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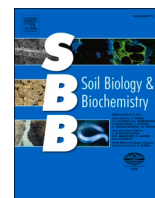
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## Controls of microbial carbon use efficiency along a latitudinal gradient across Europe

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### ABSTRACT

Microbial carbon use efficiency (CUE) describes the partitioning of carbon (C) between respiration and growth, and this defines the soil-atmosphere C balance. Despite its importance, CUE is not properly represented in soil biogeochemical models. Here, we estimated how CUE varied in soil along a continental gradient. Through a structural equation model, we found that bacterial growth, fungal community composition, and SOM quality were the main drivers of CUE variation. Biotic factors controlled CUE directly, while soil properties and climate indirectly controlled CUE via biotic factors. Surprisingly, we found that microbial assimilability of SOM had a negative relationship with CUE. High rates of microbial SOM-use coincided with a greater growth-fraction used for respiration suggesting decoupled catabolism and anabolism, probably due to nutrient limitation. Our study highlights the importance of the microbial community composition to predict CUE and that interactions between bacterial and fungal communities can have implications for CUE.

Soil microbes play a crucial role in regulating carbon (C) cycling since they are the main decomposers in soils (Schimel, 2013). They can mineralize a fraction of the organic C into CO<sub>2</sub>, via respiration, thereby contributing to the CO<sub>2</sub> that is released to the atmosphere. Simultaneously they also control how much C is stored by transforming it into microbial biomass, via growth, and eventually necromass which can become stabilized in soils (Liang et al., 2017; Camenzind et al., 2023). This partitioning of C between respiration and growth can be described by the microbial carbon use efficiency (CUE), which is defined as the ratio of microbial growth over C uptake (Geyer et al., 2019). Despite the importance of microbial CUE for regulating the soil-atmosphere C balance (Tao et al., 2023), it is still uncertain how it is controlled by abiotic and biotic factors.

Many soil biogeochemical models are built on the assumption that CUE is constant, thus disregarding environmental and biological feedbacks (Manzoni et al., 2012). Microbial CUE can be driven by abiotic factors such as temperature, moisture, and edaphic properties (Manzoni et al., 2012; Frey et al., 2013; Sinsabaugh et al., 2016; Malik et al., 2018; Qiao et al., 2019). It is expected that CUE will be negatively affected by higher temperature (Qiao et al., 2019) but this response can vary with substrate quality (Frey et al., 2013). Higher substrate quality and nutrient availability are thought to increase CUE (Manzoni et al., 2012;

Roller and Schmidt, 2015). Biotic factors such as soil biodiversity and community composition can also drive CUE (Manzoni et al., 2012; Sinsabaugh et al., 2016). Since decomposition and assimilation of C vary among microbial taxa, CUE depends on microbial community composition. Moreover, abiotic factors, can influence microbial metabolism and community composition (Fierer and Jackson, 2006; Tedersoo et al., 2014), thus indirectly impacting CUE.

Recent studies have shown that the quality of substrate and the composition of microbial communities are strongly associated with CUE. However, this has only been inferred from theory (Manzoni et al., 2012; Sinsabaugh et al., 2016; Tao et al., 2023) or shown in artificially constructed systems (Domeignoz-Horta et al., 2020; Pold et al., 2020). Here we test these suggestions in a continental scale, which has never been done before. The aim of this study was to identify the main drivers of microbial CUE variation in a continental scale. We conducted a latitudinal soil survey across Europe, including a broad range of climates, soil properties and land uses (Table S1). We measured microbial growth and respiration at stable state conditions (optimal moisture at 20 °C) and estimated CUE from microbial growth divided by microbial C use (see Supplementary Methods for details). Additionally, we measured several edaphic factors thought to affect CUE (Table S1) and sequenced the 16S and ITS2 amplicons to gather information on the microbial community

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composition. Finally, to determine the factors explaining the environmental variation of CUE, we used a structural equation model (SEM) (Fig. S1). We hypothesized that: (i) bacterial and fungal growth are determined by abiotic factors, especially pH; (ii) bacterial community composition is mainly driven by pH (Fierer and Jackson, 2006) while fungal community composition is driven by climate (Tedersoo et al., 2014); and (iii) microbial metabolism, C:N ratio, and SOM quality determine CUE.

In the surveyed latitudinal gradient, CUE ranged from 0.04 to 0.40  $\mu\text{g C } \mu\text{g}^{-1} \text{C}$  (Fig. 1), which is similar to values that have been reported for other substrate-independent methods (Sinsabaugh et al., 2013; Geyer et al., 2019; Soares and Rousk, 2019). We could not detect that climate affected CUE along the latitudinal gradient (Fig. 1). We found that bacterial growth, fungal community composition, and SOM quality were the main drivers of CUE variation (Fig. 2). It was expected that microbial growth will be an important driver of CUE as it is one of its main components. A previous survey of soil systems found that bacterial growth positively affected CUE and was the main explanatory variable (Soares and Rousk, 2019). It has also been shown that variation in CUE is mainly driven by differences in microbial growth rates (Smith et al., 2021) or microbial biomass C (Sinsabaugh et al., 2016), rather than respiration rates. A plausible explanation was that microbial growth rate is a decisive component of fitness. An organism's ability to translate resources into growth relative to other organisms in the same environment is very close to a direct measure of relative fitness, and thus a direct proxy of ecological or evolutionary success. In contrast, respiration, although essential for providing energy for growth and other cellular processes, is not directly linked to fitness (Manzoni et al., 2012). Consistent with this, variation in CUE was mainly determined by slow-growing microbial communities with low CUE probably due to relatively high maintenance energy costs (Soares and Rousk, 2019) or fast-growing communities with high CUE associated with high yield life history strategies (Malik et al., 2020).

We resolved both bacterial and fungal growth, but only bacterial growth influenced CUE. It was likely that bacterial growth had a

stronger impact on CUE since bacterial communities contributed more to microbial growth ( $\bar{X} = 0.26 \mu\text{g C h}^{-1} \text{g}^{-1}$ ) than fungal communities ( $\bar{X} = 0.07 \mu\text{g C h}^{-1} \text{g}^{-1}$ ). In contrast, the fungal community composition was a significant driver of CUE (Fig. 2). The importance of microbial diversity and community composition on CUE variation has been recently recognized, where an artificially constructed soil was used to show that climate affected CUE indirectly through changes in the microbial community composition (Domeignoz-Horta et al., 2020). It is also known that decomposition responses to changing environmental factors can depend on the composition of the microbial community (Glassman et al., 2018). Additionally, CUE is known to differ between taxa (Roller and Schmidt, 2015; Pold et al., 2020; Smith et al., 2021), generating community differences.

The SEM also showed that the bacterial community composition was the main driver of the fungal community composition albeit the effect on CUE was indirect (Fig. 2). This suggested that biotic interactions could be important drivers of CUE. Surprisingly little is known about the role of biotic interactions on changes in CUE. While negative interactions like competition or antagonism can reduce CUE (Rousk et al., 2010; Bahram et al., 2018), CUE can also be enhanced by indirect competition and positive interactions (Iven et al., 2023). However, a greater microbial complexity and interkingdom associations (e.g., bacteria and fungi) can also strengthen soil multifunctionality due to metabolic labor division leading to niche complementarity in the support of multiple simultaneous ecosystem functions (Wagg et al., 2019). Therefore, interactions between fungal and bacterial communities should be considered when evaluating soil functions such as C sequestration.

Soil C:N ratios can also be a predictor for CUE variation (Soares and Rousk, 2019; Oliver et al., 2021). Since microbial communities need to maintain their stoichiometry within physiological boundaries, ecological stoichiometric theory predicts that microorganisms will adjust their CUE in response to substrate elemental ratios (Manzoni et al., 2012). In our study, we did not find a significant effect of soil C:N ratio on CUE, matching recent findings (Takriti et al., 2018) that the absence of this

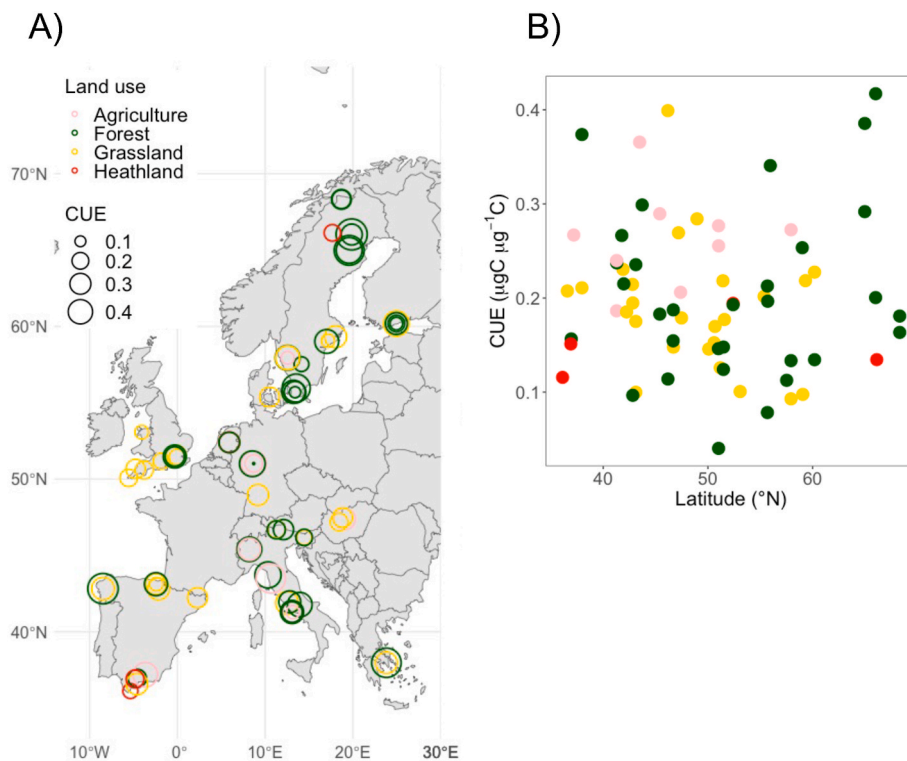
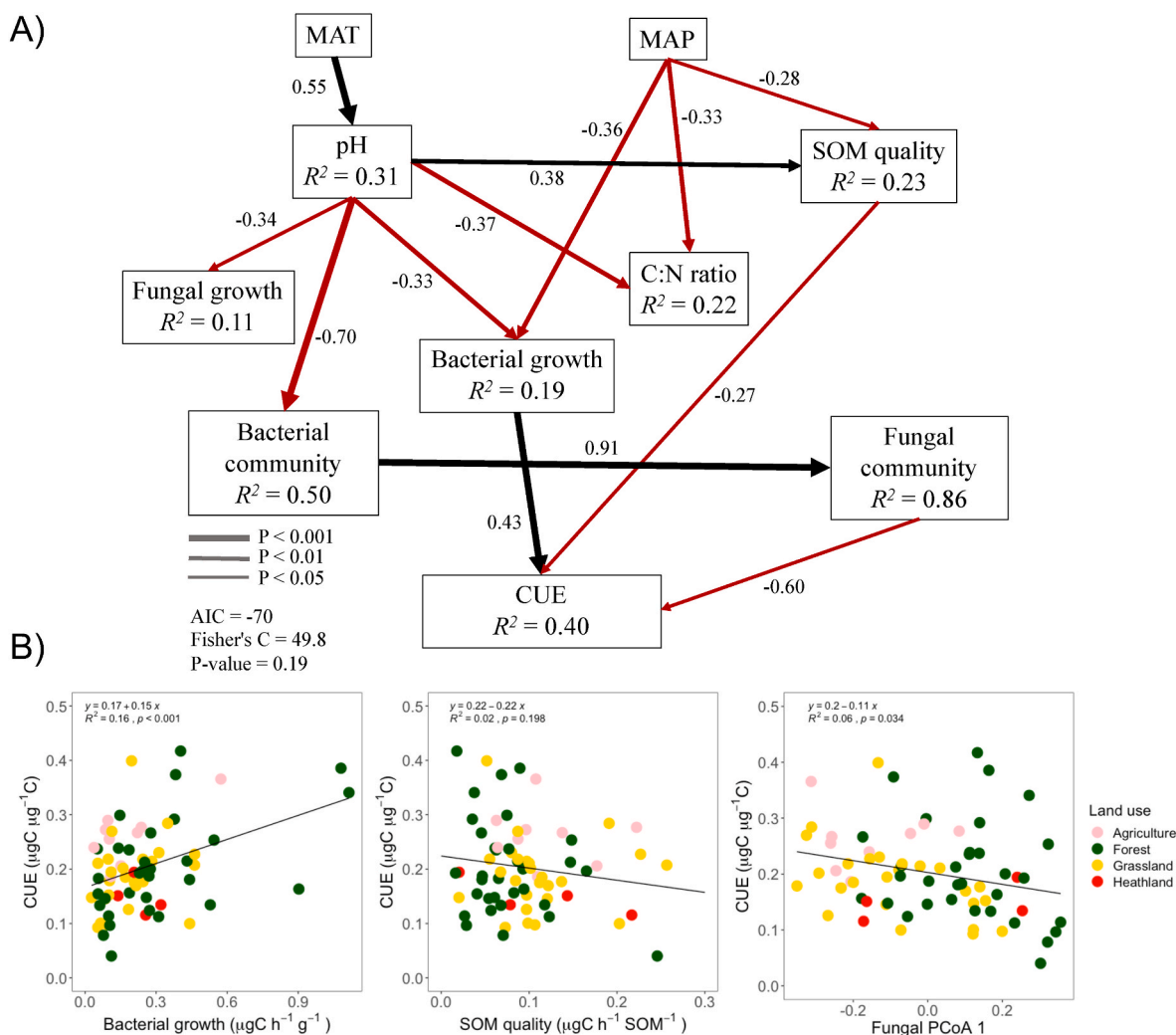


Fig. 1. Microbial carbon use efficiency along the latitudinal gradient studied. A) Map representing the sampling points and values of CUE. B) CUE along the latitudinal gradient studied and the different types of land use studied.



**Fig. 2.** A) Structural equation model showing the influence of soil abiotic and biotic factors on CUE. Significant paths are shown in black if positive or in red if negative. Path width corresponds to the degree of significance as shown in the lower left. The amount of variance explained by the model ( $R^2$ ) is shown for each response variable, and measures of overall model fit are shown in the lower left. MAT: mean annual temperature, monthly mean historical temperatures of ten years (2009–2018); MAP: mean annual precipitation, monthly mean historical precipitations of ten years (2002–2011); pH: soil pH measured in a 1:5 (w:v) soil/water extraction; Bacterial community structure: axis 1 of PCoA; Fungal community structure: axis 1 of PCoA; Bacterial growth: Growth measured at 20 °C using acetate incorporation; Fungal growth: Growth measured at 20 °C using acetate incorporation; C:N ratio: soil total C: soil total N; SOM quality: microbial growth and respiration divided by the SOM content. CUE: carbon use efficiency measured at 20 °C. Global goodness-of-fit: Fisher's C. B) Linear regressions between carbon use efficiency (CUE) and the factors driving it according to the SEM analysis.

link could be because soil C:N ratios do not reflect the resource availability since SOM can be chemically or physically protected. It is widely accepted that soil microbes are C limited (Soong et al., 2020; Yuan et al., 2022). However, the availability of nutrients, like N, can also affect their CUE (Roller and Schmidt, 2015). CUE is normally enhanced with higher nutrient availability (Sinsabaugh et al., 2013; Roller and Schmidt, 2015). Moreover, while simple substrates which are easily transported into the cell and require less activation energy can increase CUE (Ågren and Bosatta, 1987; Manzonei et al., 2012; Roller and Schmidt, 2015), low substrate quality or more complex compounds that require a larger number of enzymatic steps for degradation can decrease microbial CUE (Roller and Schmidt, 2015). Therefore, nutrient availability and SOM assimilability often are good predictors for CUE variation (Takriti et al., 2018; Li et al., 2021).

We found that CUE variation was dominated by SOM quality. Surprisingly, CUE was reduced rather than stimulated by higher SOM quality. We used the microbial assimilability of SOM (microbial use per SOM content) as a proxy for SOM quality (Fierer et al., 2005, 2006; Soares and Rousk, 2019). With higher SOM assimilability, respiration

increased more than did microbial growth, thus reducing CUE and generating a negative relationship between SOM quality and CUE. This uncoupling between catabolism and anabolism was likely due to induced nutrient limitation by a C-rich substrate (Roller and Schmidt, 2015; Yuan et al., 2022) or a low energy content (Gunina and Kuzyakov, 2022). Microbial growth requires nutrients in the synthesis of structural molecules. Therefore, when the energy source is in excess and nutrients are strongly limiting, growth will decouple from respiration, decreasing CUE (Russell and Cook, 1995). Consistent with our findings, it was recently reported that CUE increased with the ratio of hydrolytic to oxidative enzymes which is a proxy used for SOM quality (Takriti et al., 2018). Combined with our results, these findings suggest that SOM quality effects on CUE variation are more complex than previously assumed.

Even though climate did not drive CUE directly, MAP and MAT did drive other variables such as SOM quality and soil pH. The SEM indicated that pH was a driver of microbial growth and the bacterial community composition (Fig. 2). It is widely known that soil pH is one of the main factors controlling microbial activity (Rousk et al., 2009) and

bacterial community composition in a global scale (Fierer and Jackson, 2006). The SEM showed that soil pH was driven by MAT. Temperature and precipitation are important factors controlling soil formation and hence soil pH, where temperature mainly affects the rock weathering rate, while precipitation affects material flow (Jenny, 1994).

In conclusion, we found that the biotic component together with the SOM quality are the main drivers of CUE variation across Europe. Other factors such as climate and pH affected CUE indirectly through microbial activity or community composition. We show the importance of the microbial community composition to predict CUE variation and that interactions between bacterial and fungal communities can have implications for CUE.

#### CRedit authorship contribution statement

**Carla Cruz-Paredes:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Johannes Rousk:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

#### Acknowledgments

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2024.109394>.

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