Soil microbial biomass increases along elevational gradients in the tropics and subtropics but not elsewhere

9 authors, including:

Xianjin He
Chongqing University
7 PUBLICATIONS   **68** CITATIONS

SEE PROFILE

Enqing Hou
Northern Arizona University
58 PUBLICATIONS   **684** CITATIONS

SEE PROFILE

Farnon Ellwood
University of the West of England, Bristol
36 PUBLICATIONS   **1,003** CITATIONS

SEE PROFILE

Xinghua Sui
Sun Yat-Sen University
23 PUBLICATIONS   **209** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Subtropical forests in a highly-urbanized region: Potential capacities of and strategies for increasing carbon sequestration View project

Key factors impacting plant diversity dynamics in response to human activities (eutrophication and/or removing herbivores) View project

META-ANALYSIS

Soil microbial biomass increases along elevational gradients in the tropics and subtropics but not elsewhere

Xianjin He[1,2] | Enqing Hou[3,4] | G. F. Veen[5] | M. D. Farnon Ellwood[6] | Paul Dijkstra[7] |
Xinghua Sui[1] | Shuang Zhang[8] | Dazhi Wen[3,4] | Chengjin Chu[1]

[1]Department of Ecology, State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, Guangzhou, China

[2]Guangdong Open Library of Geospatial Information Technology and Application, Guangzhou Institute of Geography, Guangdong Academy of Sciences, Guangzhou, China

[3]Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

[4]Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

[5]Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

[6]Centre for Research in Biosciences, University of the West of England, Bristol, United Kingdom

[7]Center for Ecosystem Science and Society and Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona

[8]State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

Correspondence
Chengjin Chu, Department of Ecology, State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, 510275, Guangzhou, China.
Email: chuchjin@mail.sysu.edu.cn

Abstract

Aim: Our aim is to use elevational gradients to quantify the relationship between temperature and ecosystem functioning. Ecosystem functions such as decomposition, nutrient cycling and carbon storage are linked with the amount of microbial biomass in the soil. Previous studies have shown variable relationships between elevation and soil microbial biomass (SMB). Understanding the biological mechanisms linking SMB with elevational gradients will shed light on the environmental impacts of global warming.

Location: Global.

Time period: 2002–2018.

Major taxa studied: Soil microbes.

Method: We performed a global meta-analysis of the relationships between SMB and elevation. Data were collected from 59 studies of 73 elevational transects from around the world.

Results: We found no consistent global relationship between SMB and elevation. SMB increased significantly with elevation in the tropics and subtropics, but not in other climate zones. However, we found consistent positive relationships between SMB, soil organic carbon and total nitrogen concentrations.

Main conclusions: Our results suggest that global warming will impact tropical and subtropical ecosystems more severely than colder regions. Tropical ecosystems, already at risk from species extinctions, will likely experience declines in SMB as the climate warms, resulting in losses of fundamental ecosystem functions such as nutrient cycling and carbon storage.

KEYWORDS
climate change, elevation, global warming, meta-analysis, soil microbial biomass, soil organic carbon

1 | INTRODUCTION

Soil microbial biomass (SMB) accounts for much of the world's belowground living biomass (Fierer, Strickland, Liptzin, Bradford, & Cleveland, 2009) and regulates the functioning of the planet's ecosystems (Bradford et al., 2017; Capek, Starke, Hofmockel, Bond-Lamberty, & Hess, 2019). As a reservoir of soil carbon and available nutrients, SMB affects the performance of plants (Vimal, Singh, Arora, & Singh, 2017; Wardle et al., 2004) and is used as an index of soil fertility and ecosystem productivity (Singh & Gupta, 2018). Soil microorganisms are sensitive to environmental change (Bardgett & Wardle, 2010), and changes in SMB will in turn affect ecosystem functioning (Krashevska et al., 2008; Whitaker et al., 2014; Zhou, Clark, Su, & Xiao, 2015). Using elevational gradients to quantify the relationship between temperature and SMB will provide valuable insights into the effects of climate change on carbon and nutrient cycling (Sundqvist, Sanders, & Wardle, 2013; Wardle et al., 2004).

Our understanding of the causes and consequences of changes in SMB along elevational gradients at the global scale is limited and based on conflicting results (Hendershot, Read, Henning, Sanders, & Classen, 2017; Sundqvist et al., 2013). Studies from tropical (Krashevska et al., 2008; Wagai, Kitayama, Satomura, Fujinuma, & Balser, 2011; Whitaker et al., 2014) and subtropical regions (Chang, Chen, Tian, & Chiu, 2016; Cheng et al., 2013; Lin et al., 2015) observed that SMB increased with elevation and associated decreases in temperature. Similarly, experiments in tropical rain forests revealed that warming of suspended soils associated with epiphytic ferns caused significant decreases in bacterial biomass (Donald et al., 2017). Contrastingly, studies from temperate regions (Djukic, Zehetner, Mentler, & Gerzabek, 2010; Siles, Cajthaml, Minerbi, & Margesin, 2016; Zhang, Liang, He, & Zhang, 2013; Zhou et al., 2015), tundra (Kotas, Aantrůčková, Elster, & Kaštovská, 2018; Sundqvist et al., 2011; Veen et al., 2017) and the Tibetan Plateau (Cui et al., 2016; Lei, Si, Wang, & Zhang, 2017; Xu et al., 2014) concluded that SMB either decreased with elevation or exhibited no significant trends. These inconsistent results from different parts of the world suggest that the relationship between SMB and elevation varies depending on regional climates.

Despite the inconsistencies in previous studies, elevational gradients are useful for quantifying ecosystem responses to changes in temperature at spatial and temporal scales beyond those of conventional ecological experiments (Fukami & Wardle, 2005; Körner, 2007; Sundqvist et al., 2013). Using elevational patterns to understand whole-ecosystem effects of climate on the distribution, community structure and biomass of organisms could enhance our ability to predict the response of terrestrial ecosystems to global warming (Mayor et al., 2017; Sundqvist et al., 2013; Yuan et al., 2017). Although elevational changes in community composition and biomass have been studied extensively for plants (Sundqvist et al., 2013; Wang et al., 2014), far less is known about the effects of elevational changes on belowground communities (Kotas et al., 2018; Sundqvist et al., 2013).

It is almost a universal law that temperatures decrease with increasing elevation. An inconsistent relationship between SMB, temperature and elevation suggests that temperature may not be the only factor determining shifts in SMB along elevational gradients. However, elevation is also associated with changes in precipitation, soil physical and chemical properties, and vegetation productivity and type (Körner, 2007; Sundqvist et al., 2013). Any one of these factors could drive changes in SMB along elevational gradients. For example, in studies encompassing a range of biomes, SMB was most strongly correlated with soil organic carbon (SOC) and total nitrogen (TN) concentrations (Fierer et al., 2009; Wardle, 1992). At regional and local scales, SMB has been associated with soil pH (Aciego Pietri & Brookes, 2009; Rousk, Brookes, & Bååth, 2010; Wagai et al., 2011), and precipitation (Bachar et al., 2010; Drenovsky, Steenwerth, Jackson, & Scow, 2010; Ren et al., 2018). Which of these environmental factors could be used to predict elevational increases or decreases in SMB at the global scale remains unknown.

We therefore conducted a global meta-analysis of the relationships between SMB and a range of abiotic factors associated with elevation. Our hypotheses are that: (a) low temperatures associated with higher elevations will have a significant positive effect on SMB in warmer climates such as the tropics and subtropics; and (b) carbon and nitrogen levels in soils, also associated with elevation, will be positively correlated with SMB.

2 | METHODS

2.1 | Literature search, selection criteria and data acquisition

We searched the Web of Science and Google Scholar databases on 13 April 2018 using the combined keywords "elevation" or "altitud*" and "soil microbial biomass". We expanded the literature search by examining the references cited in all relevant studies. We did not include data from textbooks or grey literature (theses, annuals and meetings) in our search. To maximize our sample size we included studies that determined microbial biomass in either of the following two ways: total amounts of phospholipid fatty acids in soil (PLFAs, n mol/g soil) (Frostegård & Bååth, 1996), or soil microbial biomass carbon concentration (mg/kg) measured via the chloroform fumigation–extraction (CFE) technique (Joergensen, 1996). These two methods are commonly used to measure SMB and their results are well correlated (Leckie, Prescott, Grayston, Neufeld, & Mohn, 2004). Because these measurements use different units, the most appropriate statistical analysis was a random-effects meta-analysis with mixed effects meta-regression models. In this analysis the effect sizes are unitless, allowing us to compare two different experimental methods.

The following criteria were used to determine which studies to include in our meta-analysis:

1. We included studies conducted in natural ecosystems (i.e., excluding data from agricultural croplands).

2. We used data from the top soil (0–10 cm); we did not include estimates from litter layers because drivers of microbial biomass in litter are presumably different from those in soil (Serna-Chavez, Fierer, & van Bodegom, 2013). If a study reported data for 0–5 cm and 5–10 cm, we used the arithmetic average of the two layers.

3. Where microbial biomass at the same elevational transect was estimated more than once per year, we included one summer sample because this season was most commonly sampled. We introduced "time of sampling" as a variable in the analysis to reduce variation due to sampling season.

4. We excluded the four elevational transects that contained only two sampling sites because the sample size was insufficient to determine correlation coefficients.

5. Three studies (Bragazza, Bardgett, Mitchell, & Buttler, 2015; Chang et al., 2016; Zhou et al., 2015) used both methods of measuring SMB. As expected, the results from PLFAs and CFE were strongly correlated in these studies. To avoid pseudo-replication, we therefore included only the PLFA method in these three elevational transects. Qualitatively similar results were obtained from both PLFA and CFE methods (see Supporting Information Figure S1 in Appendix S2).

Following these criteria, we obtained data on 73 elevational transects (362 observations in total) from 59 studies in our meta-analysis (see Figure 1 and Supporting Information Appendix S1). Data sources are listed in Supporting Information Appendix S1. We recorded the SMB data, corresponding elevation, and the sample size from each study by extracting data directly from the text, tables or digitized figures.

We recorded mean annual air temperature (MAT), mean annual precipitation (MAP), SOC concentration, soil TN concentration, SOC to TN ratios (C : N) and soil pH along each transect at each elevation. If climate data were absent from the source paper, we used the *extract* function in the "raster" package (v. 2.6-7; Hijmans, 2017) in R (v. 3.4.4; R Core Team, 2018) to extract MAT and MAP from the relevant latitude and longitude of the global climate layers of WorldClim (1 km^2 spatial resolution; http://www.worldclim.org/).
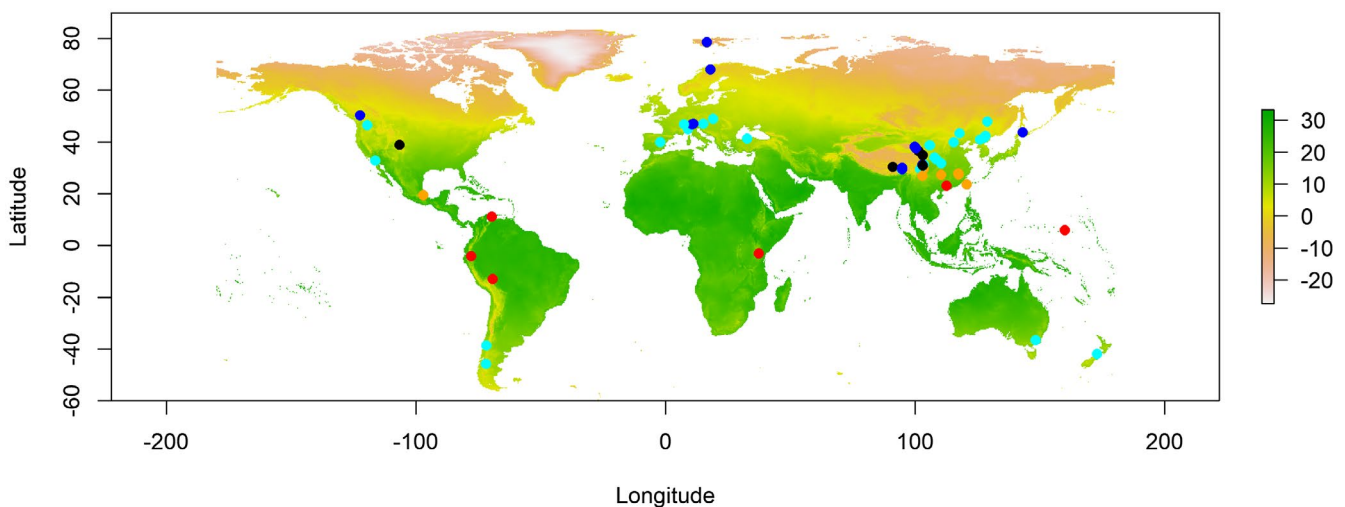
FIGURE 1 Distribution of elevational gradients reviewed in the current meta-analysis. Elevational gradients belonging to different climate zones are presented in different colours. Red points, orange points, cyan points, blue points and black points represent elevational gradients from "tropics", "subtropics", "temperate", "needleleaf deciduous forest and tundra woodland" and "tundra, highland steppe", respectively. Some sites are so close to each other that they overlap on the map. The base map is the global mean annual temperature (http://www.worldclim.org/)

2.2 | Statistical analysis

Our analysis consisted of three separate steps: random-effects meta-analysis, mixed effects meta-regression models and a series of univariate linear regression models. We ran both the multilevel mixed effects meta-analyses and the meta-regression models using the *rma.mv* function in the R package "metaphor" (v. 2.0-0; Viechtbauer, 2010). We used "~ Transect ID| Study" as a nested random factor to account for the fact that some elevational transects resulted from the same study (see Supporting Information Appendix S1 for details).

2.3 | Global relationships between elevation and soil microbial biomass

We used multilevel random-effects meta-analysis to quantify the effects of elevation on SMB at the global scale and Pearson correlation coefficients (*r*) to quantify the effect size of elevation on SMB within each elevational transect. Positive effect sizes reveal increasing SMB with elevation, while negative effect sizes reveal decreasing SMB with elevation. Most importantly, the correlation coefficient is unitless; data from PLFAs and CFE could therefore be compared directly. Effect sizes were calculated by z-transforming the Pearson correlation coefficients, which were weighted by their sample size. We assessed total heterogeneity of effect sizes using the Q statistic (*Qt*) in a random-effect model. Where *Qt* values were significant, variance between studies was greater than expected from sampling error alone, in which case moderators were used to partition the variance (Scheiner & Gurevitch, 2001). Publication bias was assessed using a regression test for funnel plot asymmetry (Egger, Smith, Schneider, & Minder, 1997). We also calculated Rosenberg's fail-safe numbers to assess the robustness of our results to publication bias (Rosenthal & Rosnow, 1991).

2.4 | Variability in the effect size of elevation on soil microbial biomass and environmental factors

We used mixed-effects meta-regression models with climate zone as a moderator to test whether the effect size of elevation on SMB differed between climate zones. Data were aggregated into five climate zones according to the Köppen–Trewartha climate classification (Baker, Diaz, Hargrove, & Hoffman, 2010; Figure 1): "tropics": T_{cold} > 18 °C; "subtropics": 8–12 months with T > 10 °C; "temperate": 4–7 months with T > 10 °C; "needleleaf deciduous forest and tundra woodland": 1–3 months with T > 10 °C; "tundra, highland steppe": T_{warm} < 10 °C. T denotes mean annual temperature (°C), T_{cold} (T_{warm}) stands for monthly mean air temperature of the coldest (warmest) month. No site was categorized into dry climate in our dataset. As above, climate zone was used as a categorical moderator in the meta-regression model, which we ran without the intercept to obtain the parameter estimates (i.e., mean effect sizes) for each climate zone. Climate zone was then used as a moderator in the meta-regression models to calculate the effect sizes of elevation on the environmental factors (i.e., MAP, SOC, TN, C : N, soil pH).We excluded MAT from this analysis because temperature decreases universally with elevation. In these mixed-effects

meta-regression models, the amount of heterogeneity explained by the moderator is also measured using Q statistic (Qm). A significant Qm value indicates that a significant proportion of the total heterogeneity among studies can be explained by the moderator (Scheiner & Gurevitch, 2001).

2.5 | Relationships between SMB and environmental factors

To establish whether global relationships existed between environmental factors, elevation and SMB, we fit a series of univariate linear regression models with SOC, TN, C : N, soil pH, MAT and MAP. Because our response variable for changing SMB with elevation was calculated as *r* (Pearson correlation coefficient), we also calculated the Pearson *r* for the relationships between elevation and the six environmental factors. We were then able to use these factors as explanatory variables in a regression model (Zhang, Chen, & Ruan, 2018). Effect size of elevation on these environmental factors was calculated by z-transforming the Pearson correlation coefficients between elevation and environmental factors. We omitted those elevational transects with missing values in any one of the six environmental factors, which reduced the dataset to 47 elevational transects from 41 studies. Having observed contrasting patterns between elevation and SMB in warmer (i.e., tropics and subtropics) and colder (i.e., temperate, "needleleaf deciduous forest and tundra woodland", "tundra, highland steppe") climate zones, we fit the environmental factors to our univariate linear regression models as variables to explain the elevational trends of SMB in warmer and colder climate zones. Relevant bivariate relationships between these variables are presented in Supporting Information Appendix S2 (Figures S2–S4). We performed all analyses in R v. 3.4.4 (R Core Team, 2018).

3 | RESULTS

SMB did not exhibit significant elevational patterns at the global scale. Meta-analysis of 73 elevational transects from 59 studies around the world indicated that the overall weighted effect size of elevation on SMB was not significantly different from zero (z = 1.809, p > .05; Figure 2a). We found no publication bias in the regression test for funnel plot asymmetry (z = −0.700, p > .05). The Rosenthal's fail-safe number (N = 732,547) was also greater than $5n + 10$ (n = 73), indicating that our results were unlikely to have been affected by non-significant, unpublished studies.

However, the test for heterogeneity was significant [Qt (df = 72) = 876,154, p < .001], indicating that variation in effect size could be explained using moderators. As a moderator, climate zone explained a significant amount of the variance in effect size between elevational transects [QM (df = 5) = 22.08, p < .001]. SMB increased with elevation in warmer zones (i.e., tropics and subtropics; Figure 2b, Supporting Information Figure S1 and Table S1). However, in colder zones (i.e., temperate, "needleleaf deciduous forest and tundra woodland" and "tundra, highland steppe") SMB exhibited no statistically significant trends (Figure 2b, Supporting Information Figure S1 and Table S1).
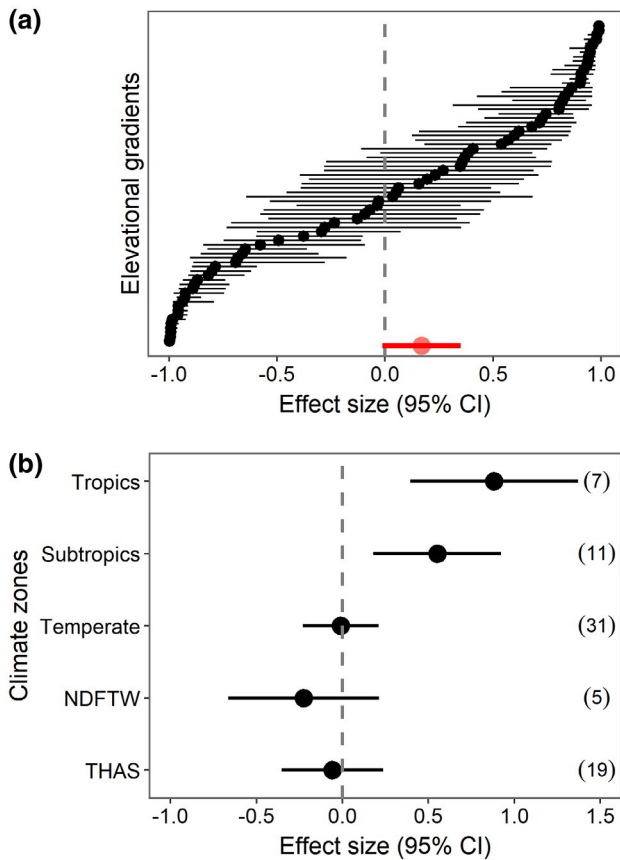
FIGURE 2 Effect size of elevation on soil microbial biomass (SMB) based on Pearson correlation coefficients. (a) Effect sizes from 73 individual elevational gradients. Black points and grey lines represent effect sizes with 95% confidence intervals (CIs). The symbol in red indicates the overall weighted mean effect size and its 95% CI. (b) Effect size of elevation on SMB at the climate zone level. Numbers in parentheses indicate the number of elevational gradients included in the corresponding climate zone. NDFTW = needleleaf deciduous forest and tundra woodland; THAS = tundra, highland steppe

As with SMB, both SOC and TN (Figure 3a,b, Supporting Information Tables S2 and S3) and the C : N ratio (Figure 3c and Supporting Information Table S4) were significantly positively associated with elevation in the tropics and the subtropics, but unaffected by elevation in the cold zones. Soil pH exhibited significant negative associations with elevation in the temperate zones while being unaffected by elevation in other climate zones (Figure 3d and Supporting Information Table S5). MAP was unaffected by elevation in any of the climate zones (Figure 3e and Supporting Information Table S6).

A series of univariate linear regression models, incorporating 47 elevational transects from 41 studies, revealed that the effect size of elevation on SMB was significantly and positively associated with the effect sizes of elevation on SOC, TN, C : N, pH and MAP at the global scale (Table 1). However, no significant associations were found between the effect size of elevation on MAT and SMB (Table 1). Within the significant moderators, SOC and TN's effect sizes explained far

more of the variation in effect size globally than soil C : N ratios, pH and MAP (Table 1). The close relationship between these environmental factors resulted in strong positive correlations between SOC and TN concentrations (Supporting Information Figure S3).

Univariate linear regression analyses showed that SOC and TN correlated most strongly with SMB in both the warm and the cold climate zones (Table 1). In warm zones, significant positive correlations described the effect of elevation on soil C : N ratios and SMB (Table 1). In cold zones, significant negative correlations described the effect of elevation on soil pH and SMB (Table 1), whereas significant positive correlations described the effect of elevation on MAP and SMB (Table 1). Significant correlations described the effect of elevation on MAT and SMB in both climatic zones, being negative in warm zones and positive in cold zones (Table 1).

4 | DISCUSSION

We looked for global patterns in SMB at different elevations in an attempt to understand how global environmental change will impact the microbial processes of the world's different climatic regions. We found only marginally significant correlations between elevation and SMB at the global scale. This result concurs with a previous global meta-analysis (Hendershot et al., 2017), which did not find a consistent relationship between soil microbial abundance and temperature gradients at the global scale. However, by separating sites based on climate zones, we found support for our first hypothesis in that SMB increased significantly with elevation in the tropics and the subtropics. Given the link between SMB and ecosystem function (Bradford et al., 2017; Capek et al., 2019), our results suggest that the effects of global warming will be particularly severe in the tropics, impacting soil chemistry (Bradford et al., 2017; Vimal et al., 2017) and soil microbial respiration (Bradford et al., 2019).

Natural elevational gradients provide information on long-term responses across centuries to millennia (Fukami & Wardle, 2005; Yuan et al., 2017). Manipulative experiments may better reflect the inherent complexity of plant–soil–microbe interactions. While some manipulative experiments reveal variable responses of SMB to warming (Pold, Grandy, Melillo, & Deangelis, 2017; Xu & Yuan, 2017), short-term warming has been shown to reduce SMB, particularly in colder and drier climates (Blankinship, Niklaus, & Hungate, 2011; Crowther et al., 2016). Other short-term experiments, on suspended soils in tropical rain forests, confirm that warming reduces bacterial biomass (Donald et al., 2017).

Although elevational patterns of SMB varied across climate zones, SMB showed a consistent positive relationship with SOC at the global scale irrespective of warmer or colder climates (Table 1). This finding is in agreement with previous studies, in which a positive correlation between SMB and SOC was found at the regional (Hu et al., 2014) and global (Cleveland & Liptzin, 2007; Fierer et al., 2009; Xu, Thornton, & Post, 2013) scales. Although microbial biomass constitutes only 1–5% of SOC, microbial necromass makes up 50–80% of SOC (Cotrufo et al., 2015; Cotrufo, Wallenstein, Boot,
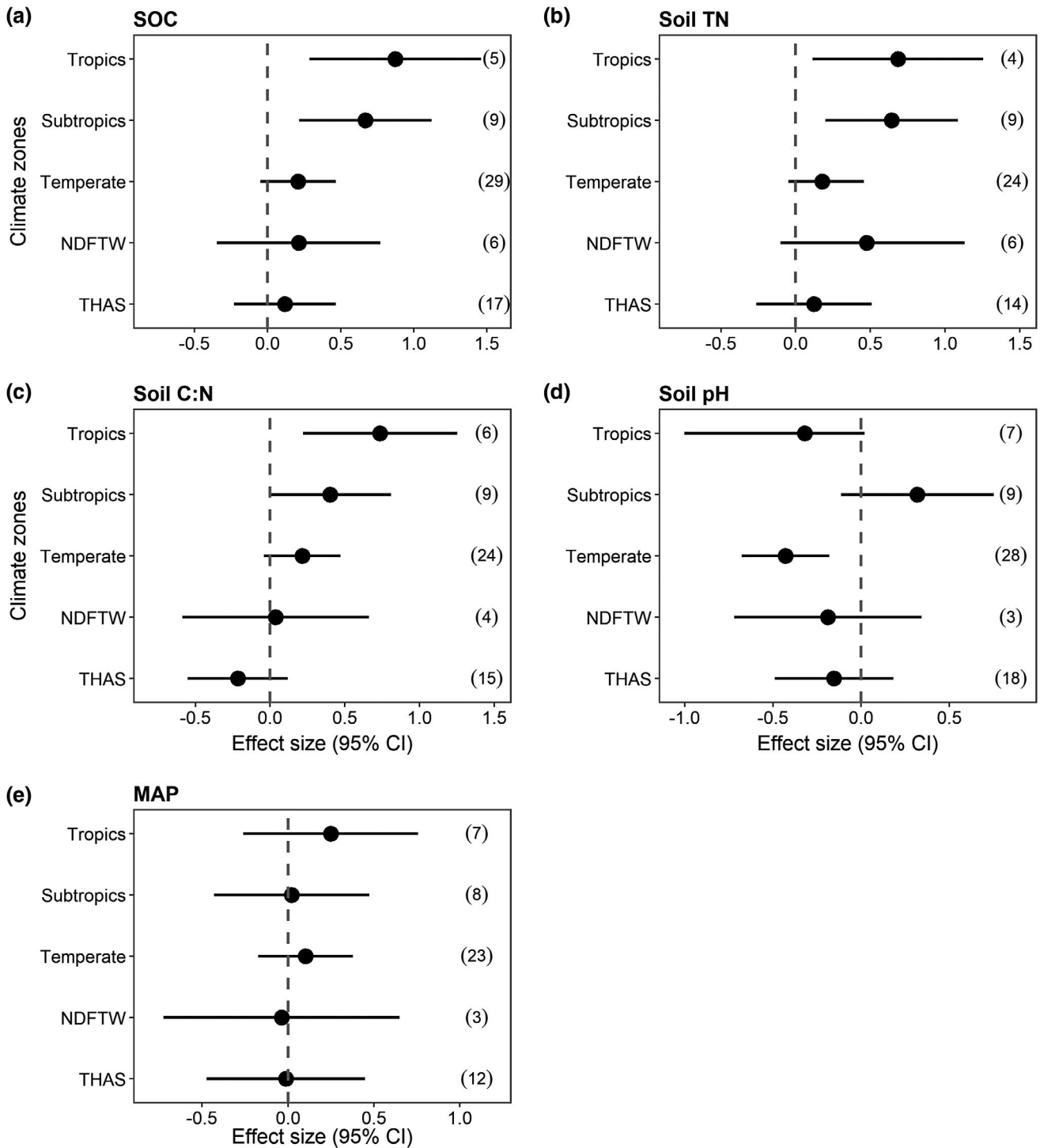
FIGURE 3 Effect size of elevation on environmental factors at the climate zone level. Effect size was quantified using Pearson correlation coefficients. The effect size of elevation on (a) soil organic carbon (SOC), (b) total nitrogen (TN), (c) soil C : N, (d) soil pH and (e) mean annual precipitation (MAP). Numbers in parentheses indicate the number of elevational gradients included in the corresponding climate zones. Abbreviations as in Figure 2

Denef, & Paul, 2013; Lehmann & Kleber, 2015). SOC is an important substrate for soil microbes, meaning that a soil with low organic matter usually has lower microbial biomass (Camenzind, Hättenschwiler, Treseder, Lehmann, & Rillig, 2018; Chen, Li, Xiao, & Wang, 2018; Traoré et al., 2016; Wardle, 1992). SOC is therefore both a substrate for and a product of microbial activity (Kitayama & Aiba, 2002; Paul,

2016; Tashi, Singh, Keitel, & Adams, 2016). Indeed, SOC provides an integrated measure of the biotic and abiotic factors regulating the size of the SMB (Fierer et al., 2009). While we cannot solve the causal relationship between SMB and SOC, our results clearly demonstrate that SOC is a good predictor for elevational patterns of SMB globally.

HE ET AL.

Global Ecology
and Biogeography

A Journal of
Macroecology

WILEY 7

TABLE 1 Results of univariate linear regressions in global, warm and cold climate zones

	Estimate	SE	t	p	Adj-R^2
Global					
SOC	0.641	0.090	7.150	**1e-09**	.435
TN	0.600	0.107	5.590	**7e-07**	.351
C : N	0.256	0.124	2.055	**.045**	.053
pH	−0.326	0.122	−2.681	**.009**	.086
MAP	0.311	0.134	2.317	**.025**	.077
MAT	0.777	1.143	0.680	.499	−.008
Warm					
SOC	0.947	0.172	5.513	**1e-06**	.677
TN	0.734	0.193	3.800	**.002**	.490
C : N	0.572	0.151	3.797	**.002**	.490
pH	−0.103	0.150	−0.687	.503	−.037
MAP	0.067	0.144	0.466	.649	−.059
MAT	−4.283	1.910	−2.243	**.039**	.192
Cold					
SOC	0.511	0.105	4.854	**1e-05**	.311
TN	0.492	0.126	3.895	**4e-04**	.257
C : N	−0.030	0.158	−0.196	.845	−.023
pH	−0.401	0.125	−3.199	**.002**	.156
MAP	0.603	0.161	3.738	**6e-04**	.260
MAT	2.207	1.094	2.018	**.049**	.055

Abbreviation: Adj = adjusted; MAP = mean annual precipitation; MAT = mean annual temperature; SOC = soil organic carbon; TN = total nitrogen. *p* values less than .05 are in bold.

The contrasting responses of SMB to elevation in different climate zones can probably be explained by several reasons. Firstly, the direct effect of temperature on the SMB may differ between climate zones. Our results showed that SMB increased marginally with MAT in cold climate zones but decreased with MAT in the (sub) tropical zones. This result was consistent with a recent meta-analysis that found a unimodal relationship between local temperature and death rate of SMB due to heat damage (Capek et al., 2019). Secondly, temperature effects on primary productivity and plant community structure may differ between climate zones (Lange et al., 2015). For example, vegetation may change from birch woodland to tundra heath with increasing elevation in the Arctic, whereas lowland rain forest changes to montane cloud forest in the tropics. These vegetation transitions may have different impacts on SMB in different climate zones. Moreover, the higher occurrence of tree lines at high elevation in the colder climates (Zhou et al., 2016) may dramatically reduce plant litter input and thus affect SOC and SMB (Mayor et al., 2017; Zhou et al., 2016). Thirdly, soils in the lowland (sub)tropics can be highly weathered and depleted in phosphorus, which can limit primary productivity and soil microbial growth, and constrain the accumulation of organic C in soil (Nottingham et al., 2015; Vitousek, Porder, Houlton, & Chadwick, 2010). Phosphorus limitation on SMB may decrease with increasing elevation in the tropics and subtropics,

associated with a reduction of rock weathering (Camenzind et al., 2018; Liu, Gundersen, Zhang, & Mo, 2012; Whitaker et al., 2014). Finally, elevational patterns of SMB in colder climates can be complicated by the occurrence of freeze–thaw cycles (Gao et al., 2018), snow melt (Flerchinger, Fellows, Seyfried, Clark, & Lohse, 2019) and microbial dormancy (Salazar, Sulman, & Dukes, 2018).

The inconsistent relationship between SMB and MAP between climate zones is consistent with the results of a recent meta-analysis (Ren et al., 2018), suggesting that temperature and precipitation may interplay on SMB. Soil pH and C : N ratio have been identified as the key ecosystem properties controlling SMB at local and regional scales (Aciego Pietri & Brookes, 2009; Manzoni, Jackson, Trofymow, & Porporato, 2008; Manzoni, Taylor, Richter, Porporato, & Ågren, 2012; Rousk, Bååth, et al., 2010; Sinsabaugh, Manzoni, Moorhead, & Richter, 2013). In the current study these two soil properties were significantly but weakly ($R^2 < 0.10$) linked to SMB along global elevational gradients. These results suggest that neither soil C : N ratio nor soil pH was the dominant factor controlling the elevational pattern of SMB, or at least less important than SOC and TN.

Note that SMB can also be affected by microbial properties such as maintenance energy demand, biochemical efficiency, microbial turnover and C use efficiency (Cotrufo et al., 2013; Kallenbach, Frey, & Grandy, 2016; Kallenbach, Grandy, Frey, & Diefendorf, 2015). How these microbial properties can be affected by the change in temperature along an elevational gradient remains unknown (Frey, Lee, Melillo, & Six, 2013; Hagerty et al., 2014; Li et al., 2019). Soil particle size may affect SMB both directly via soil microbial turnover and indirectly via its effects on SOC and other edaphic properties (e.g., soil water content; Doetterl et al., 2015; Hemingway et al., 2019). Nevertheless, few measurements of soil particle size were available in our compiled datasets, which prevents a quantitative assessment of its effect on SMB. These unknowns need to be addressed in future studies.

5 | CONCLUSION

Understanding the responses of SMB to physico-chemical conditions associated with elevational gradients is critical for predicting how ecosystems will respond to climate change and global warming. We found that SMB increased significantly with elevation in the tropics and subtropics, but not in colder regions. The elevational change in SMB was closely related to the elevational changes in SOC and TN in all climate zones. Given that elevational gradients may serve as a proxy for impacts of climate change, our study illustrates that the effects of climate change on SMB and ecosystem functioning may differ between climate zones, with increased severity in the (sub)tropics. A future challenge will be to quantify drivers, such as shifts in physico-chemical conditions, underlying these different responses of SMB to elevation.

DATA ACCESSIBILITY

Data for the meta-analysis in this study have been deposited at the Dryad website (http://datadryad.org/) with file name Appendix S1 and https://doi.org/10.5061/dryad.nc57k7g.

ORCID

Xianjin He ![iD] https://orcid.org/0000-0002-5573-607X

Xinghua Sui ![iD] https://orcid.org/0000-0001-6076-4318

REFERENCES

Aciego Pietri, J. C., & Brookes, P. C. (2009). Substrate inputs and pH as factors controlling microbial biomass, activity and community structure in an arable soil. *Soil Biology and Biochemistry*, *41*(7), 1396–1405. https://doi.org/10.1016/j.soilbio.2009.03.017

Bachar, A., Al-Ashhab, A., Soares, M. I. M., Sklarz, M. Y., Angel, R., Ungar, E. D., & Gillor, O. (2010). Soil microbial abundance and diversity along a low precipitation gradient. *Microbial Ecology*, *60*(2), 453–461. https://doi.org/10.1007/s00248-010-9727-1

Baker, B., Diaz, H., Hargrove, W., & Hoffman, F. (2010). Use of the Köppen-Trewartha climate classification to evaluate climatic refugia in statistically derived ecoregions for the People's Republic of China. *Climatic Change*, *98*(1–2), 113–131. https://doi.org/10.1007/s10584-009-9622-2

Bardgett, R. D., & Wardle, D. A. (2010). *Aboveground-belowground linkages: Biotic interactions, ecosystem processes, and global change*. New York, NY: Oxford University Press.

Blankinship, J. C., Niklaus, P. A., & Hungate, B. A. (2011). A meta-analysis of responses of soil biota to global change. *Oecologia*, *165*(3), 553–565. https://doi.org/10.1007/s00442-011-1909-0

Bradford, M. A., Mcculley, R. L., Crowther, T. W., Oldfield, E. E., Wood, S. A., & Fierer, N. (2019). Cross-biome patterns in soil microbial respiration predictable from evolutionary theory on thermal adaptation. *Nature Ecology and Evolution*, *3*(2), 223–231. https://doi.org/10.1038/s41559-018-0771-4

Bradford, M. A., Veen, G. F., Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H. C., … van der Putten, W. H. (2017). A test of the hierarchical model of litter decomposition. *Nature Ecology and Evolution*, *1*(12), 1836–1845. https://doi.org/10.1038/s41559-017-0367-4

Bragazza, L., Bardgett, R. D., Mitchell, E. A. D., & Buttler, A. (2015). Linking soil microbial communities to vascular plant abundance along a climate gradient. *New Phytologist*, *205*(3), 1175–1182. https://doi.org/10.1111/nph.13116

Camenzind, T., Hättenschwiler, S., Treseder, K. K., Lehmann, A., & Rillig, M. C. (2018). Nutrient limitation of soil microbial processes in tropical forests. *Ecological Monographs*, *88*(1), 4–21. https://doi.org/10.1002/ecm.1279

Capek, P., Starke, R., Hofmockel, K. S., Bond-Lamberty, B., & Hess, N. (2019). Apparent temperature sensitivity of soil respiration can result from temperature driven changes in microbial biomass. *Soil Biology and Biochemistry*, *135*, 286–293. https://doi.org/10.1016/j.soilbio.2019.05.016

Chang, E., Chen, T., Tian, G., & Chiu, C. (2016). The effect of altitudinal gradient on soil microbial community activity and structure in moso bamboo plantations. *Applied Soil Ecology*, *98*, 213–220. https://doi.org/10.1016/j.apsoil.2015.10.018

Chen, H., Li, D., Xiao, K., & Wang, K. (2018). Soil microbial processes and resource limitation in karst and non-karst forests. *Functional Ecology*, *32*(5), 1400–1409. https://doi.org/10.1111/1365-2435.13069

Cheng, F., Peng, X., Zhao, P., Yuan, J., Zhong, C., Cheng, Y., … Zhang, S. (2013). Soil microbial biomass, basal respiration and enzyme activity of main forest types in the Qinling Mountains. *PLoS ONE*, *8*(6), e67353. https://doi.org/10.1371/journal.pone.0067353

Cleveland, C. C., & Liptzin, D. (2007). C:N:P stoichiometry in soil: Is there a "Redfield Ratio" for the microbial biomass? *Biogeochemistry*, *85*(3), 235–252. https://doi.org/10.1007/s10533-007-9132-0

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, *8*(10), 776–779. https://doi.org/10.1038/ngeo2520

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*(4), 988–995. https://doi.org/10.1111/gcb.12113

Crowther, T. W., Todd-Brown, K. E. O., Rowe, C. W., Wieder, W. R., Carey, J. C., Machmuller, M. B., … Bradford, M. A. (2016). Quantifying global soil carbon losses in response to warming. *Nature*, *540*(7631), 104–108.

Cui, H., Wang, G., Yang, Y., Yang, Y., Chang, R., & Ran, F. (2016). Soil microbial community composition and its driving factors in alpine grasslands along a mountain elevational gradient. *Journal of Mountain Science*, *13*(6), 1013–1023. https://doi.org/10.1007/s11629-015-3614-7

Djukic, I., Zehetner, F., Mentler, A., & Gerzabek, M. H. (2010). Microbial community composition and activity in different Alpine vegetation zones. *Soil Biology and Biochemistry*, *42*(2), 155–161. https://doi.org/10.1016/j.soilbio.2009.10.006

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., … Boeckx, P. (2015). Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geoscience*, *8*(10), 780–783. https://doi.org/10.1038/ngeo2516

Donald, J., Bonnett, S., Cutler, M., Majalap, N., Maxfield, P., & Ellwood, M. D. F. (2017). Physical conditions regulate the fungal to bacterial ratios of a tropical suspended soil. *Forests*, *8*(12), 474. https://doi.org/10.3390/f8120474

Drenovsky, R. E., Steenwerth, K. L., Jackson, L. E., & Scow, K. M. (2010). Land use and climatic factors structure regional patterns in soil microbial communities. *Global Ecology and Biogeography*, *19*(1), 27–39. https://doi.org/10.1111/j.1466-8238.2009.00486.x

Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *BMJ*, *315*(7109), 629–634.

Fierer, N., Strickland, M. S., Liptzin, D., Bradford, M. A., & Cleveland, C. C. (2009). Global patterns in belowground communities. *Ecology Letters*, *12*(11), 1238–1249. https://doi.org/10.1111/j.1461-0248.2009.01360.x

Flerchinger, G. N., Fellows, A. W., Seyfried, M. S., Clark, P. E., & Lohse, K. A. (2019). Water and carbon fluxes along an elevational gradient in a sagebrush ecosystem. *Ecosystems*. https://doi.org/10.1007/s10021-019-00400-x

Frey, S. D., Lee, J., Melillo, J. M., & Six, J. (2013). The temperature response of soil microbial efficiency and its feedback to climate. *Nature Climate Change*, 3(4), 395–398. https://doi.org/10.1038/nclimate1796

Frostegård, Å., & Bååth, E. (1996). The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biology and Fertility of Soils*, 22(1–2), 59–65. https://doi.org/10.1007/BF00384433

Fukami, T., & Wardle, D. A. (2005). Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B: Biological Sciences*, 272(1577), 2105–2115.

Gao, D., Zhang, L., Liu, J., Peng, B. O., Fan, Z., Dai, W., … Bai, E. (2018). Responses of terrestrial nitrogen pools and dynamics to different patterns of freeze-thaw cycle: A meta-analysis. *Global Change Biology*, 24(6), 2377–2389. https://doi.org/10.1111/gcb.14010

Hagerty, S. B., van Groenigen, K. J., Allison, S. D., Hungate, B. A., Schwartz, E., Koch, G. W., … Dijkstra, P. (2014). Accelerated microbial turnover but constant growth efficiency with warming in soil. *Nature Climate Change*, 4(10), 903–906. https://doi.org/10.1038/nclimate2361

Hemingway, J. D., Rothman, D. H., Grant, K. E., Rosengard, S. Z., Eglinton, T. I., Derry, L. A., & Galy, V. V. (2019). Mineral protection regulates long-term global preservation of natural organic carbon. *Nature*, 570(7760), 228–231.

Hendershot, J. N., Read, Q. D., Henning, J. A., Sanders, N. J., & Classen, A. T. (2017). Consistently inconsistent drivers of microbial diversity and abundance at macroecological scales. *Ecology*, 98(7), 1757–1763. https://doi.org/10.1002/ecy.1829

Hijmans, R. J. (2017). Raster: Geographic data analysis and modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster

Hu, Y., Xiang, D., Veresoglou, S. D., Chen, F., Chen, Y., Hao, Z., … Chen, B. (2014). Soil organic carbon and soil structure are driving microbial abundance and community composition across the arid and semi-arid grasslands in northern China. *Soil Biology and Biochemistry*, 77, 51–57. https://doi.org/10.1016/j.soilbio.2014.06.014

Joergensen, R. G. (1996). The fumigation-extraction method to estimate soil microbial biomass: Calibration of the kEC value. *Soil Biology and Biochemistry*, 28(1), 25–31. https://doi.org/10.1016/0038-0717(95)00102-6

Kallenbach, C. M., Frey, S. D., & Grandy, A. S. (2016). Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nature Communications*, 7(1), 13630. https://doi.org/10.1038/ncomms13630

Kallenbach, C. M., Grandy, A. S., Frey, S. D., & Diefendorf, A. F. (2015). Microbial physiology and necromass regulate agricultural soil carbon accumulation. *Soil Biology and Biochemistry*, 91, 279–290. https://doi.org/10.1016/j.soilbio.2015.09.005

Kitayama, K., & Aiba, S. (2002). Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology*, 90(1), 37–51. https://doi.org/10.1046/j.0022-0477.2001.00634.x

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology and Evolution*, 22(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Kotas, P., Aantrůčková, H., Elster, J., & Kaštovská, E. (2018). Soil microbial biomass, activity and community composition along altitudinal gradients in the High Arctic (Billefjorden, Svalbard). *Biogeosciences*, 15(6), 1879–1894. https://doi.org/10.5194/bg-15-1879-2018

Krashevska, V., Bonkowski, M., Maraun, M., Ruess, L., Kandeler, E., & Scheu, S. (2008). Microorganisms as driving factors for the community structure of testate amoebae along an altitudinal transect in tropical mountain rain forests. *Soil Biology and Biochemistry*, 40(9), 2427–2433. https://doi.org/10.1016/j.soilbio.2008.06.004

Lange, M., Eisenhauer, N., Sierra, C. A., Bessler, H., Engels, C., Griffiths, R. I., … Gleixner, G. (2015). Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications*, 6(1), 6707. https://doi.org/10.1038/ncomms7707

Leckie, S. E., Prescott, C. E., Grayston, S. J., Neufeld, J. D., & Mohn, W. W. (2004). Comparison of chloroform fumigation-extraction, phospholipid fatty acid, and DNA methods to determine microbial biomass in forest humus. *Soil Biology and Biochemistry*, 36(3), 529–532. https://doi.org/10.1016/j.soilbio.2003.10.014

Lehmann, J., & Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*, 528(7580), 60–68.

Lei, T., Si, G., Wang, J., & Zhang, G. (2017). Microbial communities and associated enzyme activities in alpine wetlands with increasing altitude on the Tibetan plateau. *Wetlands*, 37(3), 401–412. https://doi.org/10.1007/s13157-017-0876-6

Li, J., Wang, G., Mayes, M. A., Allison, S. D., Frey, S. D., Shi, Z., … Melillo, J. M. (2019). Reduced carbon use efficiency and increased microbial turnover with soil warming. *Global Change Biology*, 25(3), 900–910.

Lin, Y., Whitman, W. B., Coleman, D. C., Shi, S., Tang, S., & Chiu, C. (2015). Changes of soil bacterial communities in bamboo plantations at different elevations. *FEMS Microbiology Ecology*, 91(5), fv033. https://doi.org/10.1093/femsec/fiv033

Liu, L., Gundersen, P., Zhang, T., & Mo, J. (2012). Effects of phosphorus addition on soil microbial biomass and community composition in three forest types in tropical China. *Soil Biology and Biochemistry*, 44(1), 31–38. https://doi.org/10.1016/j.soilbio.2011.08.017

Manzoni, S., Jackson, R. B., Trofymow, J. A., & Porporato, A. (2008). The global stoichiometry of litter nitrogen mineralization. *Science*, 321(5889), 684–686.

Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Ågren, G. I. (2012). Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*, 196(1), 79–91. https://doi.org/10.1111/j.1469-8137.2012.04225.x

Mayor, J. R., Sanders, N. J., Classen, A. T., Bardgett, R. D., Clément, J., Fajardo, A., … Wardle, D. A. (2017). Elevation alters ecosystem properties across temperate treelines globally. *Nature*, 542(7639), 91–95.

Nottingham, A. T., Whitaker, J., Turner, B. L., Salinas, N., Zimmermann, M., Malhi, Y., & Meir, P. (2015). Climate warming and soil carbon in tropical forests: Insights from an elevation gradient in the Peruvian Andes. *BioScience*, 65(9), 906–921. https://doi.org/10.1093/biosci/biv109

Paul, E. A. (2016). The nature and dynamics of soil organic matter: Plant inputs, microbial transformations, and organic matter stabilization. *Soil Biology and Biochemistry*, 98, 109–126. https://doi.org/10.1016/j.soilbio.2016.04.001

Pold, G., Grandy, A. S., Melillo, J. M., & Deangelis, K. M. (2017). Changes in substrate availability drive carbon cycle response to chronic warming. *Soil Biology and Biochemistry*, 110, 68–78. https://doi.org/10.1016/j.soilbio.2017.03.002

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ren, C., Chen, J. I., Lu, X., Doughty, R., Zhao, F., Zhong, Z., … Ren, G. (2018). Responses of soil total microbial biomass and community compositions to rainfall reductions. *Soil Biology and Biochemistry*, 116, 4–10. https://doi.org/10.1016/j.soilbio.2017.09.028

Rosenthal, R., & Rosnow, R. L. (1991). *Essentials of behavioral research: Methods and data analysis* (2nd ed.). New York, NY: McGraw Hill.

Rousk, J., Bååth, E., Brookes, P. C., Lauber, C. L., Lozupone, C., Caporaso, J. G., … Fierer, N. (2010). Soil bacterial and fungal communities across a pH gradient in an arable soil. *The ISME Journal*. https://doi.org/10.1038/ismej.2010.58

Rousk, J., Brookes, P. C., & Bååth, E. (2010). The microbial PLFA composition as affected by pH in an arable soil. *Soil Biology and Biochemistry*, 42(3), 516–520. https://doi.org/10.1016/j.soilbio.2009.11.026

Salazar, A., Sulman, B. N., & Dukes, J. S. (2018). Microbial dormancy promotes microbial biomass and respiration across pulses of drying-wetting stress. *Soil Biology and Biochemistry*, 116, 237–244. https://doi.org/10.1016/j.soilbio.2017.10.017

Scheiner, S. M., & Gurevitch, J. (2001). Meta-analysis: Combining the results of independent experiments. In J. Gurevitch, & L. V. Hedges (Eds.), *Design and analysis of ecological experiments* (pp. 347–369). UK: Oxford University Press.

Serna-Chavez, H. M., Fierer, N., & van Bodegom, P. M. (2013). Global drivers and patterns of microbial abundance in soil. *Global Ecology and Biogeography*, 22(10), 1162–1172. https://doi.org/10.1111/geb.12070

Siles, J. A., Cajthaml, T., Minerbi, S., & Margesin, R. (2016). Effect of altitude and season on microbial activity, abundance and community structure in Alpine forest soils. *FEMS Microbiology Ecology*, 92(3), fiw008. https://doi.org/10.1093/femsec/fiw008

Singh, J. S., & Gupta, V. K. (2018). Soil microbial biomass: A key soil driver in management of ecosystem functioning. *Science of the Total Environment*, 634, 497–500. https://doi.org/10.1016/j.scitotenv.2018.03.373

Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L., & Richter, A. (2013). Carbon use efficiency of microbial communities: Stoichiometry, methodology and modelling. *Ecology Letters*, 16(7), 930–939. https://doi.org/10.1111/ele.12113

Sundqvist, M. K., Giesler, R., Graae, B. J., Wallander, H., Fogelberg, E., & Wardle, D. A. (2011). Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. *Oikos*, 120(1), 128–142. https://doi.org/10.1111/j.1600-0706.2010.18811.x

Sundqvist, M. K., Sanders, N. J., & Wardle, D. A. (2013). Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. *Annual Review of Ecology, Evolution and Systematics*, 44(1), 261–280. https://doi.org/10.1146/annurev-ecolsys-110512-135750

Tashi, S., Singh, B., Keitel, C., & Adams, M. (2016). Soil carbon and nitrogen stocks in forests along an altitudinal gradient in the eastern Himalayas and a meta-analysis of global data. *Global Change Biology*, 22(6), 2255–2268. https://doi.org/10.1111/gcb.13234

Traoré, O. Y. A., Kiba, D. I., Arnold, M. C., Fliessbach, A., Oberholzer, H. R., Nacro, H. B., … Bünemann, E. K. (2016). Fertilization practices alter microbial nutrient limitations after alleviation of carbon limitation in a Ferric Acrisol. *Biology and Fertility of Soils*, 52(2), 177–189. https://doi.org/10.1007/s00374-015-1061-9

Veen, G. F. C., De Long, J. R., Kardol, P., Sundqvist, M. K., Snoek, L. B., & Wardle, D. A. (2017). Coordinated responses of soil communities to elevation in three subarctic vegetation types. *Oikos*, 126(11), 1586–1599. https://doi.org/10.1111/oik.04158

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36(3), 1–48.

Vimal, S. R., Singh, J. S., Arora, N., & Singh, S. (2017). Soil-plant-microbe interactions in stressed agriculture management: A review. *Pedosphere*, 27(2), 177–192. https://doi.org/10.1016/S1002-0160(17)60309-6

Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. A. (2010). Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen–phosphorus interactions. *Ecological Applications*, 20(1), 5–15. https://doi.org/10.1890/08-0127.1

Wagai, R., Kitayama, K., Satomura, T., Fujinuma, R., & Balser, T. (2011). Interactive influences of climate and parent material on soil microbial community structure in Bornean tropical forest ecosystems. *Ecological Research*, 26(3), 627–636. https://doi.org/10.1007/s11284-011-0822-7

Wang, G., Ran, F., Chang, R., Yang, Y., Luo, J., & Jianrong, F. (2014). Variations in the live biomass and carbon pools of Abies georgei along an elevation gradient on the Tibetan Plateau, China. *Forest Ecology and Management*, 329, 255–263. https://doi.org/10.1016/j.foreco.2014.06.023

Wardle, D. (1992). A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biological Reviews*, 67(3), 321–358. https://doi.org/10.1111/j.1469-185X.1992.tb00728.x

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304(5677), 1629–1633.

Whitaker, J., Ostle, N., Nottingham, A. T., Ccahuana, A., Salinas, N., Bardgett, R. D., … McNamara, N. P. (2014). Microbial community composition explains soil respiration responses to changing carbon inputs along an Andes-to-Amazon elevation gradient. *Journal of Ecology*, 102(4), 1058–1071. https://doi.org/10.1111/1365-2745.12247

Xu, M., Li, X., Cai, X., Gai, J., Li, X., Christie, P., & Zhang, J. (2014). Soil microbial community structure and activity along a montane elevational gradient on the Tibetan Plateau. *European Journal of Soil Biology*, 64, 6–14. https://doi.org/10.1016/j.ejsobi.2014.06.002

Xu, W., & Yuan, W. (2017). Responses of microbial biomass carbon and nitrogen to experimental warming: A meta-analysis. *Soil Biology and Biochemistry*, 115, 265–274. https://doi.org/10.1016/j.soilbio.2017.08.033

Xu, X., Thornton, P. E., & Post, W. M. (2013). A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography*, 22(6), 737–749. https://doi.org/10.1111/geb.12029

Yuan, Z. Y., Jiao, F., Shi, X. R., Sardans, J., Maestre, F. T., Delgado-Baquerizo, M., … Peñuelas, J. (2017). Experimental and observational studies find contrasting responses of soil nutrients to climate change. *eLife*, 6, e23255. https://doi.org/10.7554/eLife.23255

Zhang, B., Liang, C., He, H., & Zhang, X. (2013). Variations in soil microbial communities and residues along an altitude gradient on the northern slope of Changbai Mountain, China. *PLoS ONE*, 8(6), e66184. https://doi.org/10.1371/journal.pone.0066184

Zhang, T. A., Chen, H. Y. H., & Ruan, H. (2018). Global negative effects of nitrogen deposition on soil microbes. *The ISME Journal*, 12(7), 1817–1825. https://doi.org/10.1038/s41396-018-0096-y

Zhou, J., Wu, Y., Bing, H., Yang, Z., Wang, J., Sun, H., … Luo, J. I. (2016). Variations in soil phosphorus biogeochemistry across six vegetation types along an altitudinal gradient in SW China. *Catena*, 142, 102–111. https://doi.org/10.1016/j.catena.2016.03.004

Zhou, Y., Clark, M., Su, J., & Xiao, C. (2015). Litter decomposition and soil microbial community composition in three Korean pine (Pinus koraiensis) forests along an altitudinal gradient. *Plant and Soil*, 386(1–2), 171–183. https://doi.org/10.1007/s11104-014-2254-y

BIOSKETCHES

Xianjin He is a research associate whose research focuses on soil biodiversity and biogeochemical cycles.

Enqing Hou is a soil scientist focusing on nutrient dynamics in natural terrestrial ecosystems.

Chengjin Chu is a plant community ecologist whose primary research involves understanding biodiversity maintenance mechanisms and responses of biodiversity to climate change.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: He X, Hou E, Veen GF, et al. Soil microbial biomass increases along elevational gradients in the tropics and subtropics but not elsewhere. *Global Ecol Biogeogr*. 2019;00:1–10. https://doi.org/10.1111/geb.13017