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Global Pattern and Controls of Soil Microbial Metabolic Quotient

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Abstract

The microbial metabolic quotient (MMQ), microbial respiration per unit of biomass, is a fundamental factor controlling heterotrophic respiration, the largest carbon flux in soils. The magnitude and controls of MMQ at regional scale remain uncertain. We compiled a comprehensive dataset of MMQ

to investigate the global patterns and controls of MMQ in top 30 cm soils. Published MMQ values, generally measured in laboratory microcosms, were adjusted on ambient soil temperature using long-term (30 y) average site soil temperature and a Q_{10} = 2. The area-weighted global average of MMQ_Soil is estimated as 1.8 (1.5 ~ 2.2) µmol C · h^{-1} per mmol microbial biomass C (MBC) with substantial variations across biomes and between cropland and natural ecosystems. Variation was most closely associated with biological factors, followed by edaphic and meteorological parameters. MMQ_Soil was greatest in sandy clay and sandy clay loam and showed a pH maximum of 6.7 ± 0.1. At large scale, MMQ_Soil varied with latitude and mean annual temperature (MAT), and was negatively correlated with microbial N:P ratio, supporting growth rate theory. These trends led to large differences in MMQ_Soil between natural ecosystems and cropland. When MMQ was adjusted to 11°C (MMQ_Ref), the global MAT in top 30 cm soils, the area-weighted global averages of MMQ_Ref was 1.5 (1.3 ~ 1.8) µmol C· mmol MBC^{-1} · h^{-1}. The values, trends and controls of MMQ_Soil add to our understanding of soil microbial influences on soil carbon cycling and could be used to represent microbial activity in global carbon models.

Key words: Basal Respiration, Edaphic Factor, Meteorology, Microbial Metabolic Quotient, pH, Soil Microbial Biomass

INTRODUCTION

Soil microbial processes are critical for the global carbon cycle (Schimel and Schaeffer 2012), particularly heterotrophic respiration, possibly the largest carbon flux in soils (Bardgett et al. 2008). Respiration rates are determined by the biomass and activity of the soil microbes (Moorhead et al. 2014). The microbial respiration per unit of microbial biomass is defined as the microbial metabolic quotient (MMQ) (Anderson and Domsch 1993). Although the distribution of soil microbial biomass has been well quantified (Jenkinson 1977, Beck et al. 1997, Serna-Chavez et al. 2013, Xu et al. 2013), the MMQ at various scales is largely unknown (Anderson and Domsch 1993, Spohn 2015).

The metabolic processes driving heterotrophic respiration depend on many environmental and biological factors (Anderson and Domsch 1993, Wardle 1993). The environmental factors include substrate availability and quality (Blagodatskaya et al. 2011); (Jiang et al. 2013), soil texture and water content (Van Veen and Kuikman 1990, Jiang et al. 2013), and temperature (Hagerty et al. 2014). Biologically, the MMQ is affected by microbial community structure (Jiang et al. 2013), microbial biomass and basal respiration (Wardle 1993). The MMQ at global- and biome- scales in relation to these biological, edaphic, and meteorological controls is invaluable for understanding and predicting heterotrophic respiration within global carbon cycle models (Jenkinson and Ladd 1981, Hagerty et al. 2014, Steinweg et al. 2014).

The global soil carbon modeling community has long recognized the importance of microbial carbon biogeochemistry (Parton et al. 1987, Jenkinson et al. 1990, Schimel 2001). Traditional ecosystem models implicitly simulate the microbial contribution to soil carbon cycling, mostly using first order differential equations (Parton et al. 1987, Raich et al. 1991, Schimel 2001), however, this simple modeling approach does not explicitly consider microbial regulation of soil organic carbon mineralization (Schimel 2001). In recent years, a number of microbial models have been developed that explicitly simulate microbial processes and their controls on soil carbon cycling (Schimel and Weintraub 2003, Allison et al. 2010, Wang et al. 2013, Wieder et al. 2013, Sulman et al. 2014, Xu et al. 2014). Microbial activities in these models are typically represented as a single parameter, which is determined from microbial biomass turnover rate measurements, obtained with traditional soil incubations (Jenkinson and Ladd 1981, Wieder et al. 2013, Xu et al. 2014). Microbial enzymatic models simulate microbial control of the carbon cycle with enzyme kinetics, while the enzyme production rate depends on MMQ (Allison et al. 2010, Wang et al. 2013). The *in-situ* microbial biomass turnover rate mathematically equals MMQ under steady state conditions, i.e. when there is no net biomass change (Jenkinson and Ladd 1981, Van Veen et al. 1984). Therefore, the magnitude

and controls of MMQs are essential for accurately calibrating these microbial models and assessing their sensitivity to global change factors (Steinweg et al. 2014), within larger scale carbon cycling models.

However, traditional incubation methods for estimating basal microbial respiration have long been questioned because the temperature during incubations is typically different from the ambient soil temperature (Jenkinson and Ladd 1981). Reported MMQ based on laboratory soil incubations become more representative for soil microbial activity, and more useful in process modeling, if they are adjusted to ambient soil temperature (Fig. 1). This temperature-corrected MMQ is a more relevant metric for assessing the dependency of MMQ on local edaphic, meteorological, and biological factors. In addition, MMQ can also be normalized to a global reference temperature for broad comparisons among biomes that differ in plants, microbes and soil composition.

In this study, we present a comprehensive global synthesis of published MMQs, temperature-adjusted MMQs, global and biome-level MMQs, and the biological and environmental controls over MMQ. We first report the global dataset of basal respiration (BR), soil microbial biomass carbon (MBC), and the MMQ. Then we report the temperature-corrected MMQs at global and biome scales. Third, we analyze the controls on MMQs at a global scale, with a focus on comparing cropland and natural ecosystems. Last, we discuss the implications of the knowledge for microbial soil carbon models.

MATERIALS AND METHODS

Data compilation

We collected publications by searching for: “soil microbial turnover rate”, “basal respiration”, “soil microbial metabolic quotient”, “soil microbial residence time”, and “soil microbial biomass” in Google Scholar in December 2013; in December 2015 we repeated the search to expand the dataset to cover the period of 1970s-2015. Candidate studies were included in this study if 1) soil

microbial metabolic quotient was reported or both basal microbial respiration and biomass carbon were reported; 2) and the incubation period for measuring basal respiration was <40 d. Long incubation experiments normally result in reduced basal respiration. In addition, soil microbial biomass carbon is unlikely to change over short periods, which is the fundamental assumption for the MMQ correction based on soil temperature as applied in this study. More than 95% of the values identified in our search were from the incubation experiments <40 days (Appendix S1: Fig. S1). Many studies set 35 ~ 42 d as the threshold for short-term versus long-term incubations when studying labile carbon limitation to microbial respiration (Shi et al. 2006, Birge et al. 2015). Basal respiration was measured without substrate addition, because substrate addition enhances microbial activity, but not necessarily microbial biomass, thereby altering MMQ (Lu et al. 2014). The soil microbial biomass, basal respiration, and MMQs data represent the top 30 cm of soils across the globe; the reasons for using top 30 cm are (1) more than 70% soil microbial biomass are in top 30 cm (Xu et al. 2013), and (2) this portion of microbial biomass is the most active along soil profile (Fierer et al. 2003).

A total of 2444 observations from 14 biomes across the globe were retrieved from 210 papers (Fig. 2). The data were further aggregated into ten biome types: Cropland (CL), Grassland (GL), Shrubland (Shr), Temperate Broadleaf Forest (Brof), Temperate Coniferous Forest (Conf), Tropical/Subtropical Forest (T/STF), Natural Wetland (W), Boreal Forest (Borf), Pasture (P), and Bare soil and others (BS). No data were available for Tundra ecosystems (Fig. 2). Metadata for each site included latitude, longitude, mean annual air temperature, mean annual precipitation, bulk density, soil pH, vegetation type, incubation temperature, basal respiration, soil microbial biomass carbon, nitrogen, and phosphorus, soil organic carbon, soil total nitrogen, soil available phosphorus (all reported available phosphorus including Olson P etc.), sampling date, and sampling depth (Data S1).

Other metadata, not measured *in situ*, were extracted from spatial datasets. When not available at a site level, we extracted point-level soil data (soil pH, soil texture (silt, clay, and sand), and bulk density) from the Re-gridded Harmonized World Soil Database v1.2 in the Oak Ridge

National Laboratory Distributed Active Archive Center for Biogeochemical Dynamics (https://daac.ornl.gov/SOILS/guides/HWSD.html). Soil temperature and moisture data for the top 10 cm were downloaded from the NCEP/DOE AMIP-II Reanalysis (Reanalysis-2) Monthly Average dataset at: http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.surfaceflux.html on June 12, 2015. The corresponding grid values were extracted based on geographical coordinates. The extraction of soil temperature and moisture was based on a 30y average of 1981-2010; the retrieved climate data are from CRU TS version 3.23 (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_3.23/) on 30 March 2016, the 30-year average was used to represent the site-level meteorology condition.

Equation 1 was used to compute MMQ from basal respiration (BR) and microbial biomass carbon (MBC) if MMQ was not reported in the literature. The 3-D scatter plots for BR, MBC, and MMQ_Inc are shown in Fig. 3.

$$MMQ = \frac{BR}{MBC} \qquad (1)$$

Temperature correction of MMQ

Temperature correction is necessary for comparing MMQ across studies due to the differences between long-term average site soil temperature and incubation temperature. Approximately 91% of the published incubation experiments were carried out at temperatures higher than the long-term average ambient soil temperature at the sampling locations ($P < 0.001$; Fig. 4). We adjusted these reported MMQs to their long-term average site soil temperature and to the global-averaged mean soil temperature (Table 1 & Appendix S1: S1), using a $Q_{10} = 2$ (Eq. 2). This function has been previously used to mathematically simulate the temperature dependence of microbial respiration (Rey and Jarvis 2006, Wei et al. 2014).

$$MMQ_1 = MMQ_2 \times Q_{10}^{\frac{T1-T2}{10}} \qquad (2)$$

T_1 and T_2 are the temperatures in Celsius, MMQ_1 and MMQ_2 is the microbial metabolic quotient at T_1 and T_2, respectively. Based on MMQ_Inc, we calculated the MMQ_Soil using the incubation temperature and the 30 y average soil temperature at the sampling site. Therefore, MMQ_Soil represents the site's average MMQ in relation to MAT (mean annual temperature). This equation was used to calculate MMQ_Ref representing MMQ at soil temperature of 11 °C. The corrections were carried out under the assumption that basal respiration is temperature-dependent, while soil microbial biomass remains unchanged during the typically short soil incubations. The Q_{10} value of 2 was used because (1) recent synthesis studies have reported that Q_{10} = 2 is indeed the best value for the temperature sensitivity of microbial activities (Fierer et al. 2006, Koch et al. 2007); (2) an incubation experiment under a gradient of temperatures further supported the Q_{10} = 2 of basal respiration (Xu et al. 2015a) (Appendix S1: Fig. S2); and (3) a sensitivity analysis confirmed that Q_{10} for MMQ has a median value of 2, albeit ranging between 1.5 ~ 3.0 (Appendix S1: Table S2 & Appendix S1: Fig. S3).

Correlations between MMQs

Due to the temperature correction, there are three terms for MMQ in this study. (1) The MMQ_Inc, i.e. MMQ based on incubation data, is the reported microbial metabolic quotient; (2) MMQ_Soil is the adjusted microbial metabolic quotient at long-term average site soil temperature; and (3) MMQ_Ref is the reference microbial metabolic quotient based on the global soil MAT of 11°C. The global MAT is determined from the output of the Community Earth System Model/Community Land Model (CESM/CLM) (Oleson et al. 2013). The connections among the three MMQs are illustrated in Fig 1. Due to the short duration of the incubation experiments (all incubations were <40 d with more than half <7 d (Appendix S1: Fig. S1)), it is assumed that the soil microbial biomass did not substantially change during incubation. In this paper, we focus on the magnitudes and controls of MMQ_Soil, and discuss the MMQ_Inc and MMQ_Ref from a modeling perspective.

Statistical analysis

The statistical analyses used in this study included simple linear regression, generalized linear regression, polynomic regression, Duncan's new multiple range test, generalized linear regression, and structural equation modeling. Generalized linear regression was used to quantify the standardized contributions of various environmental factors to variation in the MMQs. Polynomial regression was used to estimate the pH and soil texture controls on MMQ_Soil. Duncan's new multiple range test was used to quantify the significance of inter-biome differences in MMQ (Table S1). All statistical analyses were carried out with R.13.1 in Mac OS X.

Structural equation modeling (SEM) was used to quantify the relative importance of biological, edaphic and meteorological factors in controlling MMQ variation. The lavaan package (https://cran.r-project.org/web/packages/lavaan/index.html) in R was used for the SEM. Redundant factors were removed from the SEM model. While basal respiration (BR), microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP), and microbial N:P ratio (MB_NP) are all important biological factors controlling MMQ_Soil (Appendix S1: Fig S4), they were significantly correlated so only one of these biological factors was used in the SEM. Due to the strong multiconllinearity among variables, the Variance Inflation Factor (VIF) was used to quantitatively select the right factor for SEM analysis (VIF < 5). Considering the strong correlation of BR with several other factors and the lacking of MBN and MBP data from many studies (i.e. microbial biomass N:P ratio), we used BR in the SEM to represent the biological factors. For the edaphic factors, (Appendix S1: Fig S4), there were strong correlations between carbon, nitrogen, and phosphorus. Therefore, we used soil organic carbon density (SOC, g m^{-2}) as a factor representing nutrient concentrations. Soil pH was included as an important soil chemical condition (Appendix S1: Fig S5). For soil texture, only silt and clay contents were included because the sand content could be determined if soil silt and clay are known. For soil meteorological factors, soil temperature and moisture were included (Appendix S1: Fig S6).

The SEM results were evaluated with the Comparative Fit Index (CFI), the Normed Fit Index (NFI), and the Chi Square Test (χ^2). The Chi-Square value is the traditional measure for evaluating the overall model fit and accessing the magnitude of discrepancy between the sample and fitted covariance matrices; NFI is an incremental fit index that assesses the model by comparing the Chi-Square value of the model to the null model that assumes that all variables are uncorrelated; CFI is a revised form of the NFI that takes into account sample size; model fits with NFI > 0.95 and CFI > 0.95 indicate a good SEM (Hooper et al. 2008). The SEM was applied to data from cropland, natural ecosystems, and cropland + natural ecosystems to attribute the variations in MMQ_Soil to meteorological, edaphic and biological factors.

The figures for variable correlation and ternary graphics were produced with OriginPro 8.5 and Microsoft Excel 2016 in Windows. The spatial maps were produced with ArcGIS 10.2 in Windows. All data for basal respiration, soil microbial biomass, microbial biomass N:P ratio, MMQs were log-transformed before statistical analysis, the average and 95% confidence intervals were transformed back to original values for reporting. This log-transformation was used to make the data population follow a normal distribution for robust statistical analysis.

RESULTS

Global and biome-level MMQ_Inc and MMQ_Soil

The arithmetic mean values for MMQ_Inc and MMQ_Soil are 3.7 (95% CI: 3.5 ~ 3.9)and 2.0 (95% CI: 1.9 ~ 2.1) μmol C· mmol MBC^{-1} · h^{-1}, respectively. The global average of MMQ_Inc is significantly greater than MMQ_Soil (Table 1). The biome area-weighted global mean MMQ_Inc and MMQ_Soil were 3.4 (95% CI: 1.9 ~ 4.1) and 1.8 (95% CI: 1.5 ~ 2.2) μmol C· mmol MBC^{-1} · h^{-1} (Table 1), which is primarily attributable to the fact that > 90% of the studies were conducted on soils where the incubation temperature was higher than long-term average site soil temperature (Fig. 4).

Both MMQ_Inc and MMQ_Soil showed substantial variations across biomes (Table 1). Tropical/Subtropical had the lowest MMQ_Inc (1.6 (95% CI: 1.4 ~ 1.8) μmol C· mmol MBC^{-1} · h^{-1}), while natural wetlands the highest MMQ_Inc (8.0 (95% CI: 6.1 ~ 10.4) μmol C· mmol MBC^{-1} · h^{-1}). Temperate conifer forests had the lowest MMQ_Soil (1.0 (95% CI: 0.8 ~ 1.1) μmol C· mmol MBC^{-1} · h^{-1}), while natural wetlands the highest MMQ_Soil (3.8 (95% CI: 2.9 – 4.8) μmol C· mmol MBC^{-1} · h^{-1}) (Table 1). This large inter-biome variation of MMQ_Soil has previously been attributed to biome-specific differences in soil texture, substrate quality, and microbial community (Larsen et al. 2012, Schimel and Schaeffer 2012, Karhu et al. 2014, Xu et al. 2014).

Controls on MMQ_Soil shown as linear regression

Variations in MMQ_Soil are controlled by various factors that could be categorized as biological, meteorological and edaphic. We analyzed the effects of biological factors on MMQ_Soil using a simple linear regression approach (Fig. 5; Appendix S1: Fig S4). All biological factors were significantly correlated with MMQ_Soil (Appendix S1: Fig. S4). Across the whole dataset, the MMQ_Soil was positively correlated with BR ($r = 0.50$; $p < 0.01$), negatively correlated with soil MBC ($r = -0.35$; $p < 0.01$), MBN ($r = -0.38$; $p < 0.01$), MBP ($r = -0.30$; $p < 0.01$), and N:P ratio ($r = -0.60$; $p < 0.01$) (Appendix S1: Fig. S4). In addition, most of these factors were correlated with each other. For example, the MBC is significantly correlated with MBN ($r = 0.92$; $p < 0.01$) (Appendix S1: Fig. S4).

Among the edaphic factors, MMQ_Soil was significantly correlated with bulk density ($r = 0.053$; $p < 0.01$), silt content ($r = -0.25$; $p < 0.01$), clay content ($r = 0.084$; $p < 0.01$), sand content ($r = 0.099$; $p < 0.01$), organic carbon density ($r = -0.09$; $p < 0.01$), total nitrogen density ($r = -0.14$; $p < 0.01$), soil pH values ($r = 0.11$; $p < 0.01$), and marginally correlated with total phosphorus ($r = 0.11$; $p = 0.078$) (Appendix S1: Fig. S5). Among climate factors, MMQ_Soil was positively correlated with soil temperature ($r = 0.34$; $p < 0.01$), MAP ($r = 0.098$; $p < 0.01$), and MAT ($r = 0.38$; $p < 0.01$), and negatively correlated with soil moisture ($r = -0.072$; $p < 0.01$) (Appendix S1: Fig. S6).

Of the three groups of factors controlling MMQs, biological factors were the most important, followed by edaphic and meteorological factors. Based on the multiple linear regressions, BR, temperature, moisture, organic carbon density, pH, and texture, explained 76% of the MMQ_Soil variation in croplands, 49% in natural ecosystems, and 53% in all ecosystems (Table 2).

Controls of MMQ_Soil inferred with structural equation modeling

The dominant effect of BR on MMQ_Soil was supported by SEM analysis (Fig. 6). For MMQ_Soil, the standardized coefficient (β), a quantitative parameter for specific association, was 0.94 for cropland ($P < 0.001$), 0.60 for natural ecosystems ($P < 0.001$), and 0.74 for all ecosystems combined ($P < 0.001$) (Fig. 6C). The impact of soil temperature on MMQ_Soil was significant in croplands ($\beta = 0.26$, $P < 0.001$), natural ecosystems ($\beta = 0.25$, $P < 0.001$), and for the whole dataset. The impact of soil moisture on MMQ_Soil was significant in natural ecosystems ($\beta = -0.38$, $P < 0.001$) and for the whole dataset ($\beta = -0.17$, $p < 0.001$) (Fig. 6), but not for croplands ($\beta = 0.01$, $P = 0.65$). This is consistent with the GLM results, which also showed a contrasting effect of soil temperature (0.004, $P = 0.910$) for cropland vs. (-0.142, $P = 0.001$) natural ecosystems and a marked difference in soil moisture, 0.016 ($P = 0.661$) vs. -0.420 ($P < 0.001$) (Table 2). In summary, the GLM and SEM approaches agreed on the overall ranking of the factors determining MMQ_Soil: biological factors > edaphic factors > meteorological factors (Table 2).

Edaphic factors on MMQ_Soil

Among the edaphic variables, SOC had the strongest impact on MMQ with negative effects on MMQ_Ref in both cropland and natural ecosystems. The effects of pH, silt and clay content on MMQ_Ref were not significant (Table 2). Soil temperature, latitude, soil texture, microbial biomass carbon, nitrogen, and N:P ratio, and soil pH were all identified as important factors contributing to the variation in MMQ_Soil (Fig. 5; Appendix S1: Fig. S4, S5, and S6). Temperature was a primary factor controlling microbial activities (Lloyd and Taylor 1994, Davidson and Janssens 2006), and MMQ_Soil was positively correlated with soil temperature (Appendix S1: Fig. S5). There was a negative correlation between soil microbial biomass N:P ratio and MMQ_Soil ($P < 0.001$) (Fig. 5B),

which was consistent with the growth rate theory, the higher growth rate is associated with higher P concentration and lower C:P and N:P ratios (Sterner and Elser 2002). Lower N:P supports higher MMQ_Soil with a slope of -0.6496 ± 0.0930).

Significant correlations were found between all single soil texture factors and the MMQs (Appendix S1: Fig. S5). Particularly, soil pH and texture had a significant correlation with MMQ_Soil (Fig. 5 & 6, Appendix S1: Fig. S5). The relationships between MMQ_Soil and silt or sand followed a concave curve (Fig. 7B & 7D), while the correlation between clay content followed a convex curve (Fig. 7C); both were best described by polynomial equations (Fig. 7). To further analyze the soil texture effects on MMQ_Soil and identify the soil types with high or low MMQ_Soil, we plotted the MMQ_Soil on the soil texture class ternary diagram. Sandy clay and sand clay loam had higher MMQ_Soil than the other soils. Because data were lacking for silt-dominated soils, some potential texture impacts remain unclear. In addition, MMQ_Soil showed a significant association with soil pH (Appendix S1: Fig S5). We found that the relation between soil pH and MMQ_Soil followed a unimodal curve with a maximum at pH = 6.7.

Natural Ecosystems vs. Cropland

The MMQ_Soil was higher in cropland than natural ecosystems (3.1 vs. 1.4 μmol C· mmol $MBC^{-1} \cdot h^{-1}$) (Fig. 9). A further separation analysis showed that forests had significantly lower MMQs compared to non-forest ecosystems (1.2 vs. 2.6 μmol C· mmol $MBC^{-1} \cdot h^{-1}$ for MMQ_Soil) (Fig. 9). The higher MMQ_Soil in cropland is driven by cultivation, which stimulates microbial activity (Srivastava and Singh 1989, Xu et al. 2013). Because substrate availability is lower in cropland soils, soil microbial biomass is largely lower than that of natural ecosystems (18.4 vs. 47.2 mmol C · (Kg dry $soil)^{-1}$; $P < 0.001$), while basal respiration is slightly lower (93.3 vs. 134.7 μmol C · (Kg dry $soil)^{-1} \cdot h^{-1}$; $P < 0.001$) (Appendix S1: Table S2).

Large differences were also found in the environmental controls on MMQ_Soil between croplands and natural ecosystems (Table 1 & 2, Fig. 5, 6 & 8). For example, the impacts of soil temperature and pH on MMQ_Soil were similar for croplands and natural ecosystems (β = 0.26 vs.

0.25 for temperature and β = -0.01 vs. 0.04 for pH) (Fig. 6B & 6C), while the effect of soil moisture was significantly different (β = 0.01 vs. -0.38) (Fig. 6B & 6C). Significantly different impacts were found for soil pH as well; the three parameters for a second order polynomial equation describing soil pH impact on MMQ_Soil were all significantly different (Fig. 6C), while the effects of microbial biomass N:P ratio on MMQ_Soil were similar between cropland and natural ecosystems (Fig. 6B). Soil texture impacts were also different between natural ecosystems and croplands (Fig. 8). Sandy clay and sandy loam soils had higher MMQ_Soil than other soils in cropland, while they had relatively lower MMQ_Soil than other soil types in natural ecosystems. This finding has indicated that the biological controls on microbial processes are similar for croplands and natural ecosystems; the differences are likely caused by edaphic and meteorological factors.

MMQ_Ref: MMQ adjusted to global average soil temperature

The arithmetic mean value for MMQ_Ref was 1.6 (95% CI: 1.5 ~ 1.7) μmol C· mmol MBC^{-1} · h^{-1}. The global average of MMQ_Inc was significantly larger than MMQ_Soil, which was significantly larger than MMQ_Ref (Table 1 & Appendix S1: Table S1). The biome area-weighted global mean MMQ_Ref was 1.5 μmol C· mmol MBC^{-1} · h^{-1}. MMQ_Soil was thus significantly greater than MMQ_Ref ($P < 0.001$) on a global scale (Table 1), which is primarily attributable to the fact that > 90% of the studies were conducted on soils where the ambient soil temperature was higher than global mean temperature (Fig. 4). The differences between MMQ_Soil and MMQ_Ref varied with biomes along latitude. MMQ_Ref was significantly higher than MMQ_Soil in high latitude ecosystems (e.g. boreal forest) ($P < 0.001$), while it was significantly lower at low latitudes (e.g. subtropical and tropical forest) ($P < 0.001$), and quite similar at mid-latitudes (e.g. temperate broadleaf and temperate conifer forests) (Table 1).

The MMQ_Ref showed substantial variations across biomes (Table 1). Natural wetlands had the highest MMQ_Ref (3.4 (95% CI: 2.6 – 4.4) μmol C· mmol MBC^{-1} · h^{-1}), while subtropical and tropical forests had the lowest MMQ_Ref (0.6 (95% CI: 0.5 – 0.7) μmol C· mmol MBC^{-1} · h^{-1}) (Table 1). Similarly, the large inter-biome variations of MMQ_INc, MMQ_Soil, and MMQ_Ref are attributable

to biome-specific differences in basal respiration and soil microbial biomass caused (Table S2) by soil texture, substrate quality, and microbial community (Larsen et al. 2012, Schimel and Schaeffer 2012, Karhu et al. 2014, Xu et al. 2014). The MMQ_Ref are higher in cropland than natural ecosystems (2.1 vs. 1.3 μmol C· mmol $MBC^{-1} \cdot h^{-1}$) (Fig. 9). A further separation analysis illustrated that forests had significantly lower MMQ_Ref compared to non-forest ecosystems (1.2 vs. 2.0 μmol C· mmol $MBC^{-1} \cdot h^{-1}$) (Fig. 9).

DISCUSSIONS

MMQs vs. microbial respiratory carbon turnover

MMQ is defined as microbial respiration per unit of biomass (Anderson and Domsch 1993). Theoretically, if soil microbial biomass is at steady state, there is no net growth, carbon assimilation equals maintenance respiration plus production, and MMQ equals respiratory carbon turnover rate (Van Veen et al. 1984). Over the course of laboratory incubations (up to 40d), it is assumed that MMQ equals microbial biomass turnover rate because microbial biomass does not show substantial change.

Our mean value for MMQ_Ref (1.5 μmol C· mmol $MBC^{-1} \cdot h^{-1}$) was similar to the turnover rate reported in many experiments and incorporated in microbial models. A recent meta-analysis reported a mean soil microbial biomass turnover rate of 67 ± 22 days based on production data (Sinsabaugh et al. 2017), which was equivalent to specific biomass turnover rate (μ/B) of 0.6 ± 0.2 μmol C· mmol $MBC^{-1} \cdot h^{-1}$, and a mean microbial carbon use efficiency (CUE) of 0.25 ~ 0.27. These values are equivalent to our mean value for MMQ_Soil (1.8 ± 0.6 μmol C· mmol $MBC^{-1} \cdot h^{-1}$), assuming that MMQ_Soil = (μ/B) / (CUE/(1 - CUE)).

Various controls on MMQ_Soil

The slope of the linear regression between MMQ_Soil and soil temperature was 1.2×10^{-4} mmol C· mmol $MBC^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$ (Fig. 5A). This value is consistent with a recent study that reported a warming-induced increase in microbial turnover rate of 1.25×10^{-4} mmol C· mmol $MBC^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$

(Hagerty et al. 2014). Proposed reasons for the positive impact of warming on MMQ_Soil primarily include: (a) warming-induced increases in activity of microbial predators, and thus fast carbon release from soil microbes, (b) warming-induced shifts in microbial community composition toward dominance of microbial species with faster turnover, (c) warming-induced acceleration of protein turnover, (d) warming-induced increases in bacteriophage activities (Hagerty et al. 2014), and (e) warming-induced smaller, more active microbial biomass (Colman and Schimel 2013).

The effect of soil texture on MMQ_Soil was consistent with a modeling study that reported a positive linear correlation between soil carbon turnover rate and clay content in a range of 10% ~ 50% (Schimel et al. 1994). In addition, a laboratory experiment found that higher clay content stimulated organic matter decomposition by increasing substrate availability and microbial biomass in artificial soils (Wei et al. 2014). Data analysis in this study confirmed that clay content was positively correlated with MMQ_Soil, although a reduction in MMQ_Soil was found above ~45% clay content (Fig 7C), which was consistent with a field study reporting a negative correlation between clay content and microbial respiration (Wang et al. 2003).

The pH effect on MMQs followed a unimodal curve for cropland soils, but not in natural ecosystems, with peak at ~6.8 (Fig. 5C), consistent with changes in microbial activity along a pH gradient (Rousk et al. 2010). One possible consideration is that croplands receive high fertilizer inputs, which may have reduced soil pH at some sites (Guo et al. 2010), with detrimental impacts on microbial activity. Because data for pH > 9 were rare, it is not clear whether the pH impact is truly unimodal, or whether the pH impact plateaus at neutral conditions, as is suggested by a study of bacterial diversity (Fierer and Jackson 2006).

Low biomass N:P ratios indicate greater cellular phosphorus content, which normally corresponds to faster microbial growth rate according to the growth rate theory (Sterner and Elser 2002), although they could also indicate very low N availability. This correlation might also indicate a shift between fungal and bacterial dominance, which differ in their mean C:N ratio (Xu et al., 2013). Greater MMQ is associated with bacteria dominated microbial communities (Fierer et al. 2007),

which will result in high N mineralization (Schimel and Bennett 2004), while lower MMQ is associated with a fungi-dominated microbial community, which normally leads to low N availability. This strong control of soil microbial N:P ratio on MMQ had two-fold implications: (1) the strong impact of N:P on microbial carbon cycling advanced our theoretical understanding of ecological stoichiometry in soil microbes, as the growth rate theory has thus far been tested primarily with autotrophic organisms (Smith 1982); 2) nitrogen and phosphorus controls on microbial carbon cycling should not be ignored in microbial models, as was common practice in the past (Wang et al. 2013, Wieder et al. 2013, He et al. 2014).

Although we confirmed that edaphic factors had significant effects on MMQ_Soil, soil sampling disturbance effect is another important mechanism that might have substantial impacts but these were not included in this analysis due to the shortage of relevant information (Data S1). Studies have found that the disturbances during soil sampling often greatly increases microbial activities (Carter and Gregorich 2007), most likely stimulating microbial activity and basal respiration (Findlay et al. 1985).

MMQ in association with carbon use efficiency

MMQs were calculated based on basal respiration and microbial biomass carbon, reflecting the specific activity of soil microbes. Microbial carbon use efficiency (CUE) is a complementary parameter relating how much carbon flow into microbial biomass is directed to biomass production (Sinsabaugh et al. 2013). Thus, a negative correlation between MMQ and CUE is expected. Our mean MMQ was similar to the microbial respiratory carbon turnover calculated from qCO_2 and CUE using an independent dataset (Sinsabaugh et al. 2017). Theoretically, higher CUE means more carbon is assimilated into microbial biomass, and less carbon enters microbial biomass respire as basal respiration, corresponding to a lower MMQ; lower CUE indicates less carbon is assimilated into microbial biomass and higher MMQ. Thus, a negative correlation between MMQ and carbon use efficiency is expected, which has been verified in Sinsabaugh et al. (2017). Sinsabaugh et al. (2017)

estimated a global mean biomass turnover time of 67 ± 22 d. based on a mean microbial CUE of 0.25 ~ 0.3. This estimate is consistent with the global average for MMQ_Soil (1.8 μmol C · h^{-1} · mmol MBC^{-1}) and MMQ_Ref (1.5 μmol C · h^{-1} · mmol MBC^{-1}), which correspond to a respiration based MBC turnover times of 23 d and 28 d, respectively, assuming that MMQ = (μ/B) / (CUE/(1 - CUE).

There was also consistency in the relative importance of environmental factors controlling MMQ and CUE between this study and Sinsabaugh et al. (2017). Biological factors, followed by edaphic factors and meteorological factors, were the dominant controls for both MMQ and CUE as shown by SEM. For example, both MMQ and CUE responded to soil pH in a second order polynomial curve, with optimal pH in a relative acid condition, 6.5 for MMQ_Soil and 5.4 for CUE. Both SEM analyses in this study and Sinsabaugh et al. (2016) agreed that soil pH had minor direct impacts on MMQ and CUE, while the indirect impacts were strong, which explained the consistency of soil pH impacts. Given the consistency between environmental controls on CUE and MMQ, it is likely the soil texture has substantial impacts on CUE, which deserves further analysis if data allow.

MMQ from experiments to models

Soil microbes are an important control of carbon flow in soils. Therefore, accurately modeling soil microbial activates is critical for modeling soil microbial processes within large-scale climate models (DeLong et al. 2011). MMQ is the direct parameter controlling soil microbial activities on carbon cycling; soil microbial turnover rate is the key mechanism for all microbial models. The majority of the recent microbial models simulate microbial turnover with a single value. The value ranges from 0.0005 h^{-1} (Wieder et al. 2013) to 0.3 h^{-1} (Sulman et al. 2014), which are largely different from the estimates in this study (Fig. 10). While the CLM-Microbe and AWB models use 0.002 h^{-1}, which is in consistent with this study.

Most microbial models do not separate the respiratory carbon release and microbial detritus production (Schimel and Weintraub 2003, Wang et al. 2013, Wieder et al. 2013, Xu et al. 2014) and define microbial activity as the microbial turnover rate at a reference temperature, which was comparable with our MMQ_Ref. Our global mean MMQ_Ref falls in the range of parameters used in extant microbial models (Allison et al. 2010, Wieder et al. 2013, He et al. 2014, Xu et al. 2014). For example, although never calibrated to measurements, the model of Schimel and Weintraub (2003) demonstrated some interesting and plausible behaviors on carbon and nitrogen cycling. The model set microbial turnover rate at 0.001 h^{-1} (equal to 1.0 μmol C· mmol MBC^{-1} · h^{-1}) for the carbon-only version of their model and at 0.0004 h^{-1} (equal to 0.4 μmol C· mmol MBC^{-1} · h^{-1}) for the carbon and nitrogen model (Schimel and Weintraub 2003), with microbial carbon being used for maintenance respiration, enzyme production, and microbial growth. The AWB model (Allison et al. 2010) and Xu et al model (Xu et al. 2014) set microbial turnover rate at 0.002 h^{-1} (equal to 2.0 μmol C· mmol MBC^{-1} · h^{-1}) which is very close to our global mean MMQ_Soil, but larger than MMQ_Ref in this study. Wieder et al (Wieder et al. 2013) set the microbial turnover rate at 0.0005 h^{-1}, (equal to 0.5 μmol C· mmol MBC^{-1} · h^{-1}), which is significantly smaller than the calculated MMQ_Ref in this study. The large range of MMQ used in microbial models infers a need for quantifying the large-scale MMQs and their environmental controls.

Meanwhile, the quantitative equations described here for the biological and edaphic controls on MMQ_Soil offer greater resolution for quantitatively modeling microbial activities at the ecosystem scale. For example, the soil texture control on MMQ had never been explicitly described mathematically in traditional or microbial models (Wieder et al. 2015), though a few modeling studies confirmed the importance of soil physical protection on carbon storage (Sulman et al. 2014); the soil pH control has been ignored in most microbial models (Xu et al. 2014, Wieder et al. 2015). While the MMQ_Ref is critically important in models that simulate microbial temperature sensitivity across various biomes, more efforts are necessary for better understanding MMQs and their environmental controls from experimental and modeling studies.

Uncertainties in present study

A comprehensive data set was compiled and analyzed for magnitude and controls of MMQ_Soil. A few simplifications during data analysis need to be considered when interpreting the results. First, the biological factors analyzed in this study excluded the root properties due to lack of data across the globe. The inclusion of root biomass and root exudation should provide more accurate information on biological controls on MMQ_Soil as root-microbe interaction has been proven an critical factors on microbial activities (Kuzyakov and Xu 2013). Second, the soil temperature used in this study was 30-year average soil temperatures at sampling location because all other environmental factors considered represented the average soil condition, we used the long-term average temperature to represent meteorological information. This treatment might have reduced the impacts of in situ soil temperature variation, and its dynamics on MMQ. Third, the MMQ_Ref is an important parameter for modeling microbial activity, and it was derived based on MMQ_Soil and a fixed $Q_{10} = 2$; this simple adjustment of invariant Q_{10} might have brought biases into this analysis considering the variation in temperature sensitivity of microbial activities (Karhu et al. 2014). Fourth, the microbial community structure is another potential factor affecting MMQ_Soil, but due to lack of data, this study did not include microbial community structure as a biological factor (Strickland and Rousk 2010, Rousk and Bååth 2011). Fifth, the C:N:P:S nutrient stoichiometry needs to be considered when estimating microbial respiration (Hartman and Richardson 2013, Xu et al. 2015b). Finally, due to the environmental controls on MMQ_Soil are similar with those on MMQ_Ref; along with the simple temperature adjustment of MMQ_Ref, this study did not report the environmental controls on MMQ_Ref. That deserves future intensive experimental and modeling studies.

FUTURE DIRECTIONS

The MMQ represents the specific microbial activity in the global soils. Therefore, it is a critically important parameter for understanding microbial controls on carbon cycling, particularly the carbon releases from soils to the atmosphere. The quantitative equations described here for the biological and edaphic controls on MMQ_Soil are a valuable source for quantitatively modeling microbial activities.

Given the progress achieved and gaps remaining, we identified three key research directions for further efforts of understanding and applying MMQ. First, a new and better methodology for quantifying MMQ is needed. Current estimation of MMQ is highly dependent on incubation experiment with measured basal respiration and soil microbial biomass carbon. Because the soil microbial biomass varies significantly over time and across space and microbes continuously assimilate and release carbon, the instant, or short-term, basal respiration and soil microbial biomass could be used to calculate the *in situ* MMQ. Due to the technical limitation, it is challenging to measure instant basal respiration and soil microbial biomass and carbon turnover in biomass. Recent measurement of microbial carbon use efficiency with isotopic technique might be partially solving this limitation (Hagerty et al. 2014). Second, how to model MMQ in a unified manner is very important for ongoing effort for incorporating microbial physiology into large-scale climate models. The mathematical equations developed in this study could be useful for modeling MMQ in a more mechanistic way, and large datasets would provide robust analysis to advance the mathematical understanding. Third, theoretical modeling of microbial physiology, particularly the MMQ might be a good way to integrate limited MMQ data; as progress being made in this direction, more convincing results are emerging. Any progress made toward these three directions would lead to robust knowledge of MMQ and reliable ways for understanding microbial contributions to carbon cycling at various scales ranging from molecular to global.

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Table 1. Global and biome-level MMQ_Inc, MMQ_Soil, and MMQ_Ref (mean and 95% confidence boundaries are reported; the different letters in one column infer difference at the significance level of P = 0.05)

Biomes	MMQ_Inc (mmol C · mol $MBC^{-1} \cdot h^{-1}$)	MMQ_Soil (mmol C · mol $MBC^{-1} \cdot h^{-1}$)	MMQ_Ref (mmol C · mol $MBC^{-1} \cdot h^{-1}$)
	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)
Bare soils/Desert	6.16 (4.83 ~ 7.86) ab	3.21 (2.50 ~ 4.13) a	2.56 (1.97 ~ 3.32) ab
Boreal Forest	3.42 (2.99 ~ 3.91) cd	1.28 (1.11 ~ 1.48) cd	1.70 (1.49 ~ 1.95) bc
Cropland	4.76 (4.31 ~ 5.25) bc	3.11 (2.79 ~ 3.47) ab	2.08 (1.87 ~ 2.31) ab
Grassland	2.31 (2.03 ~ 2.63) de	1.11 (0.97 ~ 1.27) d	1.23 (1.10 ~ 1.38) cd
Natural wetlands	7.95 (6.08 ~ 10.39) a	3.75 (2.91 ~ 4.83) a	3.36 (2.55 ~ 4.43) a
Pasture	2.05 (1.69 ~ 2.48) e	1.12 (0.91 ~ 1.38) d	0.84 (0.71 ~ 1.00) de
Shrubland	4.51 (3.55 ~ 5.74) bc	1.96 (1.56 ~ 2.47) bc	2.11 (1.74 ~ 2.56) ab
Temperate Broadleaf	2.87 (2.53 ~ 3.27) d	1.19 (1.04 ~ 1.37) cd	1.16 (1.01 ~ 1.32) cd
Temperate Conifer	2.23 (1.90 ~ 2.61) de	0.99 (0.81 ~ 1.13) d	0.96 (0.81 ~ 1.13) de
Tropical/Subtropical	1.58 (1.38 ~ 1.82) e	1.35 (1.15 ~ 1.58) cd	0.62 (0.53 ~ 0.73) e
Global average	3.67 (3.47 ~ 3.89)	2.01 (1.89 ~ 2.14)	1.64 (1.54 ~ 1.74)
Area-weighted global average	3.44 (2.89 ~ 4.12)	1.81 (1.52 ~ 2.17)	1.51 (1.27 ~ 1.80)

Table 2. Summary of the generalized linear models for the effects of biological, meteorological and soil edaphic factors on MMQ_Soil (all contribution were standardized for comparison purposes)

Source	Categories	Meteorology		Biology	Soil Edaphic Factors			
	Factors	Soil temperature	Soil moisture	BR	Soil pH	Soil organic carbon	Silt	Clay
Cropland	Standardized estimates	0.26*	0.01	0.92*	-0.01	-0.19*	-0.05	-0.03
Natural Ecosystems	Standardized estimates	0.25*	-0.39*	0.55*	0.04	-0.41*	-0.02	0.04
Combined	Standardized estimates	0.27*	-0.17*	0.68*	0.08*	-0.46*	-0.08*	0.21*

Figure legends

Fig. 1. Conceptual framework showing the correlation between MMQ_Inc, MMQ_Soil, and MMQ_Ref (positions of MMQ_Inc, MMQ_Soil, and MMQ_Ref depend on the temperatures)

Fig. 2. Distribution of the data points used in this study (2437 out of 2444 data points with geographical coordinates are shown in this map)

Fig. 3. The 3-D diagram showing the correlation between MMQ_Inc, basal respiration, and microbial biomass carbon

Fig. 4. The temperatures for the soil samples during incubation and soil and air temperatures of their sampling sites (91.5% measurements have lower air temperature than incubation temperature; 91.1% measurements have lower soil temperature than incubation temperature)

Fig. 5. Controls on MMQ_Soil in natural ecosystems and cropland (Red is for cropland, blue for natural ecosystems, and black for natural ecosystems and cropland combined; A: Cropland: Log(MMQ_Soil) = -3.0837 (0.0621) + 0.0343 (0.0034) × Tsoil; R^2 = 0.0795; P < 0.001; Natural Ecosystems: Log(MMQ_Soil) = -3.1102 (0.0281) + 0.0214 (0.0022) × Tsoil; R^2 = 0.0698; P < 0.001; All:

Log(MMQ_Soil) = -3.1670 (0.0293) + 0.0293 (0.0034) × Tsoil; R^2 = 0.1167; P < 0.001; B: Cropland: Log(MMQ_Soil) = -2.3913 (0.1081) - 0.5563 (0.1437) × Log(N:P); R^2 = 0.2256; P < 0.001; Natural Ecosystems: Log(MMQ_Soil) = -2.3049 (0.2127) – 0.6796 (0.1743) × Log(N:P); R^2 = 0.2572; P < 0.001; All: Log(MMQ_Soil) = -2.3322 (0.0926) - 0.6496 (0.0930) × Log(N:P); R^2 = 0.3468; P < 0.001; C: Cropland: Log(MMQ_Soil) = -8.5467 (0.9711) + 2.0070 (0.3082) × pH – 0.1614 (0.0239) × pH^2; R^2 = 0.0630; P < 0.001; Natural Ecosystems: Log(MMQ_Soil) = -3.4535 (0.0742) + 0.0937 (0.0127) × pH; R^2 = 0.0556; P < 0.001; All: Log(MMQ_Soil) = -5.2547 (0.3290) + 0.8153 (0.1129) × pH – 0.0631 (0.0094) × pH^2; R^2 = 0.0378; P < 0.001)

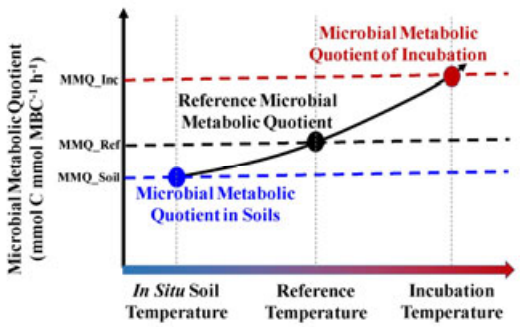
Fig. 6. Structural equation models of soil meteorology, edaphic and biology as predictors of MMQ_Soil for (A) cropland, (B) natural ecosystems, and (C) cropland and natural ecosystems combined (black lines represent significant (P < 0.05); orange lines represent not significant (P > 0.05); solid lines represent positive paths; dotted lines represent negative paths; microbial N: P ratio is not included because of lacking microbial N: P data in associated with all other variables; the width of the arrow is proportional to the factorial contribution)

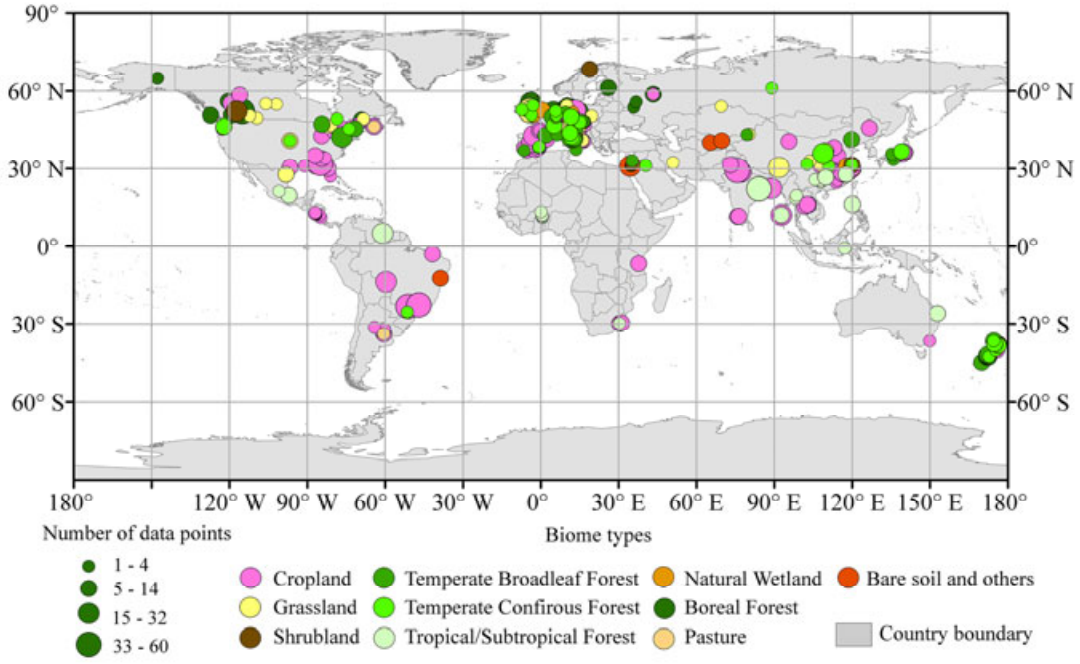
Fig. 7. Edaphic impacts on *MMQ_Soil* (A: ternary graph; correlation between MMQ_Soil and (B) silt, (C) clay, and (D) sand)

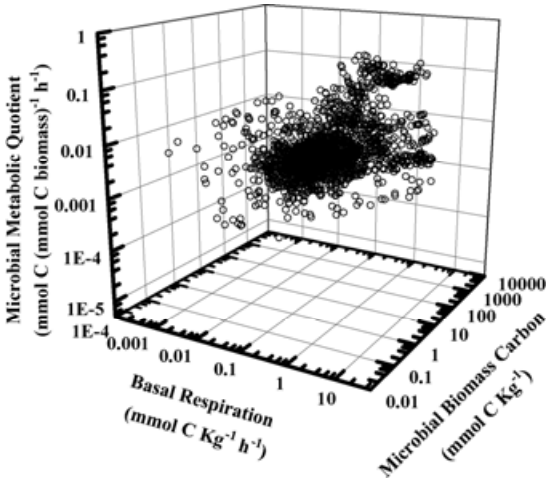
Fig. 8. Ternary graph showing silt, clay and sand impacts on *MMQ_Soil* between (A: natural ecosystem; B: cropland)

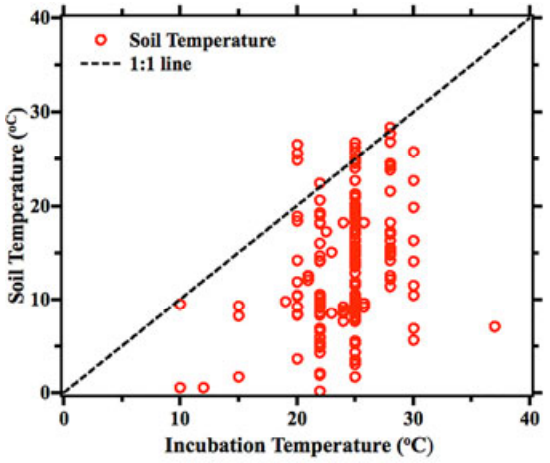
Fig 9. The MMQ_Soil and MMQ_Ref for forest vs. non-forest and cropland vs. natural ecosystems (the bar represents standard derivation)

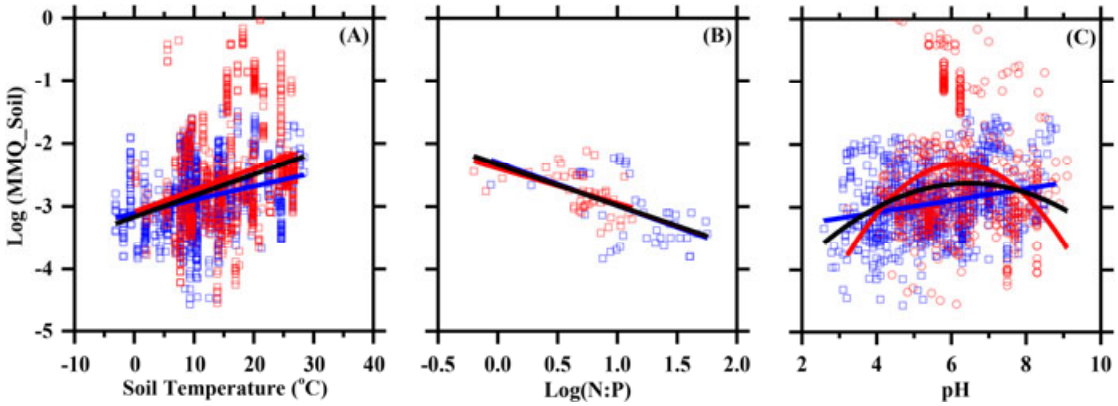
Fig. 10. Estimated respiratory carbon turnover in comparison with microbial turnover rate represented in several representative microbial models (microbial turnover rate in CORPSE ranges from 0.00046 h^{-1} to 0.04 h^{-1}, the graph assumes 90% closer to the slow carbon pool)

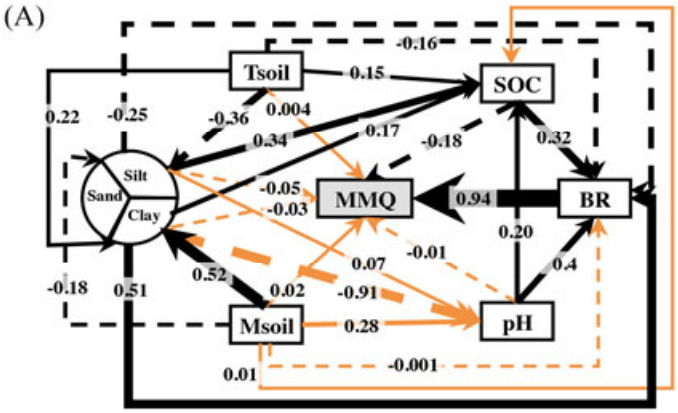




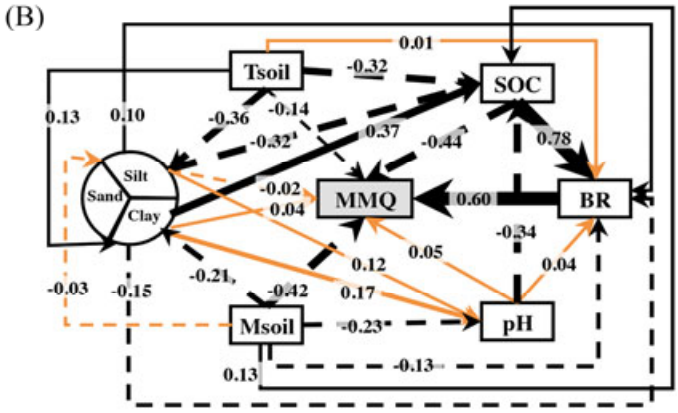




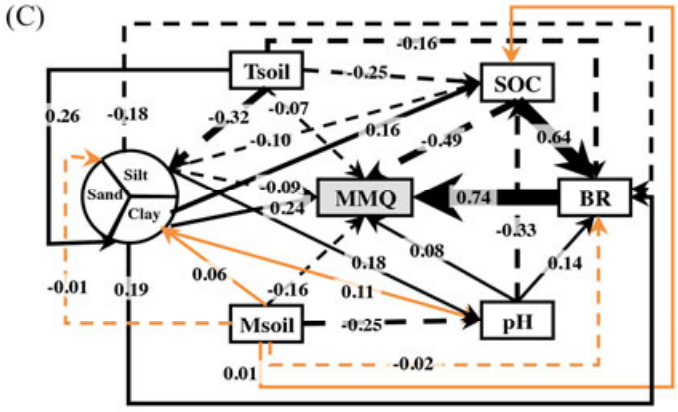




CFI = 1.00; NFI = 1.00; $\chi^2 < 0.01$; N = 274; $R^2 = 0.78$



CFI = 1.00; NFI = 1.00; $\chi^2 < 0.01$; N = 584; $R^2 = 0.39$



CFI = 1.00; NFI = 1.00; $\chi^2 < 0.01$; N = 858; $R^2 = 0.48$