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Special Section:

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Key Points:

- Soil microbial respiration rates adapt to ambient temperature with a compensatory response in global croplands
- The compensatory thermal adaptive capacity of soil microorganisms is lower in croplands than in natural ecosystems
- A warmer climate may select for microbial communities with higher carbon use efficiency in cropland soils

Supporting Information:

- Supporting Information S1

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Compensatory Thermal Adaptation of Soil Microbial Respiration Rates in Global Croplands

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Abstract Understanding whether soil microbial respiration adapts to the ambient thermal climate with an enhanced or compensatory response, hence potentially stimulating or slowing down soil carbon losses with warming, is key to accurately forecast and model climate change impacts on the global carbon cycle. Despite the interest in this topic and the plethora of recent studies in natural ecosystems, it has been seldom explored in croplands. Using two recently published independent datasets of soil microbial metabolic quotient (MMQ; microbial respiration rate per unit biomass) and carbon use efficiency (CUE; partitioning of C to microbial growth vs. respiration), we find a compensatory thermal adaptive response for MMQ in global croplands. That is, mean annual temperature (MAT) has a negative effect on MMQ. However, this compensatory thermal adaptation is only half or less of that found in previous studies for noncultivated ecosystems. In contrast to the negative MMQ-MAT pattern, microbial CUE increases with MAT across global croplands. By incorporating this positive CUE-MAT relationship (greater C partitioning into microbial growth rather than respiration with increasing temperature) into a microbial-explicit soil organic carbon model, we successfully predict the thermal compensation of MMQ observed in croplands. Our model-data integration and database cross-validation suggest that a warmer climate may select for microbial communities with higher CUE, providing a plausible mechanism for their compensatory metabolic response. By helping to identify appropriate representations of microbial physiological processes in soil biogeochemical models, our work will help build confidence in model projections of cropland C dynamics under a changing climate.

1. Introduction

The soil organic carbon (SOC) stock, the largest C pool in terrestrial ecosystems (Le Quéré et al., 2014), is sensitive to agricultural practices and climate warming (Davidson & Janssens, 2006; Lal, 2004). The conversion of noncultivated ecosystems to croplands typically causes a decline in SOC stocks because practices such as tilling break apart soil aggregates within which organic C might otherwise persist (Guo & Gifford, 2002; Sanderman et al., 2017). Croplands occupy about 12% of Earth's ice-free land (Foley et al., 2011), and store more than 140 Pg C in the top 30-cm soil depth, the most relevant layer for agricultural production (Zomer et al., 2017). This amount accounts for 19% of the global SOC stocks estimated at this depth (Foley et al., 2011; Jackson et al., 2017). Therefore, understanding how cropland SOC stocks are changing due to ongoing global warming is a pressing issue. Indeed, even subtle SOC losses through soil heterotrophic microbial respiration may represent a substantial contribution to the buildup of the atmospheric CO₂ pool (~750 Pg C, Post et al., 1990). Although climate warming is expected to accelerate the rates of soil microbial respiration in many ecosystems (Bond-Lamberty et al., 2018; Carey et al., 2016; Dorrepaal et al., 2009; Giardina et al., 2014; Heimann & Reichstein, 2008), the outcome of the microbial respiration–temperature relationship remains elusive in croplands (Karhu et al., 2014), where agricultural practices have altered the C gains to and losses from the soil.

In noncultivated ecosystems, warming-induced shifts in soil microbial physiology and community composition can compensate or enhance respiratory losses of SOC in response to warming (Bradford et al., 2019; Dacal et al., 2019; Karhu et al., 2014). Notably, two recent studies conducted across large latitudinal

gradients in mean annual temperature (MAT) found evidence for compensatory adaptation of soil microbial respiration to the ambient thermal regime (Bradford et al., 2019; Dacal et al., 2019). That is, when measured at a common assay temperature, soil microbial respiration rates were lower for soils sampled from higher MAT regimes after controlling for differences in microbial biomass and substrate depletion. Ye et al. (2019) tested competing microbial physiology-temperature relationships in SOC models and demonstrated that the compensatory thermal response found in Bradford et al. (2019) and Dacal et al. (2019) was most likely associated with greater microbial carbon use efficiency (CUE) under warmer climates.

Microbial CUE, which quantifies the partitioning of C to microbial growth versus respiration, is an important variable driving the thermal response of microbial respiration, and it is a key physiological parameter in SOC models (Allison et al., 2010; Georgiou et al., 2017; Schimel & Weintraub, 2003). With increases in temperature, the CUE of microbial communities has been reported to increase (Frey et al., 2013; Sinsabaugh et al., 2016; Takriti et al., 2018; Zheng et al., 2019), decrease (Frey et al., 2013; Qiao et al., 2019; Steinweg et al., 2008; Tucker et al., 2013), or remain unaffected (Dijkstra et al., 2011; Frey et al., 2013; Hagerty et al., 2014). These studies usually attribute changes in CUE to differential changes in rates of microbial respiration versus growth with rising temperatures. However, given the apparent lack of consensus as to how CUE responds to temperature, testing multiple competing hypotheses of CUE-temperature relationships in SOC models may provide a feasible way to advance our understanding of the mechanisms underlying changes in CUE (Ye et al., 2019).

In croplands, and beyond the effects of climate warming, soil microbial metabolism is stimulated by the disturbance and nutrient enrichment caused by agricultural practices such as tilling and inorganic fertilization (Srivastava & Singh, 1989; Xu et al., 2013; Xu et al., 2017). For example, Xu et al. (2017) compiled a global dataset of studies which measured soil microbial metabolic quotient (MMQ; respiration rate per unit biomass, or mass-specific respiration) under laboratory conditions, and found that even though the MAT regime increased soil MMQ in both croplands and natural ecosystems, MMQ was higher in croplands. The large MMQ found in cropland soils was strongly driven by a lower microbial biomass N:P content (Xu et al., 2017), suggesting that microbial growth rates are faster in croplands, potentially because inorganic fertilization increases nutrient availability. Such an explanation is consistent with observations that increased nutrient inputs promote bacterial community shifts towards more copiotrophic taxa (Fierer et al., 2011; Leff et al., 2015), which in turn might reduce the magnitude of thermal compensatory responses of microbial respiration by selecting faster-growing microbes. To examine such possibilities, the comparison of patterns revealed by large-scale empirical databases of microbial processes, with SOC model simulations of microbial physiology, represents a robust approach to advance our understanding of warming effects on SOC stocks and to elucidate the underlying microbial mechanisms (Ye et al., 2019). Such an approach has not, to the best of our knowledge, been used yet to explore relationships between soil microbial respiration and temperature in croplands.

Here we performed a data-model integration using two independent large-scale field datasets that span a MAT gradient from -1°C to 29°C (Sinsabaugh et al., 2016; Xu et al., 2017) to (i) evaluate the patterns of MMQ and CUE across a global MAT gradient in croplands and (ii) assess the potential mechanisms underlying the patterns observed using a microbial-explicit SOC model. First, we asked whether soil MMQ adapts to the ambient thermal regime with a compensatory response across the 126 global croplands compiled in Xu et al. (2017), as hypothesized in Figure 1a. Second, we assessed the thermal response of soil microbial CUE in an independent dataset of 159 cropland soils (Sinsabaugh et al., 2016), to test whether CUE increases with MAT in croplands (Figure 1a). Then, we incorporated this empirical CUE-MAT relationship into a microbial-explicit SOC model and tested whether the simulated soil MMQ versus MAT relationship can represent the patterns observed across the 126 global croplands compiled in Xu et al. (2017). Finally, we tested whether the magnitude of the compensatory thermal adaptation is smaller in global croplands (Sinsabaugh et al., 2016; Xu et al., 2017) than in noncultivated ecosystems (Bradford et al., 2019; Dacal et al., 2019) assessed across a similar MAT gradient, as hypothesized in Figure 1b.

2. Materials and Methods

2.1. Datasets Used

To test the thermal response of soil MMQ and CUE in croplands, we used two independent large-scale datasets, respectively. In the MMQ datasets, soil samples from a wide range of MAT gradient were incubated at

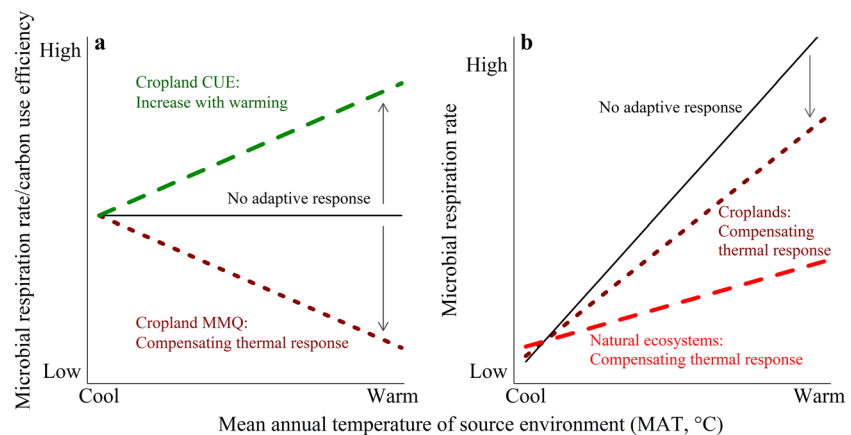


Figure 1. Hypothesized microbial physiology-temperature relationships in cropland soils consistent with a compensating thermal response across a wide mean annual temperature (MAT) gradient. (a) The soil microbial metabolic quotient (MMQ) shows compensatory thermal adaptation to increasing MAT. That is, when measured at a common assay temperature, cropland soils sampled from warmer climate have lower MMQ. Conversely, the soil microbial carbon use efficiency (CUE) is higher in warmer climates. (b) To compare the compensatory thermal adaptation in croplands versus noncultivated ecosystems, the soil MMQ is measured at the ambient temperature regime where the soil was sampled (i.e., MAT). Soil MMQ increases in warmer climates but to a lesser extent (dashed lines) than would be observed with no adaptive response (solid line). We hypothesize that high phosphorous concentrations might stimulate microbial activity and metabolism in cropland soils and hence reduce the magnitude of thermal compensatory responses of microbial respiration.

consistent assay temperatures and optimal moisture in the laboratory (Xu et al., 2017). This approach constitutes a unique and robust test of microbial thermal adaptation (Bradford et al., 2008; Karhu et al., 2014), as inferring the thermal response of microbial variables from field studies comparing, for example, warmed and control plots can be confounded by a suite of factors that might also differ between treatments, such as plant C inputs and soil moisture (Carey et al., 2016; Garcia-Palacios et al., 2018). In Xu et al. (2017), soil basal respiration rates (BRs) were measured in short-term incubations, which limit the acclimation of soil microbial respiration to the assay temperature in the laboratory (Bradford et al., 2010; Dacal et al., 2019; Hochachka & Somero, 2002). Furthermore, soil microbial biomass is unlikely to change substantively in the short-term, which is the fundamental assumption for calculating the MMQ, that is, respiration rate per unit microbial biomass (Xu et al., 2017). The dataset included 126 cropland soils with data for BR, microbial biomass carbon (MBC), MAT (usually the mean of 30-year, Fick & Hijmans, 2017), assay temperature (T), soil pH, and soil C, nitrogen (N) and phosphorous (P) contents. The 126 soils spanned a 30°C MAT gradient (from -1°C to 29°C). We calculated soil MMQ as BR/MBC (Anderson & Domsch, 1993; Xu et al., 2017) because microbial biomass is a major factor affecting the thermal response of soil respiration and thermal adaptation should be tested on a per unit biomass basis (Bradford et al., 2008; Bradford et al., 2019; Dacal et al., 2019; Walker et al., 2018).

We obtained a CUE dataset of 159 cropland soils from Sinsabaugh et al. (2016), to assess the thermal response of soil microbial CUE. These data were not available from Xu et al. (2017). The 159 cropland soils spanned a MAT gradient of ~9°C to 26°C, and included data for MAT, soil pH and soil and microbial biomass C:N ratios (see supporting information Data S1 for the dataset). Soil microbial CUE was seldom measured directly in soils due to the methodological difficulty of measuring in situ rates of microbial growth and respiration (Sinsabaugh et al., 2016). Therefore, Sinsabaugh et al. (2016) indirectly estimated CUE as a function of the difference between elemental requirements for microbial growth and the elemental composition of soil organic matter. Although soil microbial CUE and MMQ were obtained from different studies, having CUE data from an independent dataset allowed us to conduct a robust cross-validation of soil MMQ predicted by SOC models. Sinsabaugh et al. (2016) and Xu et al. (2017) extracted CUE and MMQ data from published studies. Some values were extracted as presented in the publications as means from multiple samples collected from specific sites, treatments (such as crop types and fertilizer applications), soil horizons, and/or dates. For some studies, original authors provided full datasets where each sample had independent measurements. Thus, we included the CUE and MMQ measurements as independent samples in the

multiple linear regressions, following the same approach used by Xu et al. (2017) and Sinsabaugh et al. (2016).

2.2. Assessing the Thermal Response of Soil MMQ and CUE

Soil basal respiration was measured at different assay/incubation temperatures in the studies compiled by (Xu et al., 2017), whereas thermal adaptation should be tested at a common temperature (Bradford et al., 2019; Dacal et al., 2019). To account for the lack of a common assay temperature we used three approaches to test the hypothesized compensatory thermal adaptation represented in Figure 1a, which also allowed us to evaluate whether the patterns detected were robust to the specific analytical method used. First, up to 60% of measurements (73 soils) in Xu et al. (2017) were conducted using a 25°C assay temperature. Thus, we built multiple linear regressions between soil MMQ and the controlling variables (MAT, soil C:N, C:P, and pH) identified as important for soil microbial metabolism (Bradford et al., 2019; Hou et al., 2019; Karhu et al., 2014; Xu et al., 2017). Soil C was not included in these regressions as it is highly correlated with C:N (Pearson's $r = 0.63$), and including it did not change the regression coefficient of MAT (see supporting information Table S1). We estimated the effect of MAT on soil MMQ using the regression coefficients. Second, we built the same multiple linear regression model but using the full dataset (126 soils), and statistically controlled for the influence of assay temperature by including it in the model as a predictor. For estimating the effect of MAT on soil MMQ, we could then again use the regression coefficients; in this case we fixed the assay temperature at the mean of the temperature assayed across all cropland soils by including the assay temperature coefficient. The approach is conceptually analogous to evaluating soil MMQ at a common assay temperature (Bradford et al., 2019; Dacal et al., 2019). Finally, we adjusted the full dataset of soil basal respirations at different assay temperatures to a common temperature of 25°C using equation 1 and a temperature sensitivity of $Q_{10} = 2$, as suggested in Xu et al. (2017).

$$BR_{25} = BR_T \times Q_{10}^{(25-T)/10} \quad (1)$$

where T is the assay temperature for each soil, and BR_T and BR_{25} are the soil basal respirations at T and 25°C, respectively. Then, we built a similar multiple linear regression model between soil MMQ and its controlling variables using the adjusted soil BR dataset.

We also built a multiple linear regression between soil microbial CUE and the controlling variables (MAT, soil pH, soil, and microbial biomass C:N) to assess the thermal response of CUE. All multiple linear regressions were built using R version 3.5.1 (R Core Team, 2018). We present the unstandardized coefficients for all regressions, as our objective is to compare the MMQ-MAT pattern estimated from these empirical coefficients with that simulated by SOC models (detailed below in section 2.3).

2.3. Simulating the Thermal Response of Soil MMQ and Comparisons With Observed Data

We used a microbial-explicit SOC model (Allison et al., 2010; Georgiou et al., 2017; German et al., 2012; Li et al., 2014; Ye et al., 2019) to simulate soil microbial respiration rates. In microbial-explicit SOC models, the decomposition rate of SOC depends on the size of both the soil C and microbial pools (see supporting information Figure S1 for a diagram). The model runs at an hourly time step and includes a microbial CUE that portions C into microbial biomass growth and heterotrophic respiration (Allison et al., 2010; Georgiou et al., 2017; Li et al., 2014; Wang et al., 2013). A higher CUE allocates a larger fraction of C uptake into microbial biomass growth and hence a lower fraction to CO_2 respiration. Therefore, a higher CUE should associate with a lower MMQ, and vice versa (Ballantyne & Billings, 2018). A full description of the SOC model equations and parameter values used are given in the supporting information, Method S1. To increase the consistency between our model simulations and the measured soil microbial respiration in global croplands (Xu et al., 2017), we (i) ran SOC models for a time scale of 10 hr, (ii) set the C inputs to zero during the 10-hr simulations, and (iii) set the soil C pool size (i.e., C substrate) at steady state or ambient level (see Method S1 for the value). By doing so our model outputs mimicked short-term BR and MBC to calculate soil MMQ as in Xu et al. (2017).

We established 31 “theoretical” cropland sites across the MAT gradient present in the measured data (ranging from $-1^\circ C$ to $29^\circ C$), and set one site for each $1^\circ C$ difference in MAT. We ran two types of model simulations, corresponding to the two hypotheses shown in Figure 1. First, to test the compensatory thermal adaptation of soil MMQ (Figure 1a), we incorporated the empirical CUE-MAT relationship found in global

Table 1
Unstandardized Coefficients (Mean \pm Standard Error) of the Multiple Linear Regressions Used to Assess the Thermal Response of Soil Microbial Metabolic Quotient (MMQ, $\text{mmol C} \cdot \text{mol MBC}^{-1} \cdot \text{hr}^{-1}$) in Global Croplands

	25°C assay	Full dataset	Adjusted by $Q_{10} = 2$
	$n = 73$	$n = 126$	$n = 126$
Mean annual temperature	$-0.014 \pm 0.007^*$	$-0.048 \pm 0.009^{***}$	$-0.042 \pm 0.014^{***}$
Soil pH	-0.026 ± 0.073	$-0.399 \pm 0.100^{***}$	$-0.341 \pm 0.150^*$
Soil C:N ratio	0.219 ± 0.178	$1.790 \pm 0.190^{***}$	$3.412 \pm 0.205^{***}$
Soil C:P ratio	$-0.370 \pm 0.062^{***}$	$-0.689 \pm 0.083^{***}$	$-0.458 \pm 0.121^{***}$
Assay temperature		$0.644 \pm 0.047^{***}$	
Intercept	$-4.250 \pm 0.808^{***}$	$-19.534 \pm 1.366^{***}$	$-8.860 \pm 1.729^{***}$
Adjusted R^2	0.524 ^{***}	0.884 ^{***}	0.709 ^{***}

Note. MMQ, soil C:N, and C:P ratios were natural-log-transformed to meet assumptions of normality. Model coefficients are shown for the three approaches followed to test the hypothesized compensatory thermal adaptation at a common assay temperature: (i) only data measured at a 25°C assay temperature, (ii) all studies included with the effect of assay temperature controlled for in the model (by inclusion as a predictor), and (iii) all data included and basal respiration rates adjusted to a 25°C assay temperature using $Q_{10} = 2$. MMQ data are obtained from Xu et al. (2017). C, N, and P are soil carbon, nitrogen, and phosphorous contents, respectively.
 $P < 0.001$, $^* P < 0.05$.

croplands (see section 2.2) into the SOC model, and then ran the model for the 31 sites at three increasing assay temperatures (15°C, 20°C, and 25°C). As a comparison, we also estimated empirical MMQ based on the unstandardized coefficients for MAT and assay temperature in the multiple linear regressions (see section 2.2). Second, to estimate to what extent the compensatory thermal adaptation can alter the soil MMQ-temperature relationship (Figure 1b), we simulated soil MMQ by setting an assay temperature that matched the site's MAT value, and hypothesized two scenarios: (i) a thermal adaptation scenario where soil MMQ was influenced by the empirical CUE-MAT relationship found in global croplands and (ii) a no-adaptation scenario where the slope coefficient of the CUE-MAT relationship was set to zero. We also estimated empirical MMQ with an assay temperature that matched the site's MAT value for two scenarios. We used the regression coefficients for the MAT and assay temperature for the adaptation scenario, then set the coefficient for MAT to zero for the no-adaptation scenario.

To test whether soil MMQ had consistent thermal adaptation in the longer-term, we also ran the model until all soil C stocks and fluxes reached steady state (~40 years, supporting information Figure S2). As the soil C pool could be depleted in the longer-term, we set the C inputs to steady state values (see Method S1 for the values).

2.4. Comparing the Thermal Response of Soil MMQ in Croplands Versus Noncultivated Ecosystems

We assessed whether the magnitude of the compensatory thermal adaptation is smaller in croplands (Sinsabaugh et al., 2016; Xu et al., 2017) than in noncultivated ecosystems (Bradford et al., 2019; Dacal et al., 2019), as hypothesized in Figure 1b. To test thermal adaptation of soil MMQ, Dacal et al. (2019) and Bradford et al. (2019) collected soils from 110 globally distributed drylands and from 22 sites spanning from boreal to tropical climates, respectively. They measured soil microbial respiration rates in the laboratory under standardized temperature and moisture conditions, and two C substrate levels (i.e., basal level with water only or with excess glucose addition). They built linear regression models between MMQ and the controlling variables; estimated coefficients for MAT and assay temperatures were consistent—in terms of their sign—between the two C substrate levels used (Table S2). We obtained the unstandardized (and unpublished, Table S2) regression coefficients at basal levels from these studies, and estimated empirical MMQ with an assay temperature that matched the site's MAT value under both scenarios (adaptation and no-adaptation; same as the second approach in section 2.3).

3. Results

Soil MMQ significantly decreased with increasing MAT (Table 1). This decrease occurred irrespective of the analytical methods followed to control for the different assay temperatures across studies. The decrease is

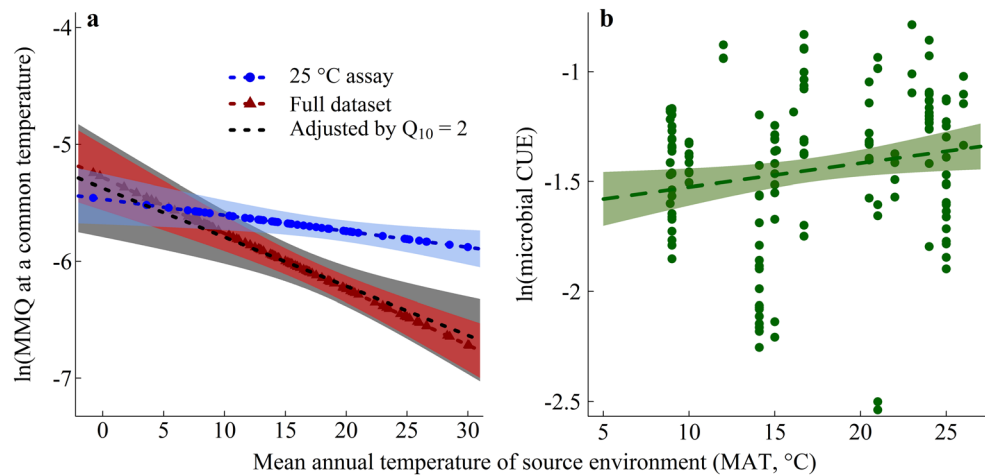


Figure 2. Thermal response of soil microbial metabolic quotient (MMQ) and microbial carbon use efficiency (CUE) based on empirical measurements in global croplands. (a) When measured at a common assay temperature, soil MMQ decreases with increasing mean annual temperature (MAT). Effect sizes of MAT on MMQ ($\text{mmol C} \cdot \text{mol MBC}^{-1} \cdot \text{hr}^{-1}$) were estimated based on coefficients of the multiple linear regressions presented in Table 1, after accounting for the effects of the other predictor variables. MMQ data were obtained from Xu et al. (2017). (b) Soil microbial CUE increases with MAT following $\ln(\text{CUE}) = -1.663(0.083) + 0.011(0.005) \times \text{MAT}$, $n = 159$, $P < 0.05$, $R^2 = 0.034$. The regression coefficient of MAT was of similar magnitude and the same sign when we also included other variables influencing CUE (0.017 ± 0.004 , $n = 159$, $P < 0.001$, $R^2 = 0.217$, see Table S3). Thus, we presented the regression of CUE versus MAT, which could be directly incorporated into soil organic carbon models (see equations (6–7) in Method S1). CUE data were obtained from Sinsabaugh et al. (2016). The shaded areas in both panels show the 95% confidence intervals.

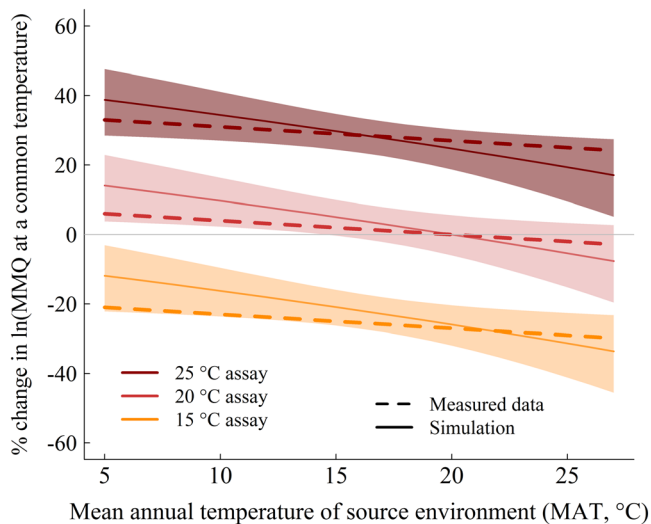


Figure 3. Simulations of the thermal response of soil microbial metabolic quotient (MMQ) using a microbial-explicit soil organic carbon (SOC) model and comparison with the pattern of MMQ measured across global croplands. We incorporated the positive CUE-MAT relationship found in the Sinsabaugh et al. (2016) dataset (Figure 2a) into the microbial-explicit SOC model. The shaded areas show the 95% confidence intervals of simulated MMQ. We calculated the measured MMQ based on the coefficients for MAT and assay temperature in the multiple linear regression shown in Table 1 (full dataset). MMQ was consistently assessed in models and measurements of soil assays with C substrate at a common basal level (no C addition) and at a short-time scale (i.e., from 1-hr to <40-day). To facilitate comparisons, we provide the relative changes (%) in simulated and measured MMQ, as compared to a reference value at 20°C (gray line).

suggestive of a significant compensatory thermal adaptive response of soil MMQ across global croplands as predicted in Figure 1a. The magnitude of compensation increased for cropland soils located in warmer climates (Figure 2a). The negative effect of MAT on soil MMQ was robust to variations in major factors driving soil microbial activity, such as assay temperature, pH, and C:N:P stoichiometry (Table 1). As expected, given that the same soil incubated at higher temperatures has larger MMQ rates, assay temperature had a positive effect on soil MMQ in the full dataset (Table 1). Soil C:N and C:P ratios played opposite roles, increasing and decreasing soil MMQ, respectively. Thus, MMQ was larger in cropland soils with higher phosphorous but lower nitrogen content. Soil pH had a negative effect on MMQ, although this effect was not significant in the subset of data measured at the 25°C assay temperature.

Soil microbial CUE significantly increased with MAT in global croplands (Figure 2b). This thermal response is opposite to the pattern found for soil MMQ (Figure 2a) and indicates that, in warmer climates, a smaller fraction of microbial C uptake is allocated to aerobic respiration as opposed to microbial growth. We next incorporated this positive CUE-MAT relationship into a microbial-explicit SOC model (see Method S1 for detail). Our SOC model fed with this CUE-MAT relationship successfully predicted the compensatory thermal response of soil MMQ (Figure 3) found in the independent empirical dataset extracted from Xu et al. (2017). MMQ at a common temperature was lower in soils sampled from croplands with higher MAT, and this pattern was consistent across the three assayed temperatures (15°C, 20°C, and 25°C). The observed soil MMQ data fell within the 95% confidence intervals of the SOC model simulations. Moreover, the compensatory thermal adaptation of soil MMQ remained consistent in the longer-term (40-year) model simulations (Figure S2).

The last set of analyses aimed to assess the magnitude of the compensatory thermal adaptation in global croplands when compared with the magnitude found in recent large-scale studies in noncultivated ecosystems. When we estimated MMQ at the assay temperature that matched the MAT value where the soil was sampled, we found that soil MMQ increased in warmer cropland sites under both the “adaptation” (using the coefficient for MAT) and “no adaptation” (the slope coefficient of MAT set to zero) scenarios (Figure 4a). Our SOC model simulation reproduced these patterns in the MMQ-temperature relationship under both scenarios (Figure 4b). However, in warmer sites, soil MMQ was lower under the adaptation scenario in both the measured and model simulated data, indicating that compensatory thermal adaptation can partially offset the positive response of MMQ to warmer temperatures across global croplands (dotted line in Figures 4a and 4b). For example, at 20°C MAT, the compensatory thermal adaptation offsets 7% and 15% of soil MMQ in the measured croplands and SOC model simulations, respectively. This offset was also found in noncultivated ecosystems (Figures 4c and 4d). However, the magnitude of the compensatory thermal adaptation was larger in noncultivated ecosystems, offsetting 18% (Figure 4c, global drylands) to 60% (Figure 4d, sites spanning boreal to tropical climates) of soil MMQ at 20°C MAT.

4. Discussion

4.1. Thermal Response of Soil MMQ and CUE

We tested the hypothesis that soil MMQ adapts to warmer thermal regimes through a compensatory response in global croplands, which is associated with increasing soil microbial CUE under warmer climates. Our analyses using published global-scale empirical data (Sinsabaugh et al., 2016; Xu et al., 2017) showed that MMQ is lower and CUE is higher for soils sampled from warmer climates (Figure 2). Further, these empirical results were cross-validated with a microbial-explicit SOC model integrating the observed positive CUE–MAT relationship, with the model simulations recreating the compensatory thermal adaptation of soil MMQ observed in global croplands (Figure 3). Our data-model integration approach suggests that a warmer climate selects for soil microbial communities with higher CUE, providing a potential mechanism for the adaptive metabolic response of microbial respiration to contrasting thermal regimes. The compensatory thermal adaptation of soil MMQ found in croplands is consistent with the adaptive responses found in noncultivated ecosystems (Bradford et al., 2019; Dacal et al., 2019). Therefore, the adaptive metabolic response to contrasting thermal regimes might be an intrinsic capacity for plants, animals, and microbes (Bradford et al., 2019; Dacal et al., 2019; Guo & Gifford, 2002; Hochachka & Somero, 2002).

Our SOC model and empirical data comparison suggested that the compensatory thermal adaptive response of soil MMQ might be associated with increasing soil microbial CUE with MAT across global croplands (Figure 3). Considering that MMQ and CUE were obtained from independent datasets (Sinsabaugh et al., 2016; Xu et al., 2017), the agreement between observed and simulated MMQ is remarkable (Figure 3). Such a “cross-dataset” comparison helps to build our confidence in the biological feasibility of the general patterns found, which are further supported by theoretical expectations. A parsimonious explanation for the greater microbial CUE observed for warmer environments is that it is a product mainly driven by microbial biomass growth outpacing increases in microbial respiration. For instance, Zheng et al. (2019) found that the response of microbial growth to increasing temperatures, measured using ^{18}O incorporation into DNA, was greater than the response of microbial respiration, ultimately leading to higher microbial CUE under elevated temperatures. However, the method of choice to measure the temperature response of CUE may influence conclusions about how CUE responds to temperature. For example, in CUE studies based on C-substrate addition (Qiao et al., 2019; Steinweg et al., 2008; Tucker et al., 2013), microbial substrate use efficiency (SUE) rather than actual microbial growth and CUE may be estimated (Sinsabaugh et al., 2013; Zheng et al., 2019). This may confound interpretation of CUE effects because microbes can intermittently store glucose and do not necessarily allocate the substrate to growth or respiration (Hill et al., 2008). Moreover, the responses of microbial SUE to temperature may depend on the substrate form added and timescale of warming, with a shift towards a more efficient community in the longer term (Frey et al., 2013). Nevertheless, the positive CUE-temperature pattern appears independent of the method used, with it being observed when derived using elemental stoichiometry (Geyer et al., 2019; Sinsabaugh et al., 2016), or estimated using ^{13}C and ^{18}O isotope tracing (Geyer et al., 2019; Takriti et al., 2018), calorimetry (Geyer et al., 2019), or the incorporation of ^{18}O into microbial DNA (Zheng et al., 2019). As most microbes live below their maximum physiological thermal limit, after long-term exposure to a higher thermal regime

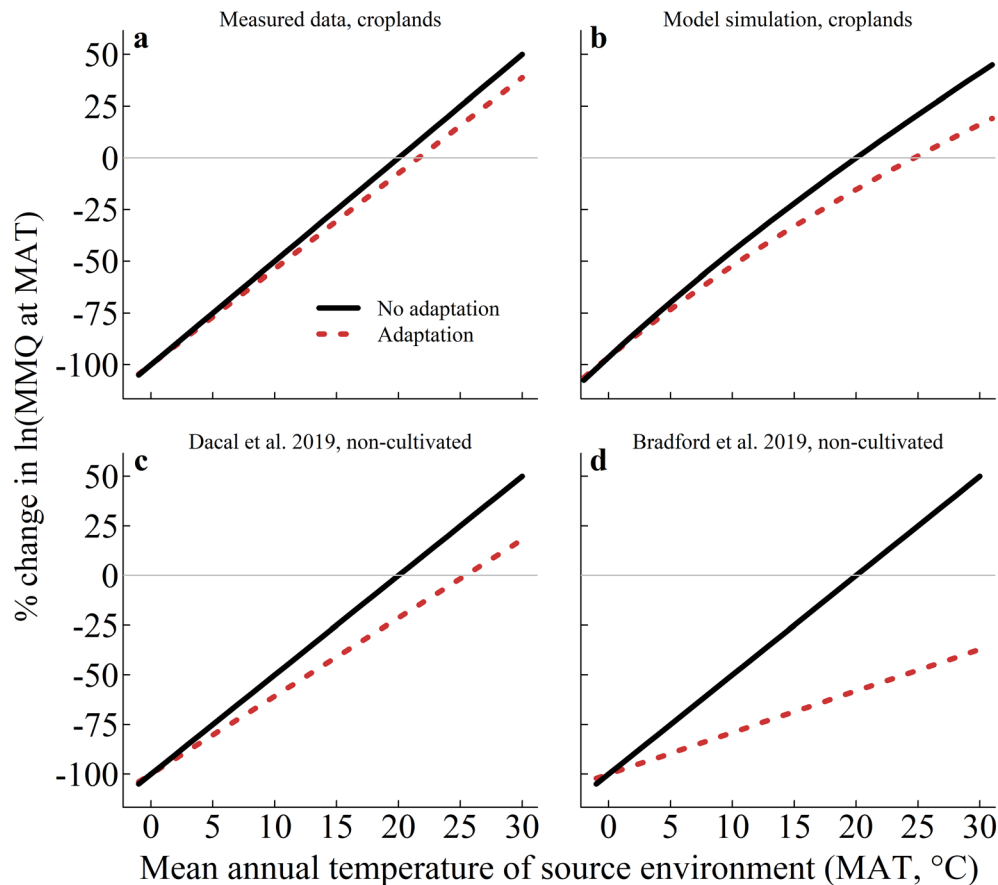


Figure 4. The effects of compensatory thermal adaptation on soil microbial metabolic quotient (MMQ)–temperature relationships in croplands and noncultivated ecosystems. MMQ was estimated for each soil at an assay temperature that matched the mean annual temperature (MAT) of its source environment. The compensatory thermal adaptation dampens the positive effect of assay temperature on MMQ. (a) We used the coefficients for the MAT and assay temperature predictors presented in Table 1 for the adaptation scenario, then set the coefficient for MAT to zero for the no-adaptation scenario. MMQ data were obtained from Xu et al. (2017). (b) In the soil organic carbon (SOC) model, we incorporated a positive CUE–MAT relationship for the adaptation scenario and then set the slope coefficient of MAT to zero for the no-adaptation scenario. CUE data were obtained from Sinsabaugh et al. (2016). (c) Same as Figure 4a, except for 110 dryland soils distributed globally (Dacal et al., 2019). (d) Same as Figure 4a, except for 22 soils collected in sites spanning boreal to tropical climates (Bradford et al., 2019). MMQ was consistently assessed in models and soil assays with C substrate at common basal level (no C addition) and a short-time scale (i.e., from 1-hr to <40-day). To facilitate comparisons among different studies, we present the relative changes (%) in measured and simulated MMQ as compared to their reference values at 20°C under the no-adaptation scenario.

microbial communities may shift towards having more efficient C use (Bradford, 2013; Frey et al., 2013; Ng, 1969; Pirt, 1965), and hence may allocate a lower fraction of C uptake to respiration (Ye et al., 2019).

It should be noted that MMQ is rarely perfectly compensatory in both natural ecosystems and croplands; instead, compensatory thermal adaptation only partially offsets the positive effect of warmer climate on soil MMQ (Bradford et al., 2019; Dacal et al., 2019; Hochachka & Somero, 2002; Figure 4). The magnitude of this partial offset was, however, lower in magnitude in croplands than in noncultivated ecosystems (Figure 4). Such a result could be indirectly caused by high soil nutrient content. For instance, high P concentration in cropland soils can result in higher soil MMQ compared with noncultivated ecosystems (Srivastava & Singh, 1989; Strickland et al., 2010; Xu et al., 2013; Xu et al., 2017). Importantly, the soil C:P ratio had a significant negative effect on MMQ (Table 1), suggesting that higher P concentration and lower C:P and N:P ratios in microbial biomass support faster microbial growth rate and higher MMQ. A reduction in the magnitude of thermal compensatory responses of microbial respiration via selection of faster-growing microbes in croplands is consistent with the growth rate theory observed primarily for autotrophic organisms (Batjes, 2016; Smith, 1982), and also with bacterial community shifts towards more copiotrophic taxa in soils subjected to elevated nutrient inputs (Fierer et al., 2011; Leff et al., 2015).

Additionally, the smaller compensatory adaptation of soil MMQ found in croplands compared with noncultivated ecosystems seems unlikely to be caused by lower available C and subsequent microbial substrate limitation in warmer climates (Bradford et al., 2019; Karhu et al., 2014). Specifically, we first evaluated this possibility with the SOC model and found that lower DOC simulated lower MMQ and thus higher thermal compensation in croplands (supporting information, Figure S4). This simulated MMQ pattern is consistent with measurements from soil incubations, whereby C substrate addition enhances microbial activity but not necessarily biomass, thereby increasing MMQ (Lu et al., 2014). Second, the negative effect of MAT on MMQ was observed despite accounting for the effect of total organic C concentration in soils (Table S1), which represents a proxy for available C due to the global spatial breadth of the cropland dataset. Lastly, soil microbial biomass C did not significantly decrease with MAT, suggesting no significant substrate limitation to microorganisms (supporting information, Figure S3).

4.2. Appropriately Representing Microbial Processes in SOC Models

Our model-data comparison helps to evaluate competing structural assumptions in microbial-explicit SOC models and hence to identify the most appropriate representation of microbial processes in these models. For example, soil microbial CUE is often assumed to be reduced by warming in microbial-explicit SOC models (Allison et al., 2010; Li et al., 2014) based on results from laboratory soil studies (Qiao et al., 2019; Steinweg et al., 2008; Tucker et al., 2013). Despite this assumption, a negative CUE-MAT relationship did not successfully predict the compensatory thermal adaptation of soil MMQ observed across global croplands (supporting information, Figure S5). Instead, our model-data comparison supported an increase in microbial CUE with warming, a pattern recently observed in both noncultivated ecosystems and croplands (Sinsabaugh et al., 2016; Takriti et al., 2018; Zheng et al., 2019; Figure 2b). Given the lack of consensus in how microbial processes are represented in SOC models due to contrasting results from field and laboratory studies, we see value in approaches such as ours that test multiple competing hypotheses and validate model assumptions using field data gathered across a wide range of environmental conditions.

Theoretically, a higher CUE should initially increase microbial biomass and generate more enzymes to decompose SOC and DOC, as simulated by the microbial-explicit model (Figure S2). Assuming that C inputs remain equal with time, the decline in soil C and hence increased microbial competition for substrate should constrain microbial biomass (Georgiou et al., 2017). Therefore, microbial biomass is expected to peak at some point and then decline until reaching a steady state (Figure S2). Our SOC model simulated these patterns on the basis of such logic of microbial physiology theory (Figure S2). Although SOC stocks are also influenced by plant C inputs (Crowther et al., 2016; Xu et al., 2014), improving the representation of soil microbial mechanisms (such as the CUE-MAT relationship) is necessary if we are to increase confidence in modeling how ongoing global warming will affect soil C stocks.

More broadly, our work suggests some avenues to explore in future modeling studies. The impacts of soil pH and C:N:P stoichiometry on microbial processes have been ignored in most microbial models (Georgiou et al., 2017; Wieder et al., 2015; Xu et al., 2014), yet we saw marked effects on soil MMQ of such variables, especially P concentration, for global croplands (Table 1). Given the potential for shifts in agricultural practices related to fertilization regimes, it may be particularly relevant to explore how external P additions, and their legacies affect soil microbial processes. Certainly, higher extractable soil P in current and historical agricultural soils has been found to be associated with faster rates of glucose mineralization (Strickland et al., 2010). Similarly, soil moisture in croplands is managed via irrigation, and in rain-fed systems is particularly sensitive to current and forecasted droughts. Notably, we measured and simulated soil microbial respiration rates under optimal moisture, suggesting the need to evaluate how limiting soil moisture might affect the patterns we observed in microbial respiration. Moreover, soil microbes consume unprotected C and shift a fraction of C uptake into persistent pools (often referred to as a microbial funnel), thereby potentially shifting soil C stocks towards proportionally more stable forms (Bradford et al., 2016; Kuzyakov et al., 2000; Tang & Riley, 2014). Incorporating the microbial funnel together with higher microbial CUE into SOC models might further improve our understating of the response of soil C stocks and fluxes in a warmer climate. Finally, there is a lot of contention about the underlying mechanisms for soil microbial thermal adaptation, with enzyme motion perhaps being the most contentious and understudied (Arcus et al., 2016; Jones et al., 2017). It is a pressing question for understanding how adaptive biochemical processes linked to enzyme conformational shifts translate to observed patterns of soil respiration across temperature gradients.

5. Conclusions

Our global-scale analysis shows a compensatory thermal adaptive response of soil microbial respiration rates in croplands that is consistent with recent findings from noncultivated ecosystems (Bradford et al., 2019; Dacal et al., 2019). However, our results also suggest that agricultural practices (e.g., inorganic fertilization) might decrease the compensatory adaptive capacity of microorganisms to changing thermal regimes. Our integrated model-observation analyses suggest that a positive CUE–MAT relationship can recreate the pattern of soil microbial respiration rates observed across a wide climatic gradient and hence provides a potential mechanism for the compensatory thermal adaptive response found in global croplands. Our integration of large datasets with modeling helps to discern appropriate representations of microbial processes in SOC models. As such, our work should help build the necessary understanding to increase confidence in projections of how cropland SOC will respond in a warmer world.

Data Availability Statement

All data used in this study, including soil microbial respiration and carbon use efficiency observations, are available at Figshare (<https://figshare.com/s/628f24145d1d599f6f44>).

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