of a trade-off between specialists and generalist strategies.

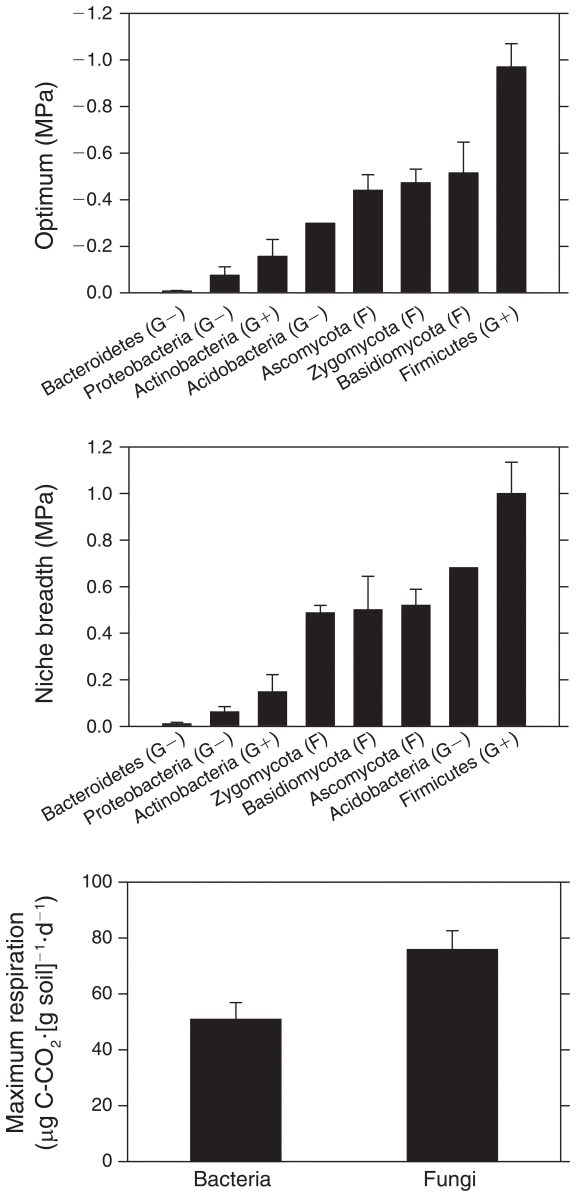

FIG. 5. Distribution of moisture niche parameters for different groups of microorganisms based on the partitioning of variance at different taxonomic scales. Abbreviations are: G+, Gram-positive bacteria; G–, Gram-negative bacteria; and F, fungi. Histogram bars show means ± SEM.

Phylogenetic signal of the moisture niche

Our results demonstrate that parameters describing the moisture niche of soil microorganisms are conserved at a relatively coarse taxonomic scale. Randomizations based on the underlying phylogenetic structure of our data set predicted that 58–65% of the variation in the niche parameters would be accounted for at the strain level. Such findings would be consistent with the idea that soil microorganisms have undergone relatively recent within-clade adaptation to moisture variability.

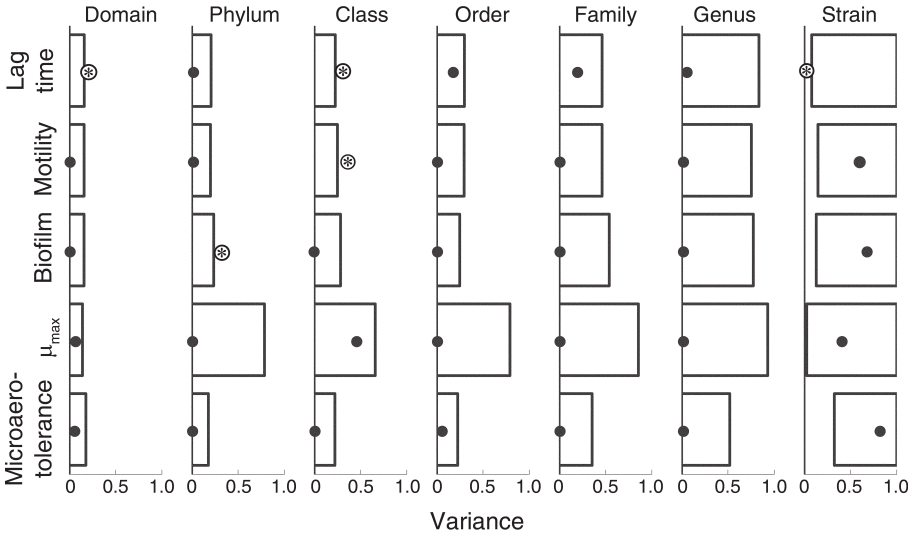

FIG. 6. Phylogenetic signal associated with functional traits for a diverse collection of soil bacterial and fungal isolates. Lag time and μ_{max} (maximum specific growth rate) are traits corresponding to parameters extracted from population growth curves. Biofilm refers to the amount of biofilm produced by each strain. Motility reflects the potential for an isolate to move within a soil matrix. Microaerotolerance assesses a strain's ability to grow under reduced (2%) relative to ambient (21.5%) oxygen concentrations. See Fig. 4 captions for a description of boxes and symbols.

This type of ecological differentiation among closely related microorganisms has been documented in other systems (Hunt et al. 2008). In contrast, we observed much less variation in niche parameters at the strain level than expected. Instead, our results suggest that adaptation to soil moisture is highly conserved. This conclusion is supported by the fact hat more than half of the variation in niche breadth (b) and optimum water potential (W_{opt}) could be assigned at the phylum level, while statistically significant amounts of variation in maximum respiration rate (R_{max}) could be explained at both the domain and genus level (22% and 57%, respectively). Our findings lend support to the view that there is ecological coherence at high taxonomic ranks (Philippot et al. 2010), which means that coarse-level taxonomy may be useful for making generalizations about the functioning of microbial taxa, at least in the context of some environmental drivers (i.e., water availability).

Our results are consistent with some general notions about the sensitivity of different groups of soil microorganisms to moisture variability. Owing to the thick peptidoglycan layer contained in their cell walls, Gram-positive bacteria are thought to be more resistant to desiccation stress than Gram-negative bacteria (see Schimel et al. 2007). Our results partially support this hypothesis. The Gram-positive Firmicutes (i.e., *Bacillus* strains) had the driest optima and broadest niche breadths of all our isolates, but the Gram-positive Actinobacteria had a relatively wet optima and narrow niche breadths (Fig. 6). Fungi may be well adapted to desiccation stress, in part, because hyphae-forming taxa can "scavenge" water by integrating over larger soil volumes as compared to individual cells (Frey 2007). Further, within the fungi, Ascomycetes and Basidiomycetes are thought to be more tolerant to dry conditions than Zygomycetes (Dix 1984). Based on the strains used in this study, our results indicate that, overall, fungi have relatively dry optima and wide niche breadths, but there is no evidence that the moisture niche varies among different fungal phyla (Fig. 5). For Gram-negative bacteria, our results are consistent with the view that these microorganisms are sensitive to desiccation and perform better under wetter soil conditions (Schimel et al. 2007), with the exception of the single Acidobacteria isolate. Although we are not aware of any bias in our cultivation strategy that would influence the moisture niche parameters, our results are based on a somewhat limited number of isolates. The decision to include representative isolates from many different phyla came at a reduction in coverage. Therefore, an appropriate amount of caution should be used when making generalizations about phyla that most likely contain thousands of taxa. Nevertheless, our results aid in the identification of microbial functional groups and contribute to a growing body of literature on the natural history of microorganisms (e.g., Newton et al. 2011).

Functional traits associated with the microbial moisture niche

There are many microbial traits that are hypothesized to be involved in adaptation to soil moisture (e.g., Potts 1994). One trait that was strongly correlated with the niche parameters of our soil microbial isolates was biofilm production. Specifically, strains that were capable of producing more biofilms had drier W_{opt}

PLATE 1. Soil bacteria and fungi were isolated from the W. K. Kellogg Biological Station (KBS) Long-Term Ecological Research (LTER) site. Photo credit: Kurt Stepnitz, Michigan State University.

and a wider niche breadth (Table 1). Furthermore, biofilm production was phylogenetically conserved at a coarse taxonomic scale (Fig. 6), similar to the moisture niche parameters. Biofilms are produced by microorganisms through the release of exopolymeric substances (EPS; polysaccharides, nucleic acids, lipids, and proteins) into their surrounding environment. EPS production allows cells to adhere to one another and to surfaces, such as soil particles. The resulting biofilm matrix provides microorganisms with physical protection from grazers, infectious viruses, and antibiotics (Flemming and Wingender 2010). In addition, many biofilms have hydrophilic properties that reduce localized fluctuations in water availability (Roberson and Firestone 1992), which minimizes microbial desiccation stress (Chang et al. 2007). However, the generation of biofilms requires an energetic investment from EPS-producing microorganisms. This cost could be reflected in reduced growth, at least under some conditions, depending on whether biofilm production is induced or constitutively expressed. We found that biofilm production was positively correlated with lag time (Table 1), which means that it took longer for biofilm-producing strains to enter exponential growth phase. In addition, biofilm production was negatively correlated with a strain's microaerotolerance, which is consistent with some observations that biofilm production is inhibited in low-oxygen environments (Reuter et al. 2010). Together, our results suggest that microorganisms may experience trade-offs between the benefits and costs of producing biofilms in soil environments with varying moisture content.

In addition to the functional traits examined in our study, there are other adaptations that may influence the moisture niche of soil microorganisms. First, it is well established that some microorganisms maintain osmotic equilibrium with their environment through the production and regulation of compatible solutes, such as sugars, polyols, and amino acids (see Schimel et al. 2007). Second, soil microorganisms may be able to tolerate unfavorable moisture conditions by entering a reversible state of reduced metabolic activity, or dormancy (Lennon and Jones 2011). Last, evidence suggests that some soil microorganisms can reduce oxidative damage that typically accompanies desiccation stress by altering their intracellular stoichiometry (Fredrickson et al. 2008). Additional research is needed to address the ecological importance and phylogenetic distribution of these functional traits in relation to soil moisture variability.

Implications for the biogeographic distributions of microorganisms

The inventory of microbial diversity has grown exponentially over the past two decades, owing in part to the development of new, high-throughput sequencing technology. In many cases, however, we still lack knowledge about the biotic and abiotic factors and processes that determine the distribution and functioning of microbial communities. Although microbial biogeography appears to be influenced by neutral (or stochastic) processes (Dumbrell et al. 2010, Ofiţeru et al. 2010), growing evidence suggests that microbial communities are structured at least in part by niche (or deterministic) processes. In particular, soil microorgan-

isms are sensitive to soil moisture and precipitation variability (Williams 2007, Blankinship et al. 2011, Hawkes et al. 2011), and some studies have shown that the distribution of bacterial assemblages tend to be correlated with natural soil moisture gradients (Steinberger et al. 1999, Fierer and Jackson 2006, Bryant et al. 2008). In this study, we demonstrated that there are generalist and specialist strategies for contending with soil moisture variability. Our findings set the stage for determining whether key functional traits, such as biofilm production, are important in determining taxa co-occurrence patterns along moisture gradients. Last, our ability to identify microbial functional groups based on taxonomy and traits provides a basis for making predictions about how microbial communities will respond (both compositionally and functionally) to existing and future soil moisture regimes.

Acknowledgments

We acknowledge S. Eichorst, T. Schmidt, L. Halverson, R. Kolter, H. Vlamakis, G. O'Toole, and D. Lindner for sharing microbial isolates. In addition, we thank S. Placella, S. Evans, and J. Palange for comments on an early version of the manuscript. This project was supported with funding from the Rackham Research Endowment and the Michigan Agricultural Experiment Station (MAES); National Research Initiative Grants (2008-35107-04481 and 2011-67019-30225) from the USDA National Institute of Food and Agriculture; and the National Science Foundation (DEB-0842441). This article is Kellogg Biological Station contribution number 1581.

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Supplemental Material

Appendix A

Information pertaining to the bacterial and fungal isolates used in our study (*Ecological Archives* E093-165-A1).

Appendix B

The relationships between population growth rates and respiration rates for a subset of the bacterial strains used in this study (*Ecological Archives* E093-165-A2).