

Consistently inconsistent drivers of microbial diversity and abundance at macroecological scales

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Abstract. Macroecology seeks to understand broad-scale patterns in the diversity and abundance of organisms, but macroecologists typically study aboveground macroorganisms. Belowground organisms regulate numerous ecosystem functions, yet we lack understanding of what drives their diversity. Here, we examine the controls on belowground diversity along latitudinal and elevational gradients. We performed a global meta-analysis of 325 soil communities across 20 studies conducted along temperature and soil pH gradients. Belowground taxa, whether bacterial or fungal, observed along a given gradient of temperature or soil pH were equally likely to show a linear increase, linear decrease, humped pattern, trough-shaped pattern, or no pattern in diversity along the gradient. Land-use intensity weakly affected the diversity-temperature relationship, but no other factor did so. Our study highlights disparities among diversity patterns of soil microbial communities. Belowground diversity may be controlled by the associated climatic and historical contexts of particular gradients, by factors not typically measured in community-level studies, or by processes operating at scales that do not match the temporal and spatial scales under study. Because these organisms are responsible for a suite of key processes, understanding the drivers of their distribution and diversity is fundamental to understanding the functioning of ecosystems.

Key words: *belowground communities; gradients; latitudinal diversity gradient; macroecology meta-analysis; microbial diversity; soil.*

INTRODUCTION

One of the most frequently asked questions, at least at global scales, is “why does the number of species vary from place to place on the planet?” It is clear that biodiversity tends to increase when moving from the poles to the tropics (Hillebrand 2004). In addition, though many early authors posited that diversity along elevational gradients simply mirrored latitudinal gradients in that diversity declined linearly with elevation (MacArthur 1972, Brown et al. 2004), biodiversity in most cases tends to peak at mid-elevations (Sanders and Rahbek 2012, Sundqvist et al. 2013). These latitudinal and elevational diversity gradients have been well

described and synthesized for aboveground organisms (Rahbek 1995, Hillebrand 2004, Westgate et al. 2014). However, how variation in the diversity of organisms belowground varies spatially has been less explored, even though soil organisms regulate many of the ecosystem services humans rely on (Fierer et al. 2009, Peay et al. 2010, Tedersoo et al. 2014, Jing et al. 2015).

Based on the accumulated evidence for the diversity of life aboveground, the operating assumption has been that diversity belowground increases toward the equator and peaks at intermediate elevations. However, a few recent studies of particular taxa in particular places have cast doubt on these assumptions (Fierer and Jackson 2006, Tedersoo et al. 2014, Beck et al. 2015), though no global syntheses of such studies have been carried out. Because most of terrestrial biodiversity is belowground, such a study would increase our understanding of the factors that govern the distribution and diversity of life, both big and small, on Earth.

Of course, soil microbes, or any taxa for that matter, are not responding to “elevation” or “latitude”; instead, their diversity patterns are driven by some factor that

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covaries with latitude or elevation. One candidate for a key driver of diversity along both elevational and latitudinal gradients is temperature (Körner 2007). Indeed, temperature generally varies systematically with elevation and latitude and is often correlated with aboveground biodiversity. The strong linkages between aboveground biodiversity, and many other attributes of ecological systems, with temperature have led to the development of the metabolic theory of ecology (MTE). The MTE predicts that the metabolism of individuals, the growth of populations, and the number of species in a local community all increase exponentially with the environmental temperature. However, the diversity of soil communities could be more strongly regulated by changes in abiotic soil factors such as pH (Fierer and Jackson 2006), land use intensity (Drenovsky et al. 2010), or by smaller-scale changes in the plant community.

We conducted a meta-analysis of soil microbial diversity measurements drawn from 325 local communities to explore large-scale patterns in the diversity of belowground taxa along latitudinal and elevational gradients, and an additional 431 communities to analyze belowground abundance patterns. The studies primarily described bacterial and fungal communities along latitudinal and elevational gradients, but also include archaea, protist, and algal communities. Specifically, we explored whether general belowground diversity patterns exist along latitudinal, elevational, and soil pH gradients and what determines spatial variation in the diversity and abundance of belowground organisms. In particular, we included biome, precipitation, land-use intensity, and the percent of the gradient sampled as predictors of belowground diversity. We predicted that the diversity of belowground communities along elevational and latitudinal gradients would be driven by site-specific changes in climate, land use intensity, and soil properties, and that the effect of these properties would vary among different taxonomic groups (i.e., communities of different taxa are structured by different factors). Finally, we tested the prediction of the metabolic theory of ecology that there is a log-linear relationship between diversity and the inverse of absolute temperature.

METHODS

To synthesize and analyze patterns of belowground biodiversity across widely varying environmental conditions, biomes, and taxa, we conducted a meta-analysis of published studies (Borenstein et al. 2009). In October 2013, we conducted a literature search on ISI Web of Science using the terms “fungi,” “bacteria,” “microbe,” or “mycorrhizae” combined with “elevational gradient,” “altitudinal gradient,” or “latitudinal gradient.” The search was constrained to include only studies published between January 1988, when early work on patterns of soil microbial communities along elevational gradients began to emerge, and October 2013, when our searching of the literature began. The search yielded >10,000 articles, which we screened for

measurements of soil microbial diversity and/or abundance along latitudinal and elevational gradients. In addition, at least four microbial communities had to be sampled along an environmental gradient to be included in the meta-analysis. Studies from 58 published papers that described ~1,000 soil communities found on all continents except Australia met these criteria (Appendix S1, Metadata S1). We classified the response variables from each article in our reduced list as measures of either belowground diversity, including taxonomic and phylogenetic indices; or abundance, including microbial biomass, PLFA abundance, and fungal colonization rate. If not provided in the manuscript, we extracted mean annual air temperature (MAT) values for all sites across all the studies using the SRTM (Jarvis et al. 2008) and Bioclim (Hijmans et al. 2005) data sets. We conducted the following analyses for diversity and abundance patterns; we display diversity patterns in the manuscript and abundance patterns in the Data S1 (see below).

Meta-analysis: finding patterns that transcend study systems

We used meta-regression methods to explore relationships between abiotic factors and diversity and abundance within and among studies. Conducting a meta-regression is only possible if raw data are available from each study, as is the case here, and is preferable to comparing single effect sizes among studies (Koricheva et al. 2013). In addition, it is likely that different methodologies used to measure species richness and abundance in these communities could lead to some inconsistencies between studies. In a step toward addressing this issue, we applied a z transformation to the response variable within each study to facilitate comparisons among diversity and abundance variables measured on different scales. Doing so standardizes the variation among studies so that they are more directly comparable. However, in an ideal world, we would use the same sampling procedures across all sites in the analysis. Unfortunately, this is rarely a possibility. In addition, we z transformed the predictor variables, MAT and soil pH, so that standardized coefficients could be compared across predictors.

We fitted a linear mixed model to the diversity and abundance data, using MAT and soil pH as predictors. We excluded all data points without soil pH recorded. We included second-degree terms for both temperature and soil pH to enable detection of unimodal or troughed patterns of diversity or abundance with changing temperature or soil pH. We fit a hierarchical model with a random intercept for each study and both first-order (linear) and second-order (quadratic) terms for temperature and soil pH ($y_{ij} \sim \text{Normal}(\theta_{ij}, \sigma_j)$; $\theta_{ij} = \beta_{0j} + \beta_{11j}T_{ij} + \beta_{21j}T_{ij}^2 + \beta_{p1j}pH_{ij} + \beta_{p2j}pH_{ij}^2$). The slope coefficients for each predictor in each study were modeled as being drawn from a normal distribution with a single global mean and variance. In the above equations, y_{ij} is the response variable, either diversity or abundance, at

location i in study j , T_{ij} is the MAT at that location, and pH_{ij} is the soil pH at that location. We estimated posterior distributions for each of the parameters using Markov chain Monte Carlo (MCMC) integration. We initialized the sampling with 5,000 warmup iterations, then sampled for 25,000 iterations, with two chains per model. One model was fitted for diversity and another one was fitted for abundance. We set wide normal priors on the μ parameters, and uniform priors with a lower bound of 0 on the σ parameters.

To explore if other soil variables influenced diversity patterns, we downloaded the following SoilGrids global data layers at 250-m resolution: soil depth, soil bulk density at soil surface, soil organic carbon content at soil surface, and soil pH at soil surface. We z transformed all of the predictor variables so that effect sizes could be compared among predictors and performed a multiple regression (mixed model) that fit these predictors to the diversity and abundance response variables of interest using study as a random effect. Finally, we used AIC model selection to select the best model. We found that none of the SoilGrids variables predicted abundance. The only variable that was retained for diversity was bulk density. While diversity may increase slightly with increasing bulk density, the r^2 was prohibitively low (<0.02), thus we do not discuss these analyses. We expected these findings because the scale of the soil variable grid does not match the scale at which soil microbial biodiversity changes. We did not analyze any additional climate variables because the Worldclim variables are transformations of temperature and precipitation, which did not predict soil microbial richness or abundance in our study.

Exploring variation in belowground diversity trends among study systems

We regressed the transformed response variables extracted from each study on MAT and on soil pH within each study, using three linear models: a linear regression estimating both slope and intercept ($y_i = \beta_1 x_i + \beta_0 + \epsilon$), a quadratic regression estimating two slope parameters and an intercept ($y_i = \beta_2 x_i^2 + \beta_1 x_i + \beta_0 + \epsilon$), and an intercept-only model ($y_i = \beta_0 + \epsilon$), assuming normally distributed residuals in all cases. We calculated Akaike's information criterion (AIC) for each regression, and selected the model fit with the lowest AIC score as the best fit in each case. Next, we divided the best-fit models for each study into five groups corresponding to possible diversity patterns: linear increase (linear regression with $\beta_1 > 0$), linear decrease (linear model with $\beta_1 < 0$), hump (quadratic regression with $\beta_2 < 0$), trough (quadratic regression with $\beta_2 > 0$), and no pattern (intercept-only regression). We grouped each comparison by predictor variable, response variable, and taxonomic group measured within the study. Within each group, we assessed the number of studies within each functional form against a chi-squared distribution to determine whether any given pattern was observed

with a greater frequency than expected by chance. We used the null hypotheses that a given study was equally likely to exhibit a linear increase, linear decrease, hump-shaped trend, trough-shaped trend, or no pattern, and that bacterial and fungal communities were equally likely to exhibit a particular functional form.

Moderator analysis: factors that explain variation in trends among systems

To explore additional factors that underlie the relationship (or lack thereof) between belowground diversity and coarse-scale environmental gradients, we fit a model similar to the above but with an additional hierarchical level. We expressed the β parameters as a linear function of the following five factors: land-use intensity averaged across each study, proportion of regional temperature variation sampled, mean annual precipitation for the entire study system, taxon, and type of gradient. For example, the first-order temperature coefficient was fit as follows: $\beta_{11j} \sim \text{Normal}(a_0 + a_1 \text{taxon}_j + a_2 \text{proportion}_j + a_3 \text{gradtype}_j + a_4 \text{precip}_j + a_5 \text{landuse}_j, \sigma_{11})$.

We used the same MCMC integration procedure to estimate posterior distributions for the hyperparameters. Details on extraction of land-use intensity data and model fitting are in Appendix S2.

Test of the metabolic theory of ecology

Our final analysis tested the prediction generated by the metabolic theory of ecology that there is a negative linear relationship between the logarithm of diversity and the inverse of absolute temperature. To test this prediction, we fit a linear mixed model where inverse of Kelvin temperature was a fixed effect and study was a random effect (i.e., we assumed the same slope, but different intercepts, across studies). We calculated a confidence interval around the effect size using the bootstrap method (1,000 permutations), and we calculated the marginal R^2 value using the `r.squaredGLMM` function (MuMIn package, Stan software). We defined the models in the Stan language and interfaced the Stan software with R using the `rstan` package. We fit the model testing the metabolic theory of ecology using the `lme4` package. The 95% posterior credible intervals are reported for all parameters below.

RESULTS

Global patterns that transcend study systems: few consistent trends

Globally, the mean effect of temperature on belowground biodiversity was not consistent across studies (Fig. 1). There was no evidence for any linear, unimodal, or inverted unimodal trend (80% credible intervals for both parameters overlapped zero). However, the mean effect of soil pH on belowground biodiversity was consistent across studies. The 95% credible interval of the

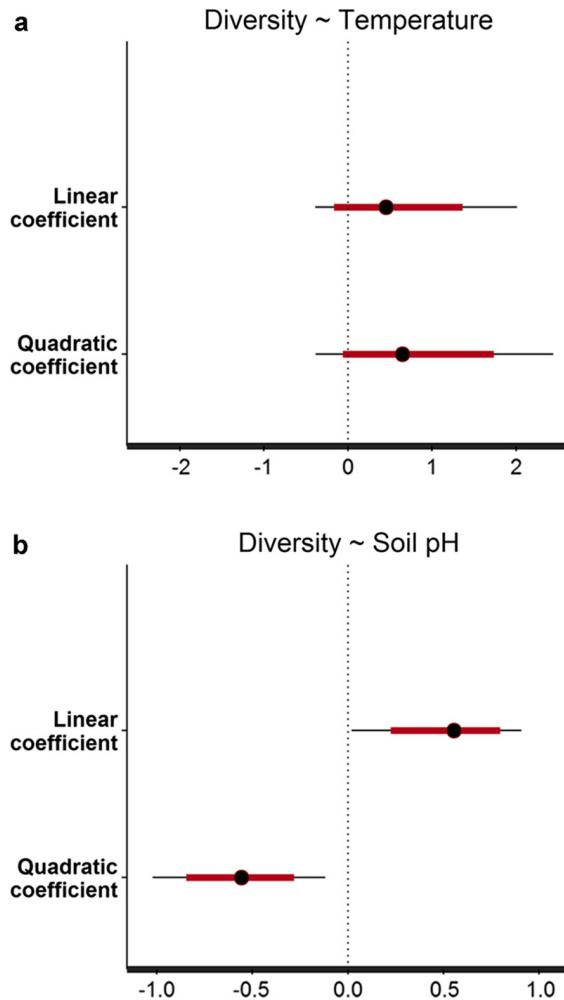


FIG. 1. Effect sizes of (a) temperature and (b) soil pH on belowground diversity across studies. For each predictor, the fitted value median effect size parameters for both the linear term and the quadratic term (black dots), along with their 80% credible intervals (thick red bars) and 95% credible intervals (thin black bars) are shown. For the effect of mean annual temperature on diversity, the 80% credible intervals of both terms overlap zero, but the effect of soil pH on diversity is positive and tending toward a hump-shaped pattern: the 95% credible interval for the linear term is greater than zero, and less than zero for the quadratic term.

quadratic term was entirely negative (median -0.58 ; credible interval $[-1.02, -0.12]$); there is a unimodal or peaked relationship between soil pH and soil biodiversity, with highly acidic soils tending to harbor reduced diversity, and moderately acidic to neutral soils harboring higher belowground diversity. In most studies, the extent of variation in pH did not extend much above 7, thus the unimodal distribution was truncated above the peak. Globally, the mean effect of temperature and pH on abundance was not consistent across sites (Appendix S3) and there was no evidence for any linear, unimodal, or inverted unimodal trend (80% credible intervals for both parameters overlapped zero).

Variation among study systems: no relationship is more common than any other

Across all groups of soil microbial diversity and abundance trends, the distributions of functional forms were never different than expected by chance (diversity by MAT, $n = 28$, $\chi^2_4 = 5.07$, $P = 0.28$; diversity by soil pH, $n = 28$, $\chi^2_4 = 5.84$, $P = 0.21$; abundance by MAT, $n = 45$, $\chi^2_4 = 2.73$, $P = 0.60$; abundance by soil pH, $n = 50$, $\chi^2_4 = 1.73$, $P = 0.79$). Belowground taxa observed along a given gradient of MAT or soil pH were equally likely to show a linear increase, linear decrease, humped pattern, trough-shaped pattern, or no pattern in diversity or abundance with respect to the abiotic gradient (Fig. 2; Appendix S4). Furthermore, bacterial and fungal taxa did not differ in their observed response of diversity and abundance to abiotic gradients; both were equally likely to increase, decrease, or follow a quadratic trend with respect to MAT or soil pH.

Factors explaining variation among study systems: drivers of variation remain unknown

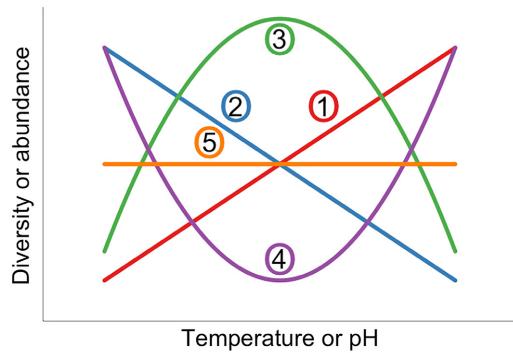
Our moderator analysis showed that virtually none of the hypothesized moderating variables had a consistent effect on the relationships between diversity or abundance and the other environmental drivers. The only exception to this no effect pattern was that the relationship between soil pH and belowground diversity tended to be weaker under high land-use intensities (Appendices S5, S6). The parameter describing the effect of land-use intensity on the linear relationship between diversity and soil pH was -21.08 (95% credible interval $[-38.06, -0.21]$), and the parameter describing the effect of land-use intensity on the hump-shaped relationship between diversity and soil pH was -1.59 (95% credible interval $[0.02, 3.96]$). To illustrate the lack of relationship for precipitation, we divided precipitation into quartiles and plotted each study's trend colored by precipitation quartile; no relationship emerged (Fig. 3, Appendix S7).

Metabolic theory of ecology: pattern is present but weak

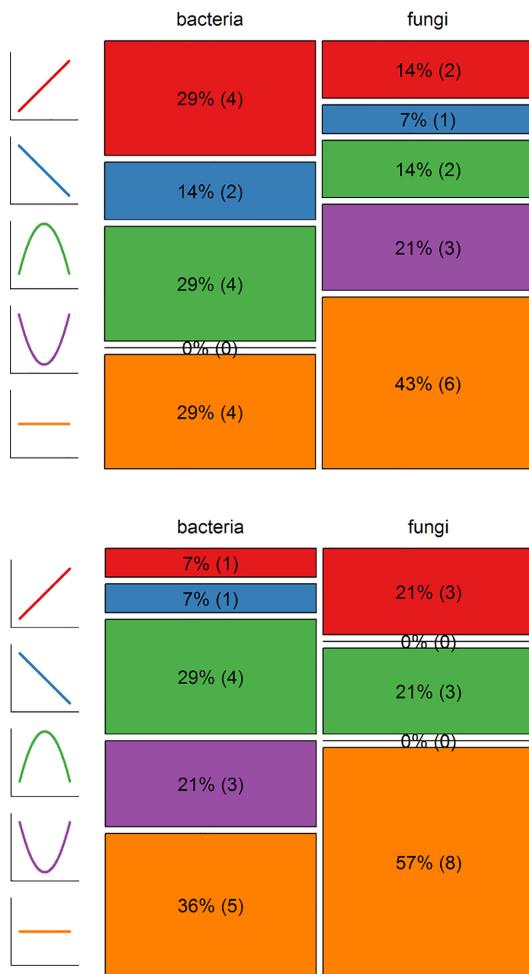
We found the expected negative relationship between the logarithm of diversity and the inverse of absolute temperature across studies (Appendix S8; slope -0.297 ; 95% confidence interval $[-0.512, -0.090]$). However, the relationship was rather weak (marginal $R^2 = 0.027$) and much lower than expected. In particular, the trend in the present study is much weaker relative to published results from microbial communities in forest soils (Zhou et al. 2016), in which R^2 values of the same relationship exceeded 0.72 for all belowground taxa.

DISCUSSION

We found a surprising lack of consensus in large-scale patterns of belowground community diversity along



a FIG. 2. (a) A schematic showing the different models that we fit to microbial abundance and diversity data vs. an environmental gradient of either mean annual temperature or soil pH. Lines 1 and 2 represent linear regression fits with a positive (red) and negative (blue) slope, respectively. Lines 3 and 4 represent quadratic regression fits with a negative or peaked (green) and positive or trough (purple) coefficient on the squared term, respectively. Line 5 (orange) represents a null model where only an intercept is fitted. (b and c) Contingency tables for within-study diversity trends in the meta-analysis for temperature and soil pH, respectively. The width of each box from left to right shows the number of studies for bacteria and fungi, respectively, and the height of each box shows the number of trends fit best by each, functional form. No functional form is significantly more common than any other for either comparison.



b linear trend, a unimodal or trough-shaped pattern, or no change in diversity patterns along a given gradient (Fig. 3). Additionally, these idiosyncratic responses occurred for both soil bacteria and fungi. None of the covariates of latitude and elevation we examined, with the exception of land-use intensity, had any utility for explaining the lack of a common large-scale microbial diversity pattern along environmental gradients. Finally, the prediction generated by the metabolic theory of ecology was only weakly supported by these data. Together, the results from this study suggest (1) that the factors driving soil diversity patterns likely depend on climatic and historical legacies of the gradient location, (2) that factors other than climate and soil properties drive large-scale patterns of belowground abundance and diversity at many sites, or (3) that large-scale and coarse measures of abiotic factors (MAT, bulked soil pH) may not be adequate to explain belowground diversity patterns occurring at much finer spatial scales, such as the scale of individual soil particles, although soil pH has some limited power to explain diversity patterns.

c Mounting evidence suggests that factors driving diversity patterns may depend on the climatic conditions of the gradient sampled (Drenovsky et al. 2010, Mathieu and Davies 2014). For example, the importance of biotic and abiotic factors that structure community assemblages differ significantly within sites at a single elevation (Sundqvist et al. 2013), as well as among sites along a gradient (McCain 2010). Microclimatic variation within sites may swamp the effects of variation in macro-scale climate among sites (Scherrer and Körner 2010), which likely influences ecological legacies and evolutionary history, factors that shape species assemblages (Sanders and Rahbek 2012). While these drivers of diversity are often acknowledged for aboveground organisms (Rahbek 1995, McCain 2010, Shi et al. 2014), they have received less attention in the soil biogeographic literature, especially when exploring patterns across many different systems (but see Mayor et al. 2017). Nonetheless, several studies have shown that ecological legacies and evolutionary history may indeed play a strong role in shaping biogeographical patterns in microbial diversity over large geographic scales (Treseder et al. 2014, Andam et al. 2016).

both elevational and latitudinal gradients. Our globally distributed data set, spanning from high arctic desert to tropical rainforests, covered an extensive range of environmental variation and allowed us to investigate abiotic factors that influence belowground diversity patterns (Appendix S1). We found that there was a weak positive to hump-shaped relationship between soil pH and belowground biodiversity globally. However, within any given study system, we found an equal likelihood of observing a

In addition to the climatic factors outlined above, other processes such as chance, disturbance history, and

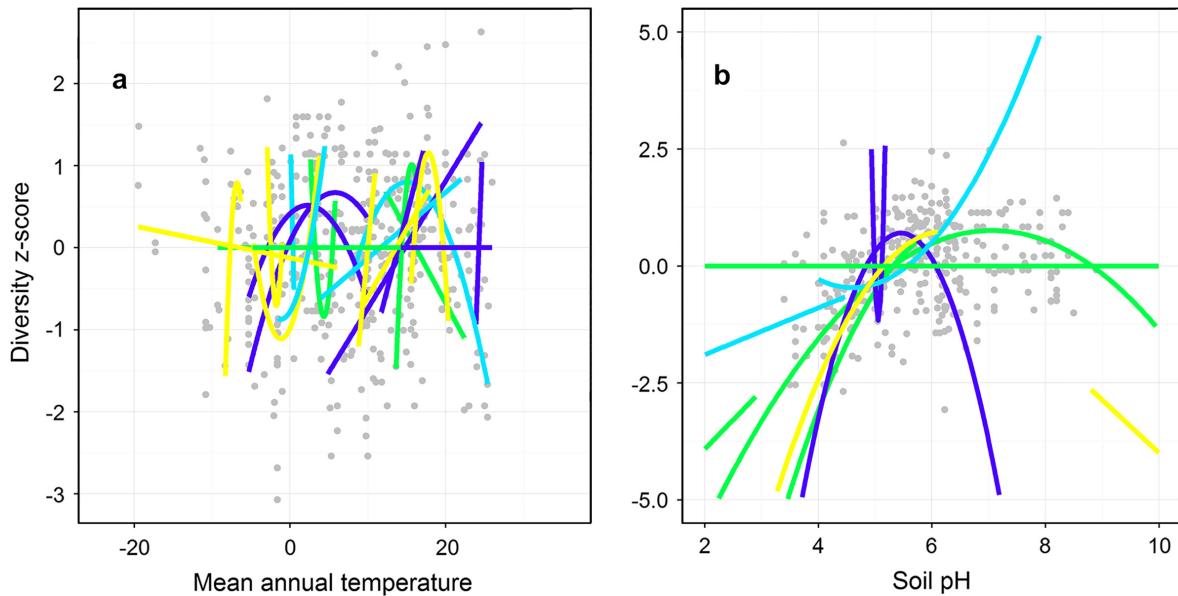


FIG. 3. Trends of diversity vs. mean annual temperature (MAT) and soil pH. For each predictor–response combination, (a) diversity by MAT and (b) diversity by soil pH, the best-fit trends of the z score of the community property vs. the environmental predictors are plotted as colored lines. Lines are colored by mean annual precipitation. We divided the precipitation levels into quartiles; yellow lines represent the driest 25% of study systems, and blue lines represent the wettest 25%. No pattern with regard to precipitation was discernible.

assembly history (Fukami 2015) may be important components of belowground community structure along elevational gradients (Peay et al. 2010, Mathieu and Davies 2014, Beck et al. 2015). This is in contrast to the deterministic view that dispersal limitation and chance play a small role relative to environmental factors. In fact, dispersal limitation at both small and large scales can be an important driver of fungal community assembly in soils (Peay et al. 2010). Early-arriving microbial species may be rapidly changing environmental factors at small scales, suggesting that the order of species arrival into a community may, in addition to climatic variables, play a role in microbial diversity patterns (Fukami 2015).

The grain of spatial variation in soil microbial communities is dramatically smaller than the grain of most large-scale gradient studies (Grundmann and Debouzie 2000). For example, spatial patterns in nitrate- and ammonia-oxidizing bacteria were observed at scales of 2–4 mm (Grundmann and Debouzie 2000). Thus, large-scale measures of abiotic factors such as MAT and bulk soil pH may not represent the heterogeneous environment under which soil microbial communities develop. Additionally, the resolution we can measure microbial diversity has been increasing and we are able to measure many more organisms in soils today than we could 20 yr ago; however, even our most advanced high throughput methods are likely under-measuring and underestimating the biodiversity in a single soil sample. As our understanding and ability to observe soil communities increases, we may be able to better predict the amount and drivers of soil diversity at both local and global scales. Further, microbial communities are dynamic,

both spatially and temporally, in part because they are short-lived and thus their diversity can change quickly (Lauber et al. 2013). Microbes may respond to fine-scale changes in soil resources, pH, oxygen, and moisture that occur at scales that current sampling protocols are not designed to capture; when samples are bulked together, microbial ecologists may be removing the environmental variation that is driving microbial diversity or abundance patterns (Classen et al. 2015). Clearly, microbial communities interact with their environment and with other organisms at very small spatial scales, and these interactions and processes may be important in determining diversity patterns, but are likely not represented in studies investigating the drivers of microbial diversity.

Here, we show that abundance and diversity patterns of belowground organisms follow no universal trend. The patterns of diversity are equally likely to linearly increase, linearly decrease, or to display a hump or trough shape, as they are to display no pattern at all. Additionally, the latitudinal and elevational covariates tested here did little to explain variation in diversity and abundance among systems. While we found support for MTE, this pattern was also weak. Instead, it is possible that local scale processes may be more important than regional processes in determining microbial diversity and abundance patterns. Recent papers that use a common suite of methods along gradients and across sites that differ in biotic and abiotic conditions are enabling researchers to disentangle how multiple drivers of diversity and abundance operate across ecosystems (Fierer and Jackson 2006, McCain 2010, Tedersoo et al. 2014). Coupling these approaches with replicated manipulative experiments at sites that

differ in biotic and abiotic conditions will allow researchers to understand how these factors shape species assemblages. By using a combination of observational and experimental approaches across scales with cutting edge molecular tools, soil macroecologists may finally be able to answer “why does the number of species in soil vary from place to place on the planet?”

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1829/supinfo>