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Increases in mean annual temperature do not alter soil bacterial community structure in tropical montane wet forests

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Abstract. Soil bacteria play a key role in regulating terrestrial biogeochemical cycling and greenhouse gas fluxes across the soil-atmosphere continuum. Despite their importance to ecosystem functioning, we lack a general understanding of how bacterial communities respond to climate change, especially in relatively understudied ecosystems like tropical montane wet forests. We used a well-studied and highly constrained 5.2°C mean annual temperature (MAT) gradient in tropical montane wet forests on the Island of Hawaii to test the hypothesis that long-term, whole-ecosystem warming and the accompanying increase in belowground carbon flux increase the diversity and alter the composition of soil bacterial communities. Across this MAT gradient, dominant vegetation, substrate type and age, soil moisture, and disturbance history are constant, allowing us to effectively isolate the influence of rising MAT on soil bacterial community structure. Contrary to our hypothesis, we found that the richness, evenness, and phylogenetic diversity of the soil bacterial community remained remarkably stable with MAT and that MAT did not predict variation in bacterial community composition despite a substantial increase in belowground soil carbon fluxes across the gradient. Our results suggest that other factors that are constant across this gradient—such as soil pH, water availability and plant species composition—may be more important than warming in influencing soil bacterial community composition and diversity, at least within the temperature range studied here (~13–18°C MAT). Ours is the first study to demonstrate stability of soil bacterial community structure with rising MAT and increased belowground carbon flux in a tropical wet forest ecosystem. Moreover, our results add to growing evidence that the diversity and composition of soil bacterial communities dominated by Proteobacteria and Acidobacteria in low-pH forest soils may be insensitive to the direct effect of climate warming.

Key words: bacteria; climate change; Hawaii; microbial diversity; tropical forests.

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INTRODUCTION

Climate warming may have both direct and indirect effects on soil bacterial communities, but the magnitude and direction of these effects remain poorly resolved (Allison and Martiny 2008, Shade et al. 2012, Cregger et al. 2014). In particular, there are surprisingly few studies on how climate warming affects soil bacterial community composition and diversity in tropical forest ecosystems. This represents a significant knowledge gap given that tropical forests play a disproportionately large role in global carbon cycling (Bonan 2008, Beer et al. 2010, Pan et al. 2011) and that soil bacterial diversity and composition are closely linked to biogeochemical cycling and greenhouse gas fluxes (Heemsbergen et al. 2004, Carney et al. 2007, Singh et al. 2014*a*). Moreover, incorporation of microbial community dynamics into soil carbon models improves their predictive capacity (Allison et al. 2010, Li et al. 2014). Understanding how climate warming affects soil bacterial community composition and diversity in carbon-dense tropical wet forest ecosystems is, therefore, a high research priority given the potentially large and rapid feedback effects on both ecosystem functioning and the global climate system (Allison and Martiny 2008).

The temperature sensitivity of bacterial communities in tropical forest soils remains poorly resolved in part because there are currently no large-scale warming experiments in tropical forest ecosystems (Cavaleri et al. 2015). It is tempting to extrapolate results from warming experiments in other forest ecosystems to the tropics, especially since there is broad overlap in bacterial community composition at the phylum level between low-pH temperate and tropical forest soils (Lauber et al. 2009). However, forest warming experiments typically do not warm the canopy (Kuffner et al. 2012, Cregger et al. 2014, DeAngelis et al. 2015), which can increase gross photosynthesis and overall carbon input belowground (Lu et al. 2013). Increasing carbon availability to bacteria can greatly affect their community composition and diversity (Carney et al. 2007, Allison and Martiny 2008, Landa et al. 2013), especially in tropical forest soils (Nemergut et al. 2010). By not incorporating the aboveground component, soil warming experiments to date in temperate forests may not accurately reflect the integrated effect of whole-ecosystem warming on forest soil bacterial communities.

Elevation gradients provide an alternative to experimentally manipulating the ambient temperature of an entire forest stand and can be a more tractable approach to examine how biota respond to climate change in tropical forest ecosystems (Malhi et al. 2010). Isolating the effect of temperature can be difficult, however, because a number of environmental variables typically covary with temperature across elevation gradients. These potentially confounding factors include moisture availability, soil pH, and plant species composition—all of which can have strong individual impacts on the diversity and composition of soil bacterial communities (Lauber et al. 2009, Cregger et al. 2014, Schlatter et al. 2015, Urbanová et al. 2015). Although several studies have reported significant relationships between elevation and soil bacterial community structure (Bryant et al. 2008, Singh et al. 2011, 2014*b*, Shen et al. 2015), including one in tropical wet forests (Fierer et al. 2011), changes in temperature along all of these elevation gradients have been confounded with changes in soil pH or plant species composition.

Here, we examine trends in soil bacterial community composition and diversity across a well-studied, highly constrained 5.2°C mean annual temperature (MAT) gradient spanning 800-m elevation in native-dominated tropical montane wet forests on Hawaii Island. Unlike other elevation gradients in the tropics, dominant plant species are constant across this Hawaii MAT gradient, as are other potentially confounding variables including soil water balance, geologic substrate, soil type, and soil pH (Litton et al. 2011, Iwashita et al. 2013). Previous work demonstrated that rates of ecosystem carbon fluxes increase substantially with rising MAT across this gradient, including soil CO_2 efflux, leaf litter decomposition, litterfall, and total belowground carbon flux (TBCF) (Litton et al. 2011, Bothwell et al. 2014, Giardina et al. 2014), while total ecosystem carbon storage remains constant (Selmants et al. 2014). Based on these findings, and on evidence that carbon availability shapes bacterial community structure (Nemergut et al. 2010, Landa et al. 2013), we hypothesized that rising MAT and the concurrent increase in belowground carbon availability would significantly increase diversity and alter the composition of soil bacterial communities across this MAT gradient.

METHODS

This Hawaii MAT gradient consists of nine permanent 20 × 20 m plots along the eastern slope of Mauna Kea volcano within the Hawaii Experimental Tropical Forest and the Hakalau Forest National Wildlife Refuge on the Island of Hawaii (Litton et al. 2011). The nine plots range in elevation from 800 to 1600 m, which corresponds to a 5.2°C difference in MAT (13–18.2°C; Table 1). The within-plot standard deviation of monthly air temperature is ~1.2°C, much

Table 1. Site characteristics across a 5.2°C mean annual temperature gradient in closed-canopy tropical montane wet forests on the Island of Hawaii, where ET is evapotranspiration and belowground carbon flux is the total amount of carbon from gross primary productivity that is partitioned to below ground.

Elevation (m)	Air temp. (°C)†	Rainfall (mm yr^{-1})‡	Potential ET (mm yr^{-1})§	Solar radiation (W m^{-2})§	Soil temp. (°C)†	Soil moisture (m^3 m^{-3})†	Soil pH†	Belowground carbon flux (g C m^{-2} yr^{-1})¶
800	18.2	4570	2298	201.1	18.0	0.55	4.1	1533
934	17.3	4292	2232	200.9	17.3	0.55	4.2	1825
1024	16.7	3975	2214	202.4	16.3	0.57	3.7	1446
1116	16.1	3734	2127	204.9	15.9	0.48	3.8	1553
1116	16.1	3433	2137	210.1	15.6	0.51	3.6	1377
1204	15.5	3181	2211	214.5	15.5	0.40	3.7	1356
1274	15.1	3101	2234	216.2	14.9	0.51	3.9	1383
1468	13.8	4119	1888	202.6	13.6	0.55	4.2	1074
1600	13.0	3282	1961	213.1	12.6	0.57	4.1	1184

† From Litton et al. (2011).
‡ From Giambelluca et al. (2013).
§ From Giambelluca et al. (2014).
¶From Giardina et al. (2014).

lower than 5.2°C range in MAT spanned by the entire gradient (Giambelluca et al. 2014). Mean annual soil temperature at 10 cm differs from MAT by only ~0.5°C on average across the gradient, and MAT explains 99% of the variance in soil temperature (Litton et al. 2011). All plots are in mature, closed-canopy tropical montane wet forest dominated by *Metrosideros polymorpha* with very similar geology and soil type. Soils are well-drained Acrudoxic Hydrudands developed from ~20 000 yr old volcanic ash (Litton et al. 2011, Giardina et al. 2014) deposited on a single Pleistocene-age Mauna Kea lava flow dominated by hawaiite and mugearite (Wolfe and Morris 1996, Litton et al. 2011). Mean annual rainfall is not constant across the MAT gradient, but both rainfall and potential evapotranspiration decline consistently with increasing elevation (Table 1). As a result, soil water content is nearly constant across the MAT gradient (Table 1) because declining rainfall with elevation is balanced by reduced evapotranspiration driven by lower air temperatures.

Within each of the nine MAT plots, we collected eight soil samples (Oa and A horizon material) in March of 2010 to a depth of 10 cm after removing undecomposed and partially decomposed litter (Oi and Oe horizon material). We extracted DNA from soil samples with the Powersoil DNA Isolation Kit (Mo-Bio Laboratories, Carlsbad, California, USA) and submitted DNA samples to the Research and Testing Laboratory (RTL, Lubbock, Texas, USA) for tag-pyrosequencing. The V1-V3 region of the 16S rRNA gene was amplified with primers Gray28F (5′ GAGTTTGATCNTGGCTCAG) and Gray519R (5′ GTNTTACNGCGGCKGCTG) by RTL. Reads were generated in the forward direction from 28F with Roche 454 Titanium chemistry sequencing. Quality trimming, denoising, and chimera removal were performed by RTL. We assigned sequences to operational taxonomic units (OTUs) using QIIME version 1.7.0 (Caporaso et al. 2010). To cluster reads into OTUs, we used the open-reference OTU picking algorithm using the UCLUST tool (Edgar 2010) at 97% sequence identity against the 13-5 release of the Greengenes database (DeSantis et al. 2006). OTUs represented by a single sequence were removed from the analysis. We rarefied samples to 2200 sequences to compare equal numbers of sequences among soil samples. The rarefaction process resulted in two soil samples with <2200 sequence reads, each from a different MAT plot, which were excluded from further analysis. We repeated the rarefaction process 10 times for each sample, with subsequent statistical analyses based on within-sample means of the 10 random iterations.

We quantified OTU richness, phylogenetic diversity, and community similarity metrics in QIIME version 1.7.0 (Caporaso et al. 2010). We used the Chao1 richness estimator (Chao 1984) to estimate OTU richness per sample and Faith's (1992) phylogenetic diversity index (Faith's PD) to estimate phylogenetic diversity. Faith's PD for a given set of taxa is the sum of all branches on the phylogenetic tree that are spanned by that set of taxa (Faith 1992, Faith and Baker 2006). Functional attributes are highly correlated with phylogeny (Langille et al. 2013), so if phylogenetic diversity varies in response to rising MAT, it may indicate a shift in the functional capacity of soil bacterial communities. To compare OTU composition across MAT plots, we constructed both taxonomic and phylogenetic community similarity matrices. We used the Bray-Curtis distance index to construct a taxonomic similarity matrix and the weighted UniFrac distance metric (Lozupone and Knight 2005) to construct a phylogenetic similarity matrix.

All statistical analyses were conducted using R version 3.0.2 (R Core Team 2015) with an α-level of 0.10 for all tests due to small sample sizes ($n = 9$). We used ordinary least-squares regression to determine whether OTU richness, phylogenetic diversity, or the relative abundance of individual phyla varied significantly as a function of MAT. To visualize similarities in community composition across the MAT gradient, we used taxonomic (Bray-Curtis) and phylogenetic (weighted UniFrac) similarity matrices to construct nonmetric multidimensional scaling (NMDS) ordinations using the vegan package (Oksanen et al. 2015) in R. We quantified whether bacterial community composition varied as a function of MAT, TBCF (Giardina et al. 2014), and soil pH with permutational multivariate analyses of variance (PERMANOVA) using taxonomic (Bray-Curtis) and phylogenetic (weighted UniFrac) measures of community similarity. We chose MAT, TBCF, and pH as predictor variables because these three factors are often highly correlated with soil bacterial community structure (Zogg et al. 1997, Lauber et al. 2009, Landa et al. 2014). We used the "adonis" function (Anderson 2001) in the vegan R package to conduct PERMANOVA tests. We estimated bacterial OTU evenness in each MAT plot using Pielou's J (Pielou 1966) and used ordinary least squares regression to determine whether OTU evenness varied as a function of MAT.

RESULTS

In contrast to our hypothesis, bacterial diversity did not vary with temperature across this well-constrained MAT gradient in tropical montane wet forests. The observed number of bacterial OTUs averaged 571 (±93; 95% CI) but did not vary with MAT ($R^2 = 0.03$, $P = 0.64$; Fig. 1). Likewise, Chao1-estimated OTU richness did not vary with MAT ($R^2 = 0.06$, $P = 0.53$), averaging 1106 (±174; 95% CI) across the MAT gradient. Similar to trends for OTU richness, OTU evenness estimated by Pielou's J did not vary as a function of MAT (adj. $R^2 = 0.16$, $P = 0.16$; mean Pielou's $J = 0.56 \pm 0.02$ across the MAT gradient). Finally, there was no relationship between MAT and phylogenetic diversity (adj. $R^2 = 0.07$, $P = 0.48$), with bacterial communities in each of the nine MAT plots spanning an average of 45 (±7; 95% CI; Fig. 1) branch lengths of the overall phylogenetic tree constructed for this study.

Similar to trends for diversity, we found no support for our hypothesis that temperature influences bacterial community composition in tropical montane wet forest soils. Soils across

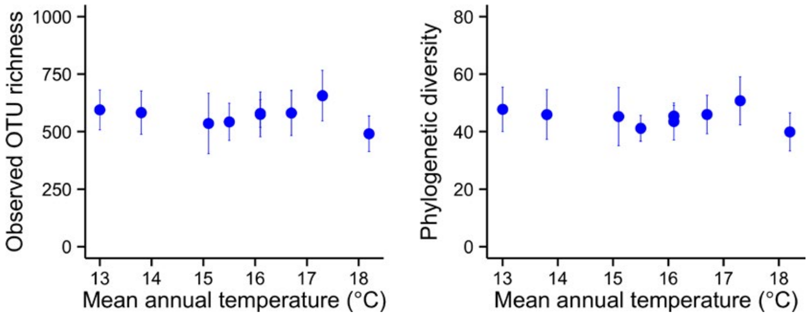

Fig. 1. Observed operational taxonomic units richness and phylogenetic diversity (Faith's PD) of soil bacteria across a 5.2°C mean annual temperature (MAT) gradient in closed-canopy tropical montane wet forests on the Island of Hawaii. Blue circles are within-plot means and error bars represent 95% confidence intervals; $n = 8$ per MAT plot.

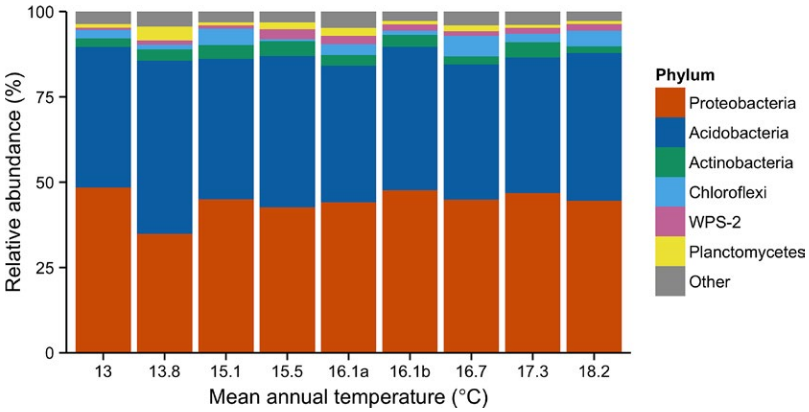

Fig. 2. Relative abundance of soil bacteria by phylum across a 5.2°C mean annual temperature gradient in closed-canopy tropical montane wet forests on the Island of Hawaii.

the MAT gradient were dominated by the phyla Proteobacteria (44% ± 4% of sequences per MAT plot) and Acidobacteria (43% ± 4% of sequences per MAT plot; Fig. 2), which is consistent with continental low-pH wet tropical forest soils (Lauber et al. 2009, Nemergut et al. 2010, Fierer et al. 2011, Lee-Cruz et al. 2013, Rodrigues et al. 2013). None of the bacterial phyla varied significantly as a function of MAT (adj. $R^2 < 0.015$, $P > 0.17$ for all phyla). Approximately 87% (±5%) of sequences within phylum Proteobacteria were in the class Alphaproteobacteria, and most Alphaproteobacteria were either in the genus Rhodoplanes (family Hyphomicrobiaceae; 18% ± 3% of sequences per MAT plot) or the family Rhodospirillaceae (10% ± 3% of sequences per MAT plot). Bacteria in phylum Acidobacteria were dominated by taxa within the family Koribacteraceae, a group of acidophilic heterotrophs, which averaged 23% (±5%) of sequences per MAT plot.

There was a large amount of overlap in community composition among MAT plots (Fig. 3). Temperature was not a significant predictor of variance in either taxonomic or phylogenetic dissimilarity between communities across the MAT gradient (Table 2). Likewise, TBCF and soil pH were not significant predictors of either taxonomic or phylogenetic dissimilarity between soil bacterial communities across the MAT gradient (Table 2). Within-plot heterogeneity in bacterial composition was lower than between-plot heterogeneity based on lower mean phylogenetic distance in soil samples within MAT plots than in soil samples between MAT plots ($t = -2.74$, $P < 0.01$).

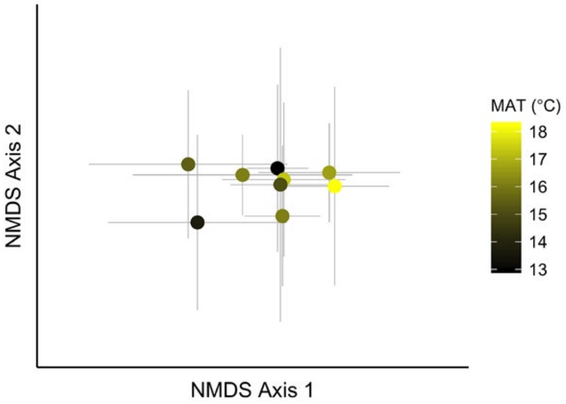

Fig. 3. Nonmetric multidimensional scaling (NMDS) ordination of soil bacterial communities across a 5.2°C mean annual temperature (MAT) gradient in closed-canopy tropical montane wet forests on the Island of Hawaii based on weighted UniFrac distances. Circles represent the centroid of replicate soil sample NMDS axis scores within MAT plots ($n = 8$ replicates per MAT plot) and gray error bars represent 95% confidence intervals. NMDS stress = 0.14.

Discussion

Quantifying the sensitivity of soil bacterial communities to rising temperature is critical to understanding how terrestrial ecosystems will respond to a changing climate. We examined how long-term, whole-ecosystem warming influences the diversity and composition of soil bacterial communities across a highly constrained MAT gradient in closed-canopy

Table 2. Variation in taxonomic and phylogenetic community composition of soil bacteria as a function of temperature, total belowground carbon flux, and soil pH across a 5.2°C mean annual temperature (MAT) gradient in closed-canopy tropical montane wet forests on the Island of Hawaii. Data were analyzed using permutational multivariate analyses of variance (PERMANOVA) on Bray-Curtis (taxonomic) and weighted UniFrac (phylogenetic) distance matrices.

	Weighted UniFrac		Bray-Curtis	
Factor	R^2	P-value	R^2	P-value
MAT	0.003	0.97	0.002	0.99
Belowground carbon flux	0.011	0.54	0.005	0.82
Soil pH	0.004	0.89	0.005	0.82
Residuals	0.982		0.988	
Total	1.00		1.00	

Hawaiian tropical montane wet forests where other potentially confounding factors, including dominant vegetation, soil chemistry, and soil moisture, were constant. Previous work along this gradient showed that increasing MAT drove sharp increases in above and belowground carbon process rates (Litton et al. 2011, Bothwell et al. 2014, Giardina et al. 2014). Increasing carbon fluxes with temperature, along with evidence from other studies indicating that bacterial diversity and community composition are sensitive to increasing carbon inputs (Carney et al. 2007, Nemergut et al. 2010, Landa et al. 2013), led us to hypothesize that rising MAT and the concurrent increase in belowground carbon availability would drive substantial shifts in the diversity and composition of soil bacteria.

In contrast to our hypothesis, we found that soil bacterial diversity and community composition were insensitive to large increases in MAT. Our results also contrast with several studies that have reported significant relationships between elevation and soil bacterial community structure (Bryant et al. 2008, Fierer et al. 2011, Singh et al. 2011, Shen et al. 2015). However, we caution that trends from these other gradients may not have been the product of changes in temperature alone. Unlike the highly constrained MAT gradient described here, all of these prior elevation gradient studies were confounded by concomitant changes in soil pH or dominant vegetation, both major factors influencing the structure of soil bacterial communities (Fierer and Jackson 2006, Lauber et al. 2009, Lynch et al. 2012, Urbanová et al. 2015). Soil pH did not vary appreciably along the Hawaii MAT gradient (Table 1), and all nine MAT plots were dominated by *M. polymorpha* in the upper canopy and by a combination of *Cheirodendron trigynum* and *Cibotium menziesii* in the mid-canopy (Selmants et al. 2014). Additionally, soil moisture was relatively constant across this MAT gradient, which may also explain the stability of soil bacterial community structure as several manipulative global change experiments have demonstrated that variation in soil moisture has a much stronger effect on bacterial community structure than variation in temperature (Castro et al. 2010, Zhang et al. 2013, Cregger et al. 2014). Because we were able to hold constant multiple environmental factors known to strongly influence soil bacterial communities, including soil pH, soil water availability, and dominant vegetation, our results provide strong evidence that soil bacterial community structure is largely insensitive to rising MAT in these tropical montane wet forests.

We also hypothesized that warming-related increases in ecosystem carbon fluxes (Litton et al. 2011, Bothwell et al. 2014, Giardina et al. 2014) would alter soil bacterial community structure based on evidence from field and laboratory experiments that increased carbon availability alters soil bacterial composition and diversity (Nemergut et al. 2010, Leff et al. 2012, Berthrong et al. 2013, Landa et al. 2013, 2014). We found no support for this hypothesis and suggest that soil bacterial community structure remained stable, despite increased belowground carbon availability, in part because of constant plant species composition across the MAT gradient. Recent evidence indicates that plant species composition is a major influence on soil bacterial community structure and that plant species effects are mediated through the chemistry of plant-derived resources (Schlatter et al. 2015, Urbanová et al. 2015). Although TBCF increased by ~50% across the MAT gradient (Giardina et al. 2014), the chemical composition of carbon inputs such as leaf litter, fine root detritus, and root exudates likely remained constant because of the lack of variation in plant species composition.

Although soil bacterial community composition and diversity appear to be insensitive to warming-related increases in carbon availability, the overall activity of the soil bacterial community may not be. Increased rates of soil CO_2 efflux and leaf litter decomposition with MAT across this gradient (Litton et al. 2011, Bothwell et al. 2014) are likely driven in part by increased activity of soil bacteria. We offer three potential explanations, none of which are mutually exclusive, as to why the functional capacity of soil bacteria may have increased across this MAT gradient with no change in community structure. First, increased carbon availability could have increased bacterial abundance without altering community composition or diversity—the forest ecosystem equivalent to the aphorism "a rising tide lifts all boats" (Litton et al. 2007). Second, the overall metabolic activity of the soil bacterial community could have increased in response to the combined effects of rising MAT and increased belowground carbon input, but without changing bacterial abundance, composition or diversity. Finally, and related to the second hypothesis, increasing MAT and belowground carbon input may have increased the active fraction of the soil bacterial community. Dormancy is a widespread strategy among soil bacteria, allowing avoidance of unfavorable environmental conditions while maintaining high levels of diversity (Jones and Lennon 2010, Shade et al. 2012). Our analysis captured any bacterial DNA without discriminating between active bacteria and the ~90% of bacterial cells in soil that are estimated to be metabolically inactive at any given time (Lennon and Jones 2011). It is possible that rising MAT and increased belowground carbon availability might increase the active fraction of existing soil bacterial communities rather than altering community composition or diversity. However, the relatively aseasonal nature of the MAT gradient and year-round favorable moisture, temperature, and carbon conditions suggest that release from dormancy is likely a minor factor.

The current study, conducted along a highly constrained 5.2°C MAT gradient in tropical montane wet forests, adds to the growing body of evidence from environmental gradients and manipulative experiments that temperature alone may not be a primary factor structuring soil bacterial communities (Fierer et al. 2009, 2011, Lauber et al. 2009, Cregger et al. 2014, DeAngelis et al. 2015). These results further suggest that climate warming, at least within the MAT range studied here, is unlikely to lead to drastic alterations of soil bacterial diversity and community composition in the absence of concomitant changes in soil pH, soil water balance, or plant community composition. These data may partially explain why soil carbon storage remains stable across this MAT gradient despite substantial increases in belowground carbon flux (Bothwell et al. 2014, Giardina et al. 2014, Selmants et al. 2014). Finally, these results bolster the suggestion posited by Fierer et al. (2011) that broad hypotheses linking biodiversity to temperature-driven variation in metabolism (sensu Brown et al. 2004) may not apply to soil bacteria.

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DATA AVAILABILITY

Data and R code for statistical analyses and figures are publicly available at: https://github.com/selmants/bacteria_MAT.