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RESEARCH ARTICLE

# Drivers of the microbial metabolic quotient across global grasslands

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## Abstract

**Aim:** The microbial metabolic quotient (MMQ; mg $CO_2$-C/mg MBC/h), defined as the amount of microbial $CO_2$ respired (MR; mg $CO_2$-C/kg soil/h) per unit of microbial biomass C (MBC; mg C/kg soil), is a key parameter for understanding the microbial regulation of the carbon (C) cycle, including soil C sequestration. Here, we experimentally tested hypotheses about the individual and interactive effects of multiple nutrient addition (nitrogen + phosphorus + potassium + micronutrients) and herbivore exclusion on MR, MBC and MMQ across 23 sites (five continents). Our sites encompassed

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a wide range of edaphoclimatic conditions; thus, we assessed which edaphoclimatic variables affected MMQ the most and how they interacted with our treatments.

**Location:** Australia, Asia, Europe, North/South America.

**Time period:** 2015–2016.

**Major taxa:** Soil microbes.

**Methods:** Soils were collected from plots with established experimental treatments. MR was assessed in a 5-week laboratory incubation without glucose addition, MBC via substrate-induced respiration. MMQ was calculated as MR/MBC and corrected for soil temperatures (MMQsoil). Using linear mixed effects models (LMMs) and structural equation models (SEMs), we analysed how edaphoclimatic characteristics and treatments interactively affected MMQsoil.

**Results:** MMQsoil was higher in locations with higher mean annual temperature, lower water holding capacity and lower soil organic C concentration, but did not respond to our treatments across sites as neither MR nor MBC changed. We attributed this relative homeostasis to our treatments to the modulating influence of edaphoclimatic variables. For example, herbivore exclusion, regardless of fertilization, led to greater MMQsoil only at sites with lower soil organic C (< 1.7%).

**Main conclusions:** Our results pinpoint the main variables related to MMQsoil across grasslands and emphasize the importance of the local edaphoclimatic conditions in controlling the response of the C cycle to anthropogenic stressors. By testing hypotheses about MMQsoil across global edaphoclimatic gradients, this work also helps to align the conflicting results of prior studies.

**KEYWORDS**

anthropogenic management, climate, herbivore exclusion, microbial biomass carbon, microbial respiration, nutrient addition, Nutrient Network: A Global Research Cooperative (NutNet), soil properties

## 1 | INTRODUCTION

Grassland ecosystems store up to 30% of the world's soil carbon (Anderson, 1991; Conant et al., 2017; Eswaran et al., 1993), with soil microbial processes playing an important role in the build-up and maintenance of this stored C (Liang et al., 2017; Schimel & Schaeffer, 2012). Microbes decompose and mineralize C and incorporate part of it into their biomass (microbial biomass C; MBC, mg C/kg soil). Microbial necromass is increasingly being shown to be important for longer-term C sequestration (Gies et al., 2021; Lehmann et al., 2020; Liang et al., 2017; Wiesmeier et al., 2019). At the same time, microbes release $CO_2$ via heterotrophic respiration (hereafter, microbial respiration, MR, mg $CO_2$-C/kg soil/h), which is determined by both the activity and abundance (biomass) of the microbes (Xu et al., 2017). The rate of MR per unit MBC is defined as the microbial metabolic quotient (MMQ; mg $CO_2$-C/mg MBC/h), also referred to as $qCO_2$ (Anderson & Domsch, 1993; Sinsabaugh et al., 2017; Xu et al., 2017; Ye et al., 2020), and is generally negatively related to the C use efficiency (CUE; the ratio of net C gain to gross C assimilation over time) of microbes (Ye et al., 2020). Given that greater MMQ implies a greater release of $CO_2$ per unit MBC, MMQ is often considered a critical parameter in soil C storage (Xu et al., 2017).

Globally, MMQ and associated variables (i.e., MR and MBC) are controlled by environmental factors such as climate and soil properties. For example, two meta-analyses that considered different ecosystem types, including grasslands, tropical to boreal forests, wetlands, shrublands, croplands and tundra (Hartman & Richardson, 2013; Xu et al., 2017), showed that MMQ was positively affected by soil pH, soil temperature and soil inorganic P availability, and negatively by soil organic C density and microbial N : P and C : P ratios across large spatial scales. In grassland ecosystems across the Inner Mongolian and Loess plateaus in China, MMQ was positively correlated with mean annual temperature, while it was negatively correlated with mean annual precipitation, soil organic C and N concentration (Cao et al., 2019; Xue et al., 2020).

MMQ, MR and MBC can also be strongly influenced by anthropogenic factors like nutrient enrichment and altered herbivore pressure. For example, MR decreased with N additions (Widdig, Schleuss, et al., 2020), while MBC remained unaffected by nutrient additions and grazing exclusion, across globally distributed grasslands (Risch et al., 2020; Widdig, Schleuss, et al., 2020). In contrast, one meta-analysis found higher MR

when N was added or herbivores were excluded, while on grazed plots with N addition, MR decreased (Zhou et al., 2019). Other meta-analyses reported a reduction in MBC in grazed grasslands (Wang et al., 2016; Zhou et al., 2017), while the responses of MBC to nutrient additions were dependent on site fertility (Wang & Fang, 2009). However, despite the extensive knowledge available about how nutrient additions and herbivore exclusions affect MR and MBC individually (e.g., Li et al., 2013, 2017; Liu et al., 2007; Stark & Kytöviita, 2006; Wang et al., 2021; Wilson et al., 2018; Zhang et al., 2015; Zhou et al., 2021), no study has so far assessed how nutrient additions and alterations in the density and composition of mammalian herbivores simultaneously affect MMQ across global grasslands, although it is increasingly acknowledged that it is crucial to study multiple disturbances and their complex interactive effects (additive, synergistic, etc.). Despite the limited information available, the heterogenous responses of MR and MBC suggest that interactions between environmental conditions and anthropogenic management could also be particularly relevant for understanding microbial processes and MMQ globally (Wang & Fang, 2009).

In this study, we sought (a) to understand how anthropogenic management (fertilization with nitrogen + phosphorus + potassium [hereafter NPK] and herbivore exclusion) affects MMQ across 23 globally distributed grassland ecosystems that are part of the Nutrient Network: A Global Research Cooperative (NutNet) research cooperative; (b) to identify the main edaphoclimatic drivers of MMQ, including soil pH, water-holding capacity, texture, bulk density, total C and N concentration, mean annual temperature, mean annual precipitation, and temperature of the wettest quarter as potential variables; and (c) to evaluate the direction and extent to which edaphoclimatic factors modulate the response of MMQ to anthropogenic management (Thébault et al., 2014).

Based on the current literature and our previous studies on C and nutrient cycling across the NutNet grasslands (Crowther, Riggs, et al., 2019; Ochoa-Hueso et al., 2020; Radujković et al., 2021; Risch et al., 2019, 2020; Sitters, Wubs, et al., 2020), we hypothesized that MMQ would be reduced by fertilization alone due to a decrease in MR, but that there would be no change in MBC (Risch et al., 2020; Widdig, Schleuss, et al., 2020; Zhou et al., 2019). We also expected an increase of MMQ with herbivore exclusion alone due to an increase in MR, but no change in MBC (Risch et al., 2020; Wang et al., 2016; Zhou et al., 2017, 2019). However, we expected to find no change in MMQ under the combined treatments (nutrients added and herbivores excluded) as the fertilization-induced decrease in MR would be cancelled out by the positive effect of herbivore removal on MR (i.e., opposing effects of treatments on MR). Finally, we expected to find large-scale macroecological patterns across our sites: we specifically predicted that sites with lower soil organic C concentration (Xue et al., 2020), lower mean annual precipitation and higher mean annual temperature would have greater MMQ (Cao et al., 2019). Our results will therefore be important to understand the role of management (fertilization and herbivore exclusion) on MMQ as well as the context dependency (edaphoclimatic factors) of the response of MMQ across global grasslands. Given that MMQ is an important parameter regulating the ability of soils to sequester and stabilize C, our results will be essential for assessing the sensitivity of soil C to global change factors such as fertilization and altered herbivory.

## 2 | METHODS

### 2.1 | Study sites and experimental design

We collected data from 23 sites that are part of the NutNet (https://nutnet.umn.edu/). The mean annual air temperature (MAT) across these sites ranged from −4 to 22 °C, mean annual precipitation (MAP) from 252 to 1,592 mm and elevations from 6 to 4,261 m above sea level (Figure 1a, Supporting Information Table S1); hence, a wide

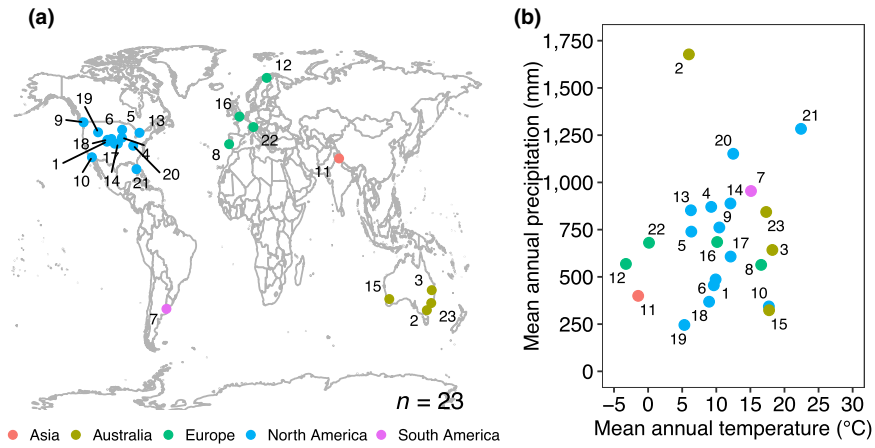


FIGURE 1 Geographic and climatic distribution of experimental Nutrient Network: A Global Research Cooperative (NutNet) sites. (a) Location of the 23 NutNet sites where the field experiment was conducted and soil samples were collected. (b) The 23 study sites represent a wide range of mean annual temperature (MAT) and mean annual precipitation (MAP) conditions that are representative of grasslands worldwide. They also cover a wide range of soil edaphic conditions as described in the main text and shown in Supporting Information Table S2. Numbers refer to # in Supporting Information Tables S1 and S2.

range of climatic conditions under which grasslands occur were covered (Figure 1b). Soil organic C concentrations ranged between 0.8 to 7.8%, soil total N concentrations between 0.1 and 0.6%, and the soil C : N ratio between 9.1 and 21.5. Soil clay content spanned from 3.0 to 35%, and soil pH from 3.4 to 7.6 (Supporting Information Table S2).

At each site, the effects of nutrient addition and herbivore exclusion were tested via a randomized-block design (Borer et al., 2014). Three blocks with 10 treatment plots each were established at each site, except for the site at bldr.us (only two blocks). Each of these 10 plots was randomly assigned to a nutrient or fencing treatment. An individual plot was 5 m × 5 m, divided into four 2.5 m × 2.5 m subplots. Each subplot was further divided into four 1 m × 1 m square sampling plots, one of which was set aside for soil sampling (Borer et al., 2014). Plots were separated by at least 1-m-wide walkways. We collected soil samples from four different treatments for this study: (a) untreated control plots (Control); (b) herbivore exclusion plots (Fence); (c) plots fertilized with N, P, K, plus nine essential macro- and micronutrients (NPK); and (d) plots with simultaneous fertilizer addition and herbivore exclusion (NPK + Fence). The experiments were established at different times in the past, with years of treatment different among sites (2–9 years since start of treatment; Supporting Information Table S1). For the nutrient additions, all sites applied 10 g $N/m^2$/year as time-release urea; 10 g $P/m^2$/year as triple-super phosphate; 10 g $K/m^2$/year as potassium sulphate. A micro-nutrient mix (Fe, S, Mg, Mn, Cu, Zn, B, Mo, Ca) was applied at 100 $g/m^2$ together with K in the first year of treatments but not thereafter.

We excluded large vertebrate herbivores (Fence) by fencing two plots, one with and one without NPK additions, within each block. The fences excluded all aboveground mammalian herbivores with a body mass of over 50 g (Borer et al., 2014). At most sites, the fences were 180 cm high, and the fence contained a wire mesh (1-cm holes) for the bottom 90 cm with a 30-cm outward-facing flange stapled to the ground to exclude burrowing animals. Climbing and subterranean animals may potentially still access these plots (Borer et al., 2014). For slight modifications in fence design at a few sites see Supporting Information Table S3. Most sites only had wild herbivores, although four sites were also grazed by domestic animals (Supporting Information Table S1).

## 2.2 | Collection of soil samples, soil microbial respiration, microbial biomass and other soil properties

Each of the 23 sites received a package containing identical material from the Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Switzerland to be used for sampling (Risch et al., 2015, 2019). We collected two soil cores of 5 cm diameter and 12 cm depth in each sampling plot and combined them to measure MR, MBC and soil chemical properties (see below). An additional sample (5 cm diameter × 12 cm depth) was collected to assess soil physical properties. This sample remained within a steel sampling core after collection and both ends were tightly closed with plastic caps to avoid disturbance. All soils were shipped cooled to the laboratory at WSL within a few days of collection. Soils were sampled roughly 6 weeks prior to peak biomass at each site during 2015 and 2016.

To assess MR ($CO_2$ production) in a laboratory incubation experiment we weighed duplicate soil samples (8 g dry soil equivalent) into 50-mL Falcon tubes. No additional substrate (glucose, sugar) was added to these samples. We adjusted the soil moisture of each sample to 60% field capacity. We then placed a 15-mL plastic test tube (Semadeni 1701A) containing 7.25 mL 0.05 M NaOH over each soil sample. The test tube was fixed with a plastic rod so that it was not in contact with the soil sample. The Falcon tubes were then sealed with a screw cap and placed in an incubator under completely dark conditions at 20 °C. The $CO_2$ produced by microbial respiration was absorbed by the 0.05 M NaOH. For 5 weeks we measured the decrease in conductivity within the 0.05 M NaOH solution on a weekly basis with a Multimeter WTW Multi 3410 (WTW GmbH, Germany) and replaced the 0.05 M NaOH with fresh solution. We included Falcon tubes without soil samples in each incubation run as blanks to test if tubes were tight and no $CO_2$ could enter or escape. We calibrated the relationship between conductivity reduction and NaOH absorbed as follows: 400 mL 0.05 M NaOH was placed in a beaker and its conductivity was measured with the multimeter. While stirring, air containing $CO_2$ was blown into the solution for approximately 1 min, which reacts with NaOH to form $Na_2CO_3$. After this process, conductivity was measured again. We then transferred 7.25 mL of the solution into a smaller beaker and added 1 mL of 0.1 M $BaCl_2$ to precipitate $Na_2CO_3$ and then titrated the solution with 0.05 M HCl to determine the remaining NaOH. We then repeated these steps with the remaining solution a total of nine times and plotted the conductivities (*y* axis) against the NaOH consumed (*x* axis, Supporting Information Figure S1). This regression line was used to infer the consumption of NaOH from the conductivity reduction in the incubation experiments and to calculate $CO_2$ evolution during incubation. In addition, we determined the optimum concentration for the NaOH solution in a series of preliminary experiments, so that the concentration was not too high to become insensitive, but also not too low so that not all NaOH reacts during incubation. We then calculated MR (mg $CO_2$-C/kg dry soil/h) as the total amount of $CO_2$ released over the 5 weeks divided by the duration of the entire incubation in hours.

Soil microbial biomass carbon (MBC; mg C/kg soil) was measured at the beginning of the experiment by measuring the maximal respiratory response to the addition of glucose solution (4 mg glucose per g soil dry weight dissolved in distilled water; substrate-induced respiration method) to approximately 5.5 g of soil (Anderson & Domsch, 1978; Eisenhauer et al., 2018; Scheu, 1992). For this purpose we used an $O_2$-micro-compensation apparatus (Scheu, 1992). More specifically, substrate-induced respiration was calculated from the respiratory response to D-glucose for 10 h at 20 °C. Glucose was added according to preliminary studies

to saturate the catabolic enzymes of microorganisms (4 mg/g soil dissolved in 400 mL deionized water). The mean of the lowest three readings within the first 10 h (between the initial peak caused by disturbing the soil and the peak caused by microbial growth) was taken as the maximum initial respiratory response (MIRR; mL $O_2$/kg soil/h) and microbial biomass (mg C/kg soil) was calculated as 38 × MIRR (Beck et al., 1997; Cesarz et al., 2022; Thakur et al., 2015).

The rest of the combined sample was dried at 65 °C for 48 h, ground and sieved (2-mm mesh) to assess the soil pH, mineral soil total C and N and C : N ratio, and mineral soil organic C (Risch et al., 2019). The undisturbed sample was used to assess water holding capacity (WHC), bulk density (BD) and soil texture [sand, silt, clay; methods in Risch et al. (2019)]. We used the percentage of sand and clay as an indicator of soil texture in this study. MAT (°C), MAP (mm) and temperature of the wettest quarter (°C) were obtained from http://www.worldclim.com (Fick & Hijmans, 2017; Hijmans et al., 2005). These variables were selected as they were found to be drivers of soil nutrient processes across these sites in earlier studies (Risch et al., 2019, 2020). Mean annual soil temperatures (MAST; °C) for the 0 to 5 cm soil layer were obtained for each site from the SoilTemp maps (Lembrechts et al., 2021, 2022), global gridded modelled products of soil bioclimatic variables for the 1979–2013 period at a 1-$km^2$ resolution, based on CHELSA (https://chelsa-climate.org/), ERA5 (https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview) and in-situ soil temperature measurements. All data used in this study can be found in Risch et al. (2023) and under https://doi.org/10.16904/envidat.379.

## 2.3 | Numerical calculations and statistical analyses

We calculated MMQ as MR/MBC. We corrected this measure using the average soil temperature of each site (MMQsoil). This temperature correction is necessary as incubation temperatures are usually much higher than site mean annual soil temperatures (see Xu et al., 2017). $MMQsoil = MMQ \times Q10^{(MAST - 20)/10}$, where Q10 was assumed to be 2 (Xu et al., 2017). See Supporting Information Figure S2 for comparison of air and soil temperatures across the 23 sites as well as the incubation temperature.

Some of the explanatory variables (clay, soil organic C, C : N ratio) were skewed and were thus log-transformed prior to analyses. All continuous explanatory variables were centred and scaled to have a mean of zero and variance of one. To avoid collinearity between them we filtered them using correlation analysis (Supporting Information Figure S3). From the variables that were strongly correlated (Pearson's $|r| > .70$; Dormann et al., 2013), we selected the ones that allowed us to minimize the number of variables (Supporting Information Figure S3). Specifically, soil total N concentration, soil total C concentration, soil sand content and soil bulk density were dropped from the dataset. We then assessed how these edaphoclimatic variables are related to MMQ across our global grasslands.

For this, we used linear mixed effects models (LMMs) fitted by maximum likelihood with the lme function in the nlme package (version 3.1-153; Pinheiro et al., 2021) in R version 3.6.3. (R Core Team, 2019). We used treatment as a fixed effect and plot nested in site as random effects to assess treatment differences in MMQsoil, as well as MR, and MBC. The number of years since the treatment started was included as a fixed effect in all the initial models but was not significant and therefore not retained in the models. To assess how differences in MMQsoil were affected by environmental factors (soil, climatic properties) we again used LMMs. Soil and climatic properties were included as fixed effects and plot nested in site as random effects. We did not include interactions between environmental variables. We then used the MuMin package (Barton, 2018; version 1.42.1) to select the best models that explained the most variation based on Akaike's information criterion (AIC; model.avg function). We used the corrected AIC (AICc) to account for our small sample size and selected the top models that fell within 4 AICc units (delta AICc < 4) (Burnham & Anderson, 2002; Johnson & Omland, 2004). We present all our top models rather than model averages. Conditional averages are provided in the Supporting Information Table S4.

Based on the findings from the analyses described above and the literature, we developed a conceptual model of direct and indirect relationships between both edaphoclimatic variables and experimental treatments (Supporting Information Figure S4) to obtain a more holistic approach in understanding how these properties affect MMQsoil. We had data from 23 sites with 272 observations. We tested this model using structural equation modelling based on a *d-sep* approach (Lefcheck, 2016; Shipley, 2009). We considered those environmental drivers that were included in our top LMMs, namely temperature of the wettest quarter (T.q.wet), soil pH, water holding capacity (WHC) and soil organic C (organic C; Supporting Information Figure S4). These factors were allowed to directly affect MMQsoil, and via their interactions with treatments. In addition, treatments were allowed to directly affect MMQsoil. Treatments were included as dummy variables in the model. We tested our conceptual model (Supporting Information Figure S4) using the piecewiseSEM package (version 2.0.2; Lefcheck, 2016) in R 3.4.0, in which a structured set of linear models are fitted individually. This approach allowed us to account for the nested experimental design, and overcome some of the limitations of standard structural equation models (SEMs), such as small sample sizes (Lefcheck, 2016; Shipley, 2009). We used the lme function of the nlme package to model response variables, including site as a random factor. Good fit of the SEM was assumed when Fisher's *C* values were non-significant ($p > .05$). For all significant interactions between soil or climate variables and treatments detected in the SEMs, we calculated treatment effect sizes, that is, the differences in MMQsoil between Control and treatments as log response ratios (LRRs) and plotted these values against the climate or soil factors. The LRRs were defined as log(Control/Treatment), where treatment

was either Fence, NPK or NPK + Fence. To assess which of the LRR-climate or soil property relationships were significant we again used LMMs, in which soil and climatic properties were included as fixed effects and plot nested in site as random effects.

## 3 | RESULTS

Contrary to our expectations, there was no evidence that fertilizer addition or herbivore exclusion directly affected MMQsoil (Figure 2a, Table 1). This was due to the lack of treatment effects on both MR ($F_{3,201}$ = 0.643, $p$ = .588, Supporting Information Figures S5–S7) and MBC ($F_{3,201}$ = 0.315, $p$ = .814, Supporting Information Figures S5–S7), rather than treatment effects cancelling each other out (homeostasis of MR and MBC). There were also no statistically significant differences in MMQsoil, MR or MBC at the individual site level (Figure 2b, Supporting Information Figure S7), but MMQsoil differed considerably across the 23 sites, ranging from 0.00018 mg $CO_2$-C/mg MBC/h at kilp.fi (Finland) to 0.0041 mg $CO_2$-C/mg MBC/h at burrawan.au (Australia; Control plots; Supporting Information Figure S8). Several of our edapho-climatic variables were correlated with MMQsoil independent of treatment (Figure 3a–h; macroecological patterns). However, only MAT, soil organic C concentration (organic C), and water holding capacity (WHC, see LMM results) contributed to simultaneously explain the variability in MMQsoil across our 23 global grasslands (Table 2, Supporting Information Table S4). MR and MBC were highly correlated across our sites ($r$ = .75), but the relationship did not differ between treatments (Supporting Information Figure S9a). The relationship was also very similar for each site (Supporting Information Figure S9b). MR and MBC increased in parallel with increasing soil organic C concentration and WHC but decreased with increasing MAT (Supporting Information Figure S10). The relationships between MMQsoil and MR and between MMQsoil and

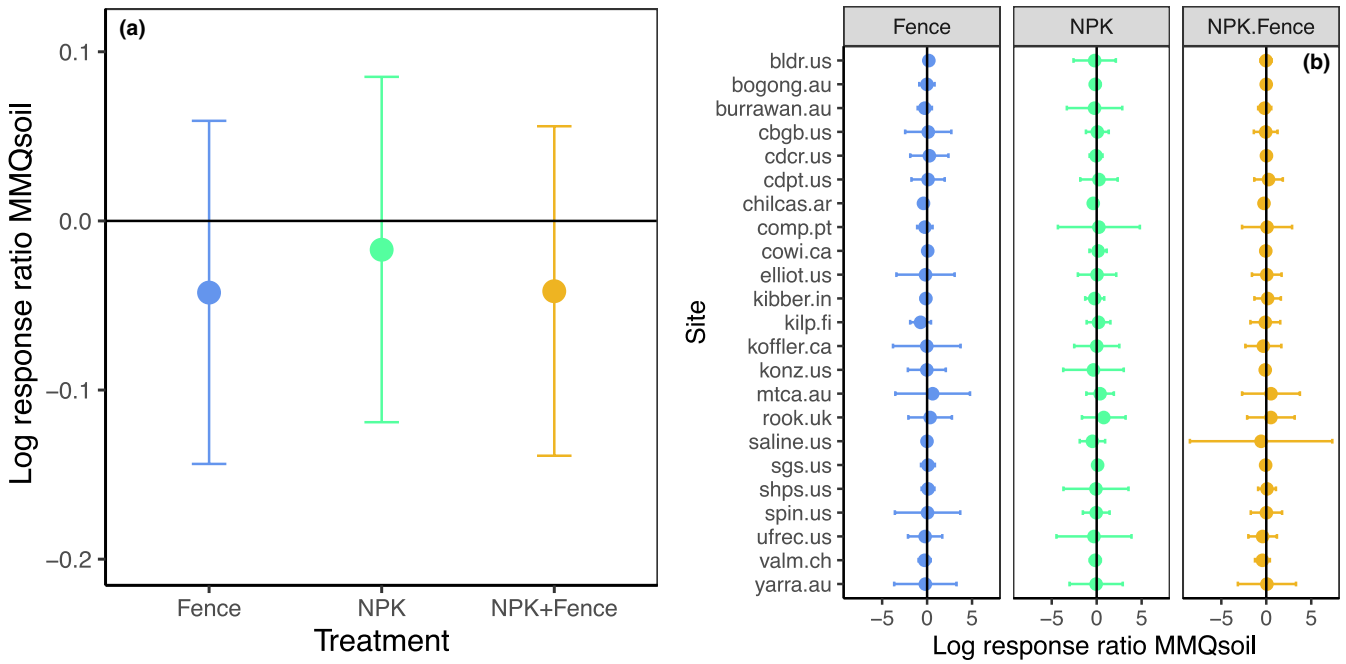


FIGURE 2 Log response ratios (LRRs) of soil microbial metabolic quotient (MMQ; mg $CO_2$-C/mg MBC/h) corrected for soil temperatures (MMQsoil). (a) Means and standard errors across sites, (b) means and standard errors for each individual site. LRR < 0 indicates higher values at control compared to treatment, LRR > 0 indicates higher values at treatments compared to control. Error bars represent the 95% confidence intervals. MMQ was calculated as MR (mg $CO_2$-C/kg dry soil/h)/MBC (mg C/kg soil). For soil temperature corrections see Methods. MBC = microbial biomass C; MR = microbial respiration; NPK = nitrogen + phosphorus + potassium.

TABLE 1 Treatment effects on soil microbial metabolic quotient corrected for soil temperature (MMQsoil) across global grasslands using linear mixed effects models (LMMs).

| Variable | *df* | Estimate | *SE* | *t*-value | *p*-value |
|---|---|---|---|---|---|
| Intercept | 201 | −7.353 | 0.127 | −57.79 | < .001 |
| Fence | 201 | −0.042 | 0.052 | −0.801 | .424 |
| NPK | 201 | −0.017 | 0.050 | −0.339 | .735 |
| NPK + Fence | 201 | −0.041 | 0.051 | −0.817 | .415 |

*Note*: The number of sites is 23.
NPK = nitrogen + phosphorus + potassium.

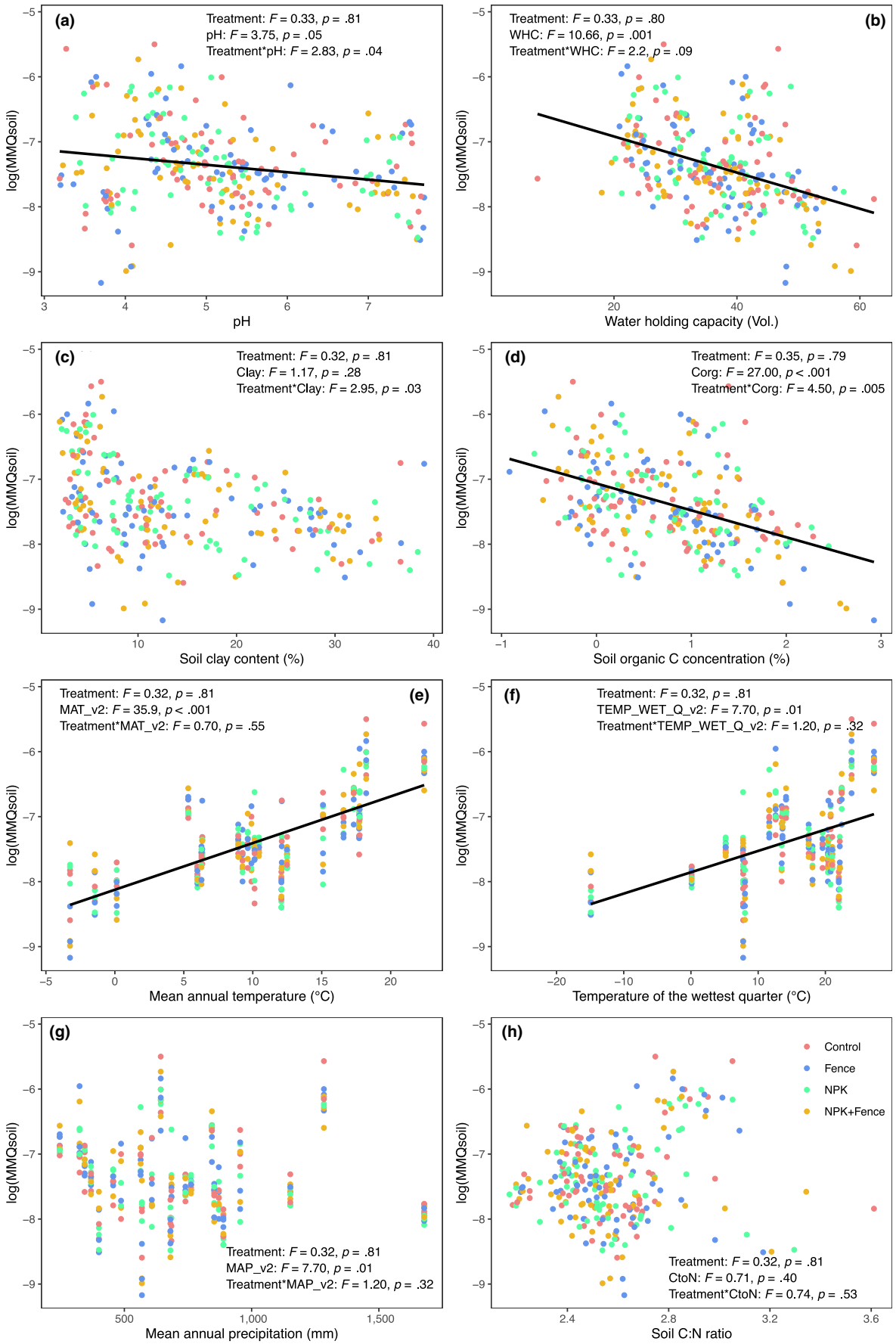

**FIGURE 3** Relationship between the soil microbial metabolic quotient (MMQ; mg $CO_2$-C/mg MBC/h) corrected for soil temperature (MMQsoil) and edaphoclimatic conditions found in our treatments across our 23 grassland sites globally. (a) pH, (b) water holding capacity (WHC), (c) soil clay content, (d) soil organic C concentration (Corg; log transformed), (e) mean annual temperature (MAT), (f) temperature of the wettest quarter (TEMP_WET), (g) mean annual precipitation (MAP), and (h) soil C : N ratio (CtoN; log transformed). MMQsoil was also log transformed. The summary of the linear mixed effect model (LMM) results for treatment, a specific edaphoclimatic variable and their interactions are provided in each figure. Different coloured points represent the four treatments (Control, NPK, Fence, NPK + Fence). The black line represents the overall relationship between log(MMQsoil) and the edaphoclimatic variable without accounting for the individual treatment. MMQ was calculated as MR (mg $CO_2$-C/kg soil/h)/MBC (mg C/kg soil). For soil temperature corrections see Methods. MBC = microbial biomass C; MR = microbial respiration.

**TABLE 2** Best models for predicting soil microbial metabolic quotient corrected for soil temperature (MMQsoil) based on edaphoclimatic variables.

| Model # | Variables | *df* | AICc | Weight |
|---|---|---|---|---|
| Model 1 | 1, 2 | 9 | 196.63 | 0.38 |
| Model 2 | 2, 3 | 9 | 197.26 | 0.28 |
| Model 3 | 2 | 8 | 197.98 | 0.19 |
| Model 4 | 1, 2, 3 | 10 | 198.56 | 0.15 |

*Note*: Variable codes: 1 = Soil organic C (log transformed), 2 = mean annual temperature, 3 = WHC.

Abbreviation: AICc, Akaike's information criterion corrected for small sample size.

MBC were very similar across the sites (Supporting Information Figure S11).

When we simultaneously considered treatments and the three most important edaphoclimatic variables (MAT, organic C, WHC) in our SEM, we found that the edaphoclimatic drivers and interactions between these and the experimental treatments explained 56% (marginal $R^2$) of the variability in MMQsoil across the 23 grasslands (Figure 4). These findings were supported by the LMMs. MMQsoil was higher at sites with higher MAT and lower WHC (Figure 4, Table 2, Supporting Information Table S4) regardless of treatments (Figures 4 and 5a,b). Soil organic C concentration did not directly affect MMQsoil in our SEM, but indirectly and negatively affected MMQsoil via interactions with herbivore exclusion (Fence, NPK + Fence, Figures 4 and 5c, Table 2, Supporting Information Table S4). Sites with soil organic C below roughly 1.7% responded with an increase in MMQsoil compared to the control when herbivores were excluded, or herbivores were excluded and NPK was added (Figure 5c). For sites with soil organic C higher than 1.7% MMQsoil was lower compared to the control in Fence and NPK + Fence plots (Figure 5c).

## 4 | DISCUSSION

In an experiment replicated in 23 grasslands worldwide, we found that MMQsoil was highly variable among sites, and that this variation was largely attributable to between-site differences in edaphoclimatic conditions. To the best of our knowledge, this is the first study that has experimentally assessed how nutrient addition and herbivore exclusion – separately and in combination – affect MMQsoil across sites spanning continents. However, we found no direct, consistent effects of these treatments on MMQsoil across sites. This was due to the homeostasis of MR and MBC in response to treatments, which was rather surprising and contrary to our initial expectations. While it theoretically would be possible that the lack of treatment effects could be related to a depletion of labile substrate during the MR measurements, this is not likely to be the case. Soil C separation has shown that in grassland topsoil, particulate organic matter (widely considered an unprotected fraction of soil C) comprises 20–45% of the total soil organic matter (Leifeld et al., 2009; Rocci et al., 2022). During our 5-week-long incubation, potentially mineralizable C represented less than 1% of total soil C, suggesting that depletion in labile C was unlikely to underlie the observed convergences.

Although different studies reporting MMQ have used a variety of methods, our results demonstrate that MMQsoil values were comparable to those previously reported for grassland ecosystems (e.g., Li et al., 2010; Stevenson et al., 2016; Wang et al., 2021; Widdig, Heintz-Buschart, et al., 2020), particularly when measurements were corrected for soil temperature (Xu et al., 2017). Only Widdig, Heintz-Buschart, et al. (2020) and Raiesi and Riahi (2014) have determined MR over several weeks as we did, while the others used much shorter incubation times (1 to 7 days; Goenster-Jordan et al., 2021; Li et al., 2005, 2010; Stevenson et al., 2016; Wang et al., 2021). In contrast to our study (measured by substrate induced respiration), many previous studies have used chloroform fumigation-extraction to determine MBC, but the two methods have been shown to result in similar findings (Beck et al., 1997). Thus, our findings provide evidence that grassland MMQsoil might be more robust to fertilization, herbivore exclusion and their interactions than previously thought. Below, we discuss potential mechanisms for our findings.

### 4.1 | Lack of fertilization effects on MMQsoil

In contrast to our expectations that MR would be more sensitive to fertilization than MBC – due to the decreasing need for microbes to mine for organic N or to respire excess C to acquire nutrients for forming microbial biomass (Manzoni et al., 2012) – we did not detect a reduction in MMQsoil with fertilization as both MR and MBC remained unaffected. Widdig, Heintz-Buschart, et al. (2020)

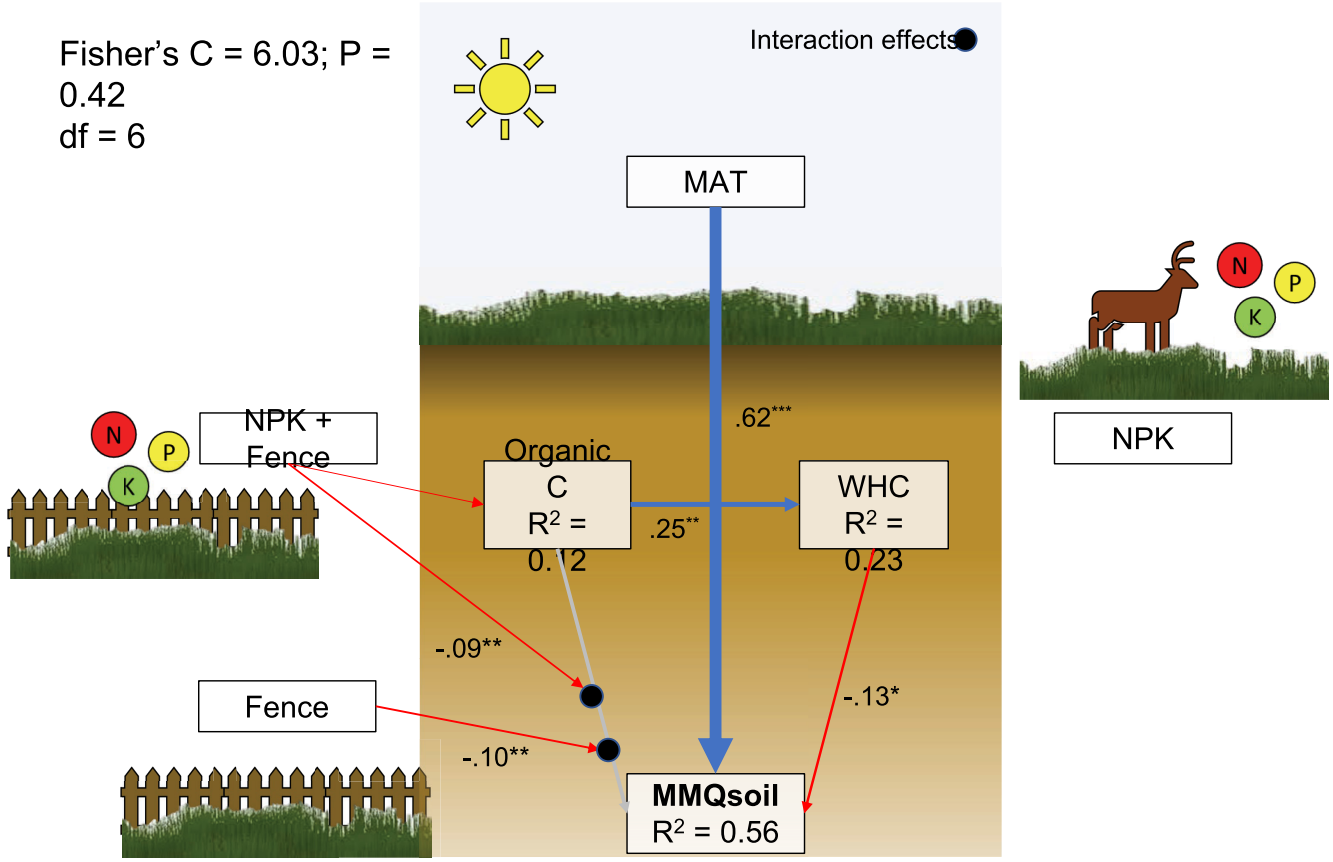


FIGURE 4 Influence of local environmental conditions on the response of soil microbial metabolic quotient (MMQ; mg $CO_2$-C/mg MBC/h) corrected for soil temperature (MMQsoil) to fertilization and herbivore exclusion. Structural equation model diagram representing connections between treatment, climatic conditions and soil properties found to influence MMQsoil. The width of the connections represents estimates of the standardized path coefficients, with blue lines representing a positive relationship and red lines a negative relationship. Interaction effects are depicted with arrows pointing to solid black dots. Significant connections and $R^2$ are shown in black. $^*p < .05$, $^{**}p < .01$, $^{***}p < .001$. MAT = mean annual temperature; Organic C = soil organic C concentration; WHC = water holding capacity; treatments: Control = control plots; Fence = herbivores excluded; NPK = fertilized with N, P, K and micronutrients; NPK + Fence = fertilized with N, P, K and micronutrients and herbivores excluded; total number of observations = 272; total number of sites = 23. MMQsoil values were log-transformed. MMQ was calculated as MR (mg $CO_2$-C/kg soil/h)/MBC (mg C/kg soil). For soil temperature corrections see Methods. MBC = microbial biomass C; MR = microbial respiration; NPK = nitrogen + phosphorus + potassium.

also did not detect any differences in MMQ, MR or MBC between control, N, P and NP plots located in a sandy, low-fertility grassland in Minnesota, USA. However, these and our results contrast with findings by Li et al. (2010) who reported an increase in MMQ after N additions due to a decrease in MBC, but no change in MR, in a semi-arid, sandy grassland in China. Yet, interestingly, when they added P or NP, MMQ no longer differed from the control plots as both MR and MBC remained unchanged (Li et al., 2010). Hence, based on our findings and the available literature there is some evidence that when N is added together with P (i.e., fertilizers are balanced), as we did in our study (NPK, NPK + Fence plots), fertilization does not affect MMQsoil, while the results are more variable when only N is added. A possible explanation for this could be that oxidative enzymes are inhibited and N mining by microbes is reduced when N is added alone. Therefore, N addition results in lower MR (Widdig, Schleuss, et al., 2020). However, when P is added, or N and P are added together, the microbes immobilize N, which prevents N from inhibiting oxidative enzymes and thus MR remains unaltered (Widdig, Schleuss, et al., 2020). In agreement with this line of thought, a recent meta-analysis reported an increase in MR when grasslands were fertilized with N (Zhou et al., 2019), while short-term (0.5 to 9 years) NP or NPK fertilization had no effect on MR across multiple grassland experiments worldwide (Li et al., 2010; Stark & Kytöviita, 2006; Widdig, Heintz-Buschart, et al., 2020). Yet, Spohn et al. (2016) found a reduction in MR when adding NPK to a temperate grassland for more than 55 years. It therefore is possible that in the short–medium term (as in our study; 2–9 years), microbes immobilize N under NP(K) fertilization and MR remains unaffected, while microbial activity may be heavily reduced in the long term, as the system becomes less dependent on microbial N mining due to the constant inorganic N input. However, how N and P additions, alone or in combination, affect N limitation and therefore MR and MMQsoil is difficult to assess due to a lack of coordinated studies, as pointed out in a recent meta-analysis (Feng & Zhu, 2021). Here, we

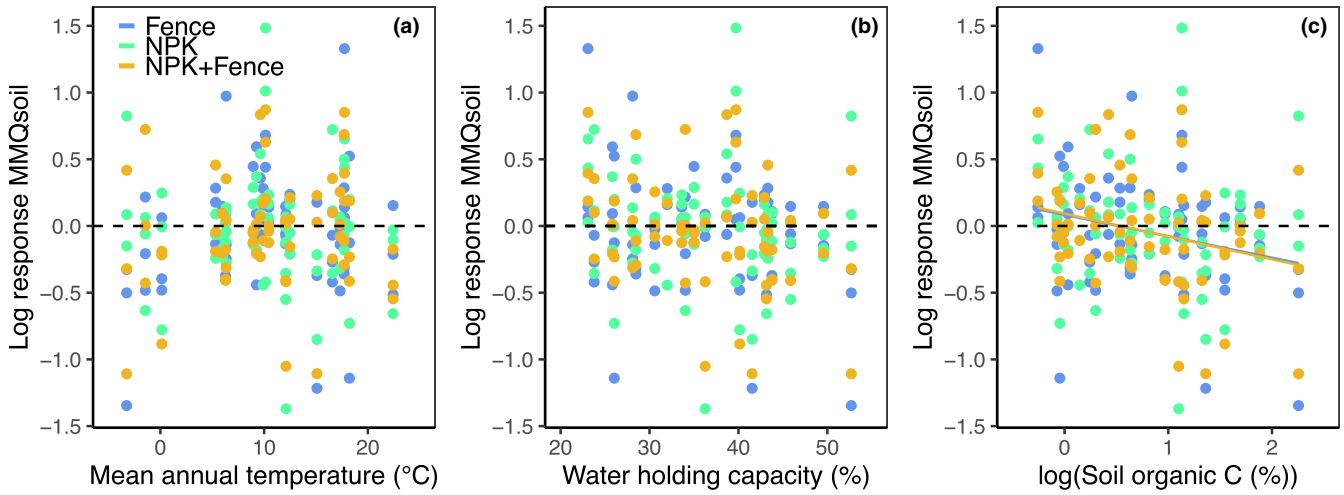


FIGURE 5 Response of soil microbial metabolic quotient (MMQ; mg $CO_2$-C/mg MBC/h) corrected for soil temperature (MMQsoil) to treatment across the landscape. Relationship between log response ratio (LRR) of MMQsoil and (a) mean annual temperature (MAT), (b) water holding capacity (WHC), and (c) soil organic C concentration (SOC; log transformed). MMQsoil is displayed as LRR, which is defined as log(treatment/control). LRR < 0 indicates higher values at control compared to treatment, LRR > 0 indicates higher values at treatments compared to control. Regression lines are shown for significant relationships only. MMQ was calculated as MR (mg $CO_2$-C/kg soil/h)/MBC (mg C/kg soil). For soil temperature corrections see Methods. Fence = herbivore exclusion; MBC = microbial biomass C; MR = microbial respiration; NPK = nitrogen + phosphorus + potassium.

only investigated how NPK (with and without herbivore exclusion) affected MMQsoil as no data were available for those plots in which N, P or NP were added separately.

## 4.2 | Lack of herbivore exclusion effect on MMQsoil

We predicted an increase in MMQsoil due to an increase in MR and no change in MBC when herbivores were excluded from grassland ecosystems. However, in our study, herbivore exclusion had no effect on MR and MBC and, consequently, MMQsoil. These findings are similar to what was reported from a Mediterranean grassland in Israel (Li et al., 2005). Other studies using laboratory incubations, however, detected a decrease in MMQ due to an increase in MBC (Goenster-Jordan et al., 2021; Raiesi & Riahi, 2014) or an increase in MMQ due to an increase in MR in grazed plots (Aldezabal et al., 2015). When MR was measured in the field via trenching or whole plant removal, again higher MR and therefore a decrease in MMQ was reported from grazed plots (Li et al., 2013; Wang, Liu, et al., 2020; Zhang et al., 2015; Zhou et al., 2019). These latter findings were explained by higher temperature sensitivities of MR and higher soil organic C concentrations due to increased plant biomass and plant litter input in ungrazed grasslands (Li et al., 2013; Wang, Liu, et al., 2020; Yunbo Wang, Wang, et al., 2020; Zhang et al., 2015). The most likely reason for the divergent findings of herbivore exclusion on MMQsoil, MR and MBC in the literature could be related to differences in grazing intensities between studies (Goenster-Jordan et al., 2021; Jiang et al., 2020), the herbivore species present, their variation in body size or functional type (Risch et al., 2013; Sitters, Kimuyu, et al., 2020), differences in the soil or microbial community composition (e.g., Peschel et al., 2015; Stark et al., 2012; Wang et al., 2019) or C : N : P stoichiometry across grasslands (e.g., Roy & Bagchi, 2021; Yu et al., 2021).

## 4.3 | Global controls of MMQsoil

As opposed to the lack of treatment effects, differences in edaphoclimatic conditions across our 23 grasslands were important drivers of MMQsoil, MR and MBC, which is similar to previous studies (Cao et al., 2019; Hartman & Richardson, 2013; He & Xu, 2021; Xu et al., 2017). MR and MBC changed in parallel across the landscape, which was also shown for other grassland ecosystems (Ananyeva et al., 2008; Gutiérrez-Girón et al., 2015; Liu et al., 2016; Wang et al., 2014). The observed positive relationship of MMQ with MAT but a negative one with MAP found in the current study is consistent with a climate gradient study across Inner Mongolian grasslands (Cao et al., 2019). Other studies considering multiple biomes (forest, tundra, grasslands, wetlands, etc.) showed that MMQ was negatively affected by soil temperature and positively by pH and inorganic P (Hartman & Richardson, 2013; Xu et al., 2017). In our study, soil pH, WHC and soil organic C concentrations had a negative effect on MMQsoil. In addition, we found that at sites with higher soil organic C concentrations (> 1.7%) MMQsoil was less vulnerable to herbivore exclusion alone, or to herbivore exclusion in combination with fertilization, than at sites with lower soil organic C concentrations (<1.7%). Generally, soils with higher organic C concentrations have higher fungi : bacteria ratios (e.g., Schmidt & Bölter, 2002; Wan et al., 2021) and therefore a higher carbon use efficiency

(Fuchslueger et al., 2019; Soares & Rousk, 2019) or a lower MMQ (Six et al., 2006). In our study, sites with high soil organic C concentrations were distributed around the globe and were found in Finland, USA, Australia and Argentina, hence under quite different edaphoclimatic conditions. To further explore and better predict the effects of nutrient addition and herbivore exclusion on C dynamics in grassland soils (Crowther, van den Hoogen, et al., 2019), future studies should also explore the role of soil microbial community composition, for example, based on major groups, as well as the local microbial nutrient status (Eisenhauer et al., 2010; Feng & Zhu, 2021), and stoichiometry (Roy & Bagchi, 2021; Xu et al., 2013; Yu et al., 2021) in driving the response of MMQsoil to varying environmental conditions.

## 5 | CONCLUSIONS

Our findings reveal that the response of MMQsoil to altered nutrient supply and herbivory is contingent on site-level edaphoclimatic conditions. MMQsoil was controlled by multiple factors, leading to higher order interactions between our treatments and site conditions. Specifically, MAT, soil WHC and soil organic C concentration determined the direction and magnitude of the MMQsoil response to environmental variation and changes in nutrient supply or herbivory. These higher order interactions among site-level edaphoclimatic factors and our treatments point to gaps in our understanding of the relationship between microbial community composition and the rate of functions such as MMQsoil. Importantly, higher order interactions may clarify why past studies have produced conflicting results about the effects of fertilization and herbivore exclusion. The results of this multi-continent experiment emphasize the importance of local edaphic and climatic context in controlling anthropogenic management impacts on C cycling processes, as recently highlighted by a meta-analysis (Beillouin et al., 2022).

### AUTHOR CONTRIBUTIONS

ACR, SZ, FH, MS and RO-H developed the overall research idea. ACR and SZ coordinated data collection and laboratory analyses. SZ and NE analysed the samples. RO-H and ACR analysed the data. ACR and RO-H wrote the paper with contributions and input from all authors. EWS and ETB are Nutrient Network coordinators. All authors collected data used in this analysis. Author contribution matrix provided as Supporting Information Table S5.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

### DATA AVAILABILITY STATEMENT

Data are available at https://www.envidat.ch/dataset/drivers-of-the-microbial-metabolic-quotient-across-global-grasslands. doi: https://doi.org/10.16904/envidat.379.

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## BIOSKETCH

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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