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► To cite this version:

Nadja Rohner, Selina Lepori, Viviana Loaiza, David Sebag, Eric Verrecchia, et al.. Erosion of community complexity increases temperature-dependency of microbial respiration, but not growth, in short-term incubations. *Elementa: Science of the Anthropocene*, 2024, 12 (1), 10.1525/elementa.2023.00100 . hal-04524684

HAL Id: hal-04524684

<https://ifp.hal.science/hal-04524684v1>

Submitted on 28 Mar 2024

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RESEARCH ARTICLE

Erosion of community complexity increases temperature-dependency of microbial respiration, but not growth, in short-term incubations

Nadja Rohner^{1,2}, Selina Lepori^{1,2}, Viviana Loaiza², David Sebag^{3,4}, Eric Verrecchia⁴, Daniel B. Nelson⁵, Ansgar Kahmen⁵, Pascal A. Niklaus², Anna-Liisa Laine^{2,6}, and Luiz A. Domeignoz-Horta^{2,7,*}

Biodiversity loss and climate change are 2 of the most alarming threats to ecosystem functioning and stability. These factors are, however, typically investigated separately, overlooking potential interactions between species extinctions and climate change on ecosystems. Here, we evaluated how different temperature regimes impact the relationship between microbial diversity and ecosystem functioning, in terms of temperature sensitivity of carbon (C) cycling functions. We hypothesized that more complex communities promote the stability of C cycling functions under both temperature regimes. We did not observe a ubiquitous response of all C-cycling processes to temperature increases within communities of distinct complexities. While growth was stable with increasing temperatures across the complexity levels, respiration rates increased more strongly at low complexity than high complexity levels at higher temperatures. Carbon use efficiency, which integrates both growth and respiration, tended to decrease with temperature at lower levels of complexity. Jointly, these results demonstrate the importance of community complexity for maintaining C-cycling thermal response under a changing climate.

Keywords: Soil carbon cycling, Microbial diversity, Ecosystem functioning, Temperature sensitivity, Carbon use efficiency, Climate change

Introduction

To date, most studies on the ecological consequences of biodiversity loss have focused on processes regarding plant diversity (Hector et al., 1999; Spehn et al., 2005; Hector and Bagchi, 2007). However, a large part of biodiversity on earth regarding its richness but also its biomass consists of microbes (Wagg et al., 2014). While

microorganisms are the most diverse and most abundant organisms on the planet and are crucial drivers of a wide range of ecosystem functions (Singh et al., 2010; Duan et al., 2023), the consequences of microbial diversity loss for ecosystem functions are not well understood. This is critical given that changes in the environment (i.e., temperature or moisture) can alter the relationship between ecosystem functioning and diversity (García et al., 2018; Domeignoz-Horta et al., 2020).

A belowground ecosystem function that is increasingly more studied due to its relevance for the climate system is soil carbon (C) cycling (Cavicchioli et al., 2019; Cappelli et al., 2022; Domeignoz-Horta et al., 2023). Empirical data provided by Kallenbach et al. (2016) suggests that soil microbial physiology may be more important for soil carbon stabilization than traditionally assumed. Accordingly, it has been recently shown that community growth efficiency was positively related to bacterial diversity under favorable environmental conditions (Domeignoz-Horta et al., 2020). Further, it was also shown that distinct microbial communities generate soil organic matter (SOM) with different chemistry that differ in decomposition potential (Domeignoz-Horta et al., 2021). These recent results suggest that even broad C-cycling-related processes might be shaped by diversity and composition of soil microorganisms

¹ Graduate Program in Quantitative Environmental Sciences, University of Zurich, Zurich, Switzerland

² Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

³ IFP Énergies Nouvelles, Rueil-Malmaison, France

⁴ Institute of Earth Surface Dynamics, Faculty of Geosciences and the Environment, University of Lausanne, Lausanne, Switzerland

⁵ Department of Environmental Sciences—Botany, University of Basel, Basel, Switzerland

⁶ Research Centre for Ecological Change, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

⁷ Current address: University of Paris-Saclay, INRAE, AgroParisTech, UMR EcoSys, Palaiseau, France

* Corresponding author:

Email: luiz.domeignoz-horta@inrae.fr

contrarily to what has been previously acknowledged (Schimel and Schaeffer, 2012; Nemergut et al., 2014).

So far, most studies focused on the relation between diversity and microbial growth (García et al., 2018) or diversity and microbial respiration separately (Nielsen et al., 2011). Carbon use efficiency (CUE) is an important parameter to characterize microbial physiology (Manzoni et al., 2012; Manzoni et al., 2018) and determines the partitioning of plant inputs into a fraction of carbon remaining in the soil (microbial growth) and a fraction respired as carbon dioxide to the atmosphere. Drivers of CUE are not fully understood, however we know that abiotic (Qiao et al., 2019; Pold et al., 2020; Liu et al., 2021) and biotic processes influence CUE (Roller et al., 2016; Iven et al., 2023). While abiotic factors have been studied more extensively, biotic factors impacting CUE have been examined to a lesser extent (Iven et al., 2023). A seminal study showed that changes in temperature systematically modified the relationship between diversity and community growth (García et al., 2018). Moreover, a recent study showed that the increase in respiration in response to warmer temperatures was higher in low diverse soils (Xu et al., 2021). These new findings suggest that more species are needed to maintain ecosystem functioning and stability under thermal stress. How all these factors interact and influence community CUE still remains largely unclear despite its importance for understanding soil-atmosphere carbon cycling feedback under global change (Pold et al., 2019). Here, our main goal was to empirically evaluate how CUE and the underlying processes growth and respiration respond to simultaneous changes in community complexity and temperature variations.

Materials and methods

In this study, we experimentally test the hypothesis that microbial community complexity ensures higher stability of CUE and the underlying processes of growth and respiration when microbial communities are subjected to fluctuations in temperature (Loreau et al., 2001). We used a solid matrix to simulate growth in soil in contrast to liquid cultures which are not able to recreate the conditions experienced by soil microorganisms, as for example nonhomogeneous substrate supply and oxygen diffusion. For that end we created a simple matrix composed of sand and clay (9:1). This matrix was initially sterile and carbon-free. Such “simple model soil” matrices have been able to provide new insights into soil microbial ecology questions of relevance for natural soils (Vogel et al., 2014; Kallenbach et al., 2016; Pronk et al., 2017; Domeignoz-Horta et al., 2020; Domeignoz-Horta et al., 2021; Cai et al., 2022). Pronk et al. (2017) review the literature on model soils and conclude that such simple systems can be used to identify the specific effects of a particular variable of interest compared to highly complex and heterogeneous natural soils. Aspects that have been studied in simple model soils spans from SOM formation, aggregation, organic matter turnover, the influence of minerals on microbial communities and microbial-derived functions, and community dynamics (Pronk et al., 2017).

Our model soil was prepared as described by Domeignoz-Horta et al. (2020). Soil microcosms consisted of 50 ml falcon tubes filled with 15 grams of model soil and inoculated with 3 ml microbe-media (tryptic soy broth; TSB) solution, reaching 70% of the water holding capacity. We created a microbial diversity gradient by serially diluting a community obtained by extracting an agricultural soil (D0; no dilution > D1; first dilution > D2; second dilution) (Figure 1, Supplementary Figures 1–3, Supplementary Tables 1–5; Diaz et al., 2003). The dilution approach has some potential biases. For example, it neglects the role of biofilms and as a result of fungal physiology, dilution accompanying disturbances may result in the damage or disruption of fungal hyphae. Nevertheless, as shown by Domeignoz-Horta et al. (2020) bacterial and fungal richness responded similarly to the dilution approach in another model soil incubation experiment. In contrast to assembling artificial communities by choosing specific strains, the resulting communities obtained through a dilution approach are sourced from naturally assembled communities and therefore should provide a more realistic scenario for testing the impact of diversity loss. Even though we did not measure the microbial richness in this experiment, previous experiments have validated this method for creating a diversity gradient (Garland and Lehman, 1999; Delgado-Baquerizo et al., 2020; Domeignoz-Horta et al., 2020; Ferreira et al., 2021). Because we did not directly measure the diversity in our microcosms, we will refer to our approach as dilution treatments.

Methods that use serial dilution approaches will result initially in distinct inoculum biomass, but an initial incubation phase has been shown to be able to allow microbial colonization and establishment of microbial communities reaching similar levels of total abundance when the resource availability is the same across communities (Phillipot et al., 2013; Schnyder et al., 2023). These previous studies have shown that pre-incubating communities resulting from a serial dilution approach allows these communities to reach similar abundance levels across different dilutions. For example, Schnyder et al. (2023) preincubated the microcosms for 28 days and observed that the communities recovered well with no significant differences in total bacterial and methanotrophic community sizes. The least diverse treatment (D3) is represented by a single bacterial strain commonly found in soils (*Streptomyces sp.* DSM 687; Supplementary Text). In preliminary experiments we evaluated that the *Streptomyces sp.* (DSM 687) grows well in the model soil under all the temperatures compared to other single strains (e.g., *Bacillus subtilis*, *Microvirgula aerodenitrificans*, and *Micromonospora sp.*). Thus, we decided to continue with this single strain for the main experiment. Regarding the dominant bacteria in natural soils, Delgado-Baquerizo et al. (2018) conducted a global analysis of bacterial communities in surface soils, identifying the Actinobacteria and Acidobacteria phylums are some of the most abundant bacteria occurring in surface soils. Furthermore, *Streptomyces sp.* which belong to the phylum Actinobacteria are important regarding carbon cycling (Barka et al., 2016). Nevertheless, it should be noted that *Streptomyces sp.* does not represent an entire phylum and our

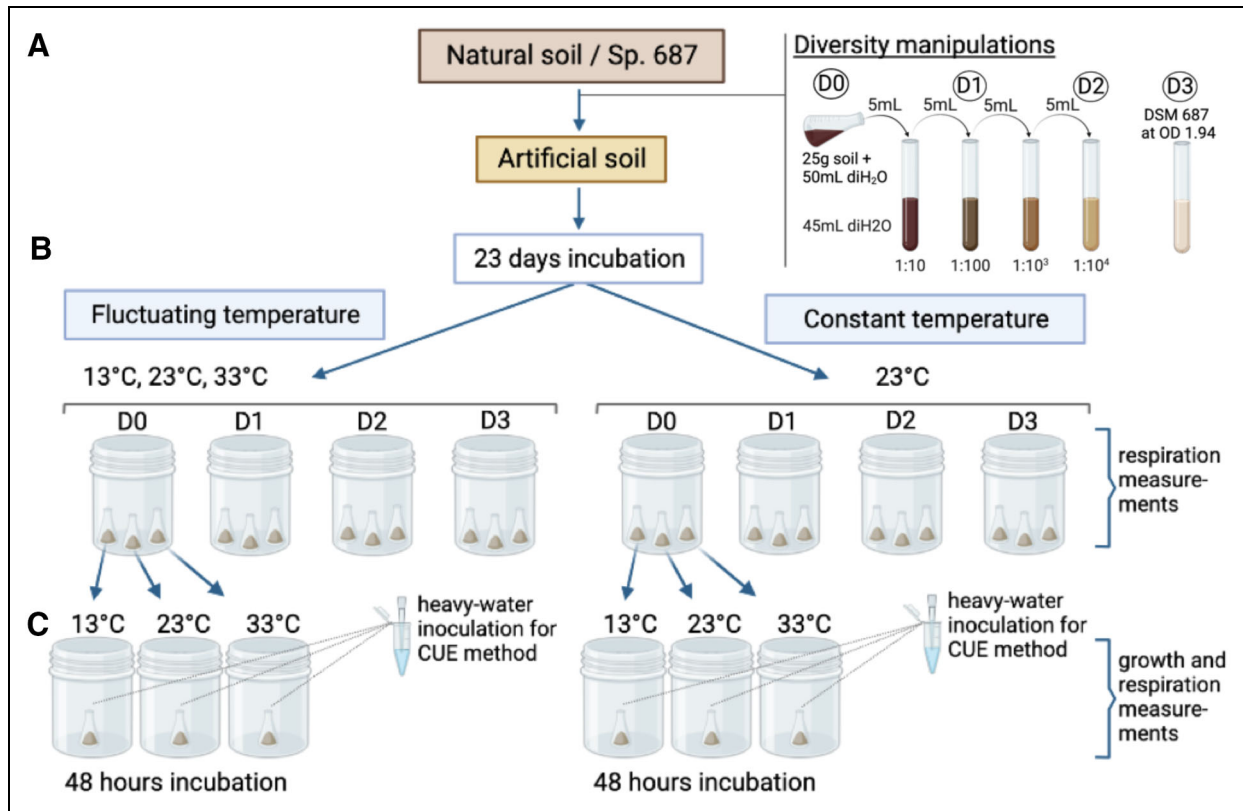


Figure 1. Experimental design. The microbial diversity manipulation of the soil suspension was performed to obtain D0, D1, and D2 inocula, while *Streptomyces sp.* DSM 687 was used for D3 treatment (A). The microbial communities obtained with the diversity manipulations were inoculated into a model soil with 5× TSB media and incubated for 23 days under 2 temperature regimes (B). Growth and respiration were measured after 48 h of incubation at all temperatures (C). TSB = tryptic soy broth.

results cannot be generalized to this whole group of bacteria.

The experiment consisted of 2 phases, community establishment (Phase I) and C-cycling evaluation (Phase II). During Phase I of the experiment (**Figure 1B**), constant temperature (CT, 23°C) and fluctuating temperatures (FT, increasing in temperature every 48 h: 13°C → 23°C → 33°C and restarting the cycle at 13°C) were applied to induce changes in the metabolism of microorganisms and select for microbial communities with distinct thermal niches (Schnyder et al., 2023). In Phase I, we used 4 biological replicates for each dilution level at each temperature regime (4 biological replicates × 4 dilution treatments × 2 temperature regimes = 32 samples) and measured respiration as a proxy for microbial activity (Supplementary Text). We anticipated that the distinct treatments would consume the substrate at different rates in Phase I (Supplementary Figure 1), therefore we added fresh substrate 3 days prior to the ¹⁸O-H₂O addition (1 mg C per g soil with a solution consisting of glucose and TSB). We recognized that glucose substrate-limitation would likely occur because our substrate amendments were not designed to remove glucose substrate-limitation across the experimental incubations but just to maintain labile C supply to ensure that there was easily available substrate for microbial activity for Phase II of the measurement. In Phase II, we measured

growth and respiration (**Figure 1C**) at 13°C, 23°C, and 33°C in all soils (4 biological replicates × 4 dilution treatments × 2 temperature regimes × 3 incubation temperatures = 96 biological samples). At the end of the 48 h incubation, we measured respiration by headspace sampling with a gas chromatograph (Agilent Technologies 7890A) and growth in a subset of 0.9 g of soil with the ¹⁸O-H₂O method (Supplementary Text) (Spohn et al., 2016). Duplicate DNA extractions for each biological replicate were performed and CUE was calculated as by Spohn et al. (2016) (Supplementary Text).

Results and discussion

Microbial activity during community establishment (Phase I)

The microbial respiration decreased over the course of the 23-day incubation of Phase I, in both CT and FT treatments. In CT, respiration decreased steadily over time, except in the D2 treatment in which respiration increased toward the end of the incubation (**Figure 2A–B**). This effect is likely due to the higher dilution and therefore smaller community inoculated into the soil which resulted in more activity toward the end of Phase I, as substrate is not limited in comparison to less diluted treatments. FT respiration clearly shows a thermal-response to incubation temperature (e.g., increasing when temperature increases and decreasing when the

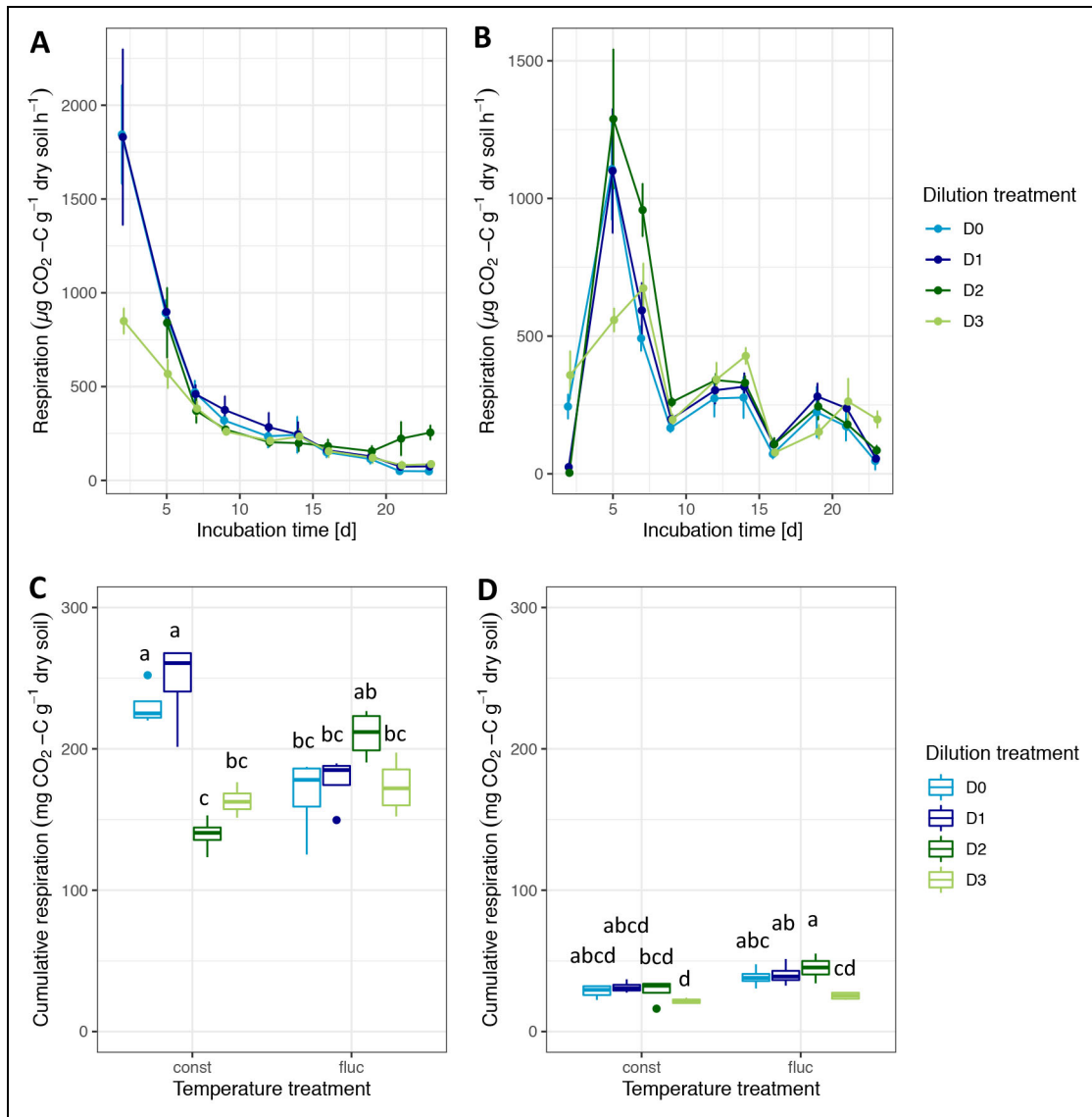


Figure 2. Microbial respiration rates and cumulative respiration during community establishment. Soil respiration of microcosms incubated at constant temperature (23°C) (A), or fluctuating temperatures (13°C, 23°C, 33°C) (B). For A and B error bars denote standard deviations of biological replicates (n = 4). Cumulative respiration for the overall incubation period (C) and cumulative respiration for the time-points chosen when the fluctuating temperature treatment was incubated at 23°C in both temperature regimes (D). For boxplots, the box denotes interquartile range, whiskers denote the 1.5× interquartile range. The horizontal line denotes the median. Points represent outliers outside of the 1.5× interquartile range. Letters indicate significant differences between diversity levels tested with the Tukey-HSD test.

temperature decreases; **Figure 2B**). The dilution effect on cumulative respiration is larger in the CT (D0 & D1 > D2 & D3) than in the FL treatment, where no clear pattern is visible (**Figure 2C**).

In addition to the total cumulative respiration, we also calculated the relative cumulative respiration for the time points in which microcosms of the CT and FT treatments were both at 23°C (**Figure 2D**). We observed a difference in the cumulative respiration by both dilution treatment ($F = 8.127, P < 0.001$) and by temperature treatment ($F = 18.215, P < 0.001$) (**Figure 2D**) showing that the temperature regime influenced microbial activity also when evaluating the activity at the same common temperature. One

possible explanation is that the 10°C temperature shift of the FT soils (as they were incubated at 13°C before 23°C) induced a stronger microbial respiration response in FT compared to CT (**Figure 2D**) as respiration is expected to respond exponentially to increases in temperature (Alster et al., 2020). The FT regime might have also resulted in a larger community size and consequently showed higher activity compared to the other treatment. Previous studies with model soils have shown that abiotic factors drive the community composition of microbial communities (Kallenbach et al., 2016; Pronk et al., 2017; Domeignoz-Horta et al., 2020). Thus, another potential explanation is that the distinct temperature regimes selected communities

with different thermal niches, and therefore these communities show distinct respiration rates at the same temperature (**Figure 2D**). Accordingly, Pold et al. (2020) showed that the response of soil isolates to temperature is strain specific varying with temperature and substrate. However, it is crucial to approach this explanation cautiously due to the short incubation period of the experiment of 23 days. Previous findings by Bradford et al. (2010) underscore the importance of temporal considerations. Thermal adaptation, as observed by Bradford et al. (2010) did not manifest until after 77 days, and differences in respiration rates only emerged after 21 days of incubation.

C-cycling response to different temperatures and community complexity levels (Phase II)

After the microbial communities were exposed to distinct temperature regimes during Phase I, in Phase II we incubated them under 3 different temperatures and measured CUE. We used linear mixed models to evaluate how the different dilution levels and the temperature regimes impacted the different soil C-cycling functions (**Figure 3**). Growth did not respond significantly to temperature in both temperature regimes and dilution levels (**Figure 3A and D**). Respiration, however, increased faster with increasing temperatures at high levels of dilution compared to lower dilution levels (**Figure 3B and E**) which has also been observed in natural soils (Xu et al., 2021). This pattern was consistently independent of previous temperature regimes. An *in-situ* soil warming experiment uncovered a decline in microbial diversity due to warming (Nottingham et al., 2022). While growth rates suggest acclimation to long-term soil warming through a community shift, the *in-situ* microbial respiration rates exceeded 3-fold the respiration predicted by their model (Nottingham et al., 2022). In agreement with this previous experiment our findings suggest a decoupling between growth and respiration in response to increasing temperatures. Interestingly, this decoupling was stronger in communities inoculated with lower levels of community complexity (**Figure 3A–D**). Even though our experiment consisted of a simple model soil and arguably cannot be projected to natural soils, insights of this study paired with our results suggest that warming accompanied by decreased microbial complexity can result in higher respiration rates than expected. It is also important to consider that microbial communities' response to long-term warming has not been ubiquitous among warming experiments (Romero-Olivares et al., 2017).

The serial dilution method could also have affected the strategies of microbial communities in the sense that higher dilutions, paired with readily available nutrients lead to a community more strongly dominated by copiotroph-strategists and, therefore a higher respiration response to temperature. While copiotrophic-related strategists have been described to be fast-growing and have a low CUE, oligotrophic-related strategists are slow-growing and have a high CUE (Fierer et al., 2007; Leff et al., 2015). The higher diluted soils likely have a low diversity of copiotrophic-species while in the less diluted

there is a higher species richness which will interact with each other (e.g., competition for resources) allowing a broader spectrum of copiotroph-related physiologies and distinct strategies to emerge (Song et al., 2017). Accordingly, Bai et al. (2017) suggested that respiration response to a 10°C increase in temperature (Q_{10}) could be controlled by the shift between copiotroph-like microbial strategies. Accordingly, in the D3 treatment where the soil was inoculated with a single *Streptomyces sp.* strain, a very strong respiration response was observed with the increase in temperature (**Figure 3B and E**). This species belongs to the phylum Actinobacteria which exhibits copiotrophic attributes (Fierer et al., 2007).

It is often considered that high diversity is required to ensure ecosystem functioning (García et al., 2018; Maron et al., 2018; Yang et al., 2021). Moreover, García et al. (2018) show that high diversity is needed to ensure growth in more extreme temperatures and that high diversity maintains high growth potential. These results were obtained from marine microorganisms under liquid cultivation, while our experiment using a model soil introduces some heterogeneity to simulate the natural gradients observed in soils (e.g., nonhomogeneous substrate availability and oxygen diffusion rates). In contrast to these previous results, we show that absolute growth and growth Q_{10} was not different between dilution treatments (**Figure 3A and D**; Supplementary Figure 2). We observed a trend of decreasing CUE with increasing temperatures and increasing dilution (**Figure 3C and F**). However, this was only significant at D3 and marginally significant at D2 dilution levels within the FT treatment (**Figure 3F**). Our results show that the Q_{10} of respiration and growth showed a different trend along the community complexity gradient, but these differences were not significant (Supplementary Figure 2) resulting in a decreasing CUE with increasing temperature as previously reported (Liu et al., 2021). CUE is the combination of growth and respiration, if respiration increases faster with temperature at high dilution levels but growth remains constant, CUE is expected to decrease at high levels of dilution (i.e., low levels of community complexity) with increasing temperatures. As growth Q_{10} was not different among diversity treatments, this trend of decreasing CUE with increasing temperatures was driven by the respiration component (**Figure 3**). Similarly, to our observed trend of decreasing CUE at higher temperatures and diminishing community complexities, a study by Steinweg et al. (2008) observed that CUE was temperature dependent but remained relatively constant over a long-term incubation period (600 days). Their findings suggest that the change in CUE attributed to temperature could be attributed to how temperature affected either cellobiose uptake or respiration. Furthermore, the study emphasized a consistent response in the shape of microbial communities' respiration and cellobiose uptake, irrespective of incubation duration or temperature. These insights provide a valuable context for our own short-term observations, shedding light on the complex interplay on how temperature influences substrate uptake affecting CUE through time in soils. We acknowledge that our experiment had a relatively short

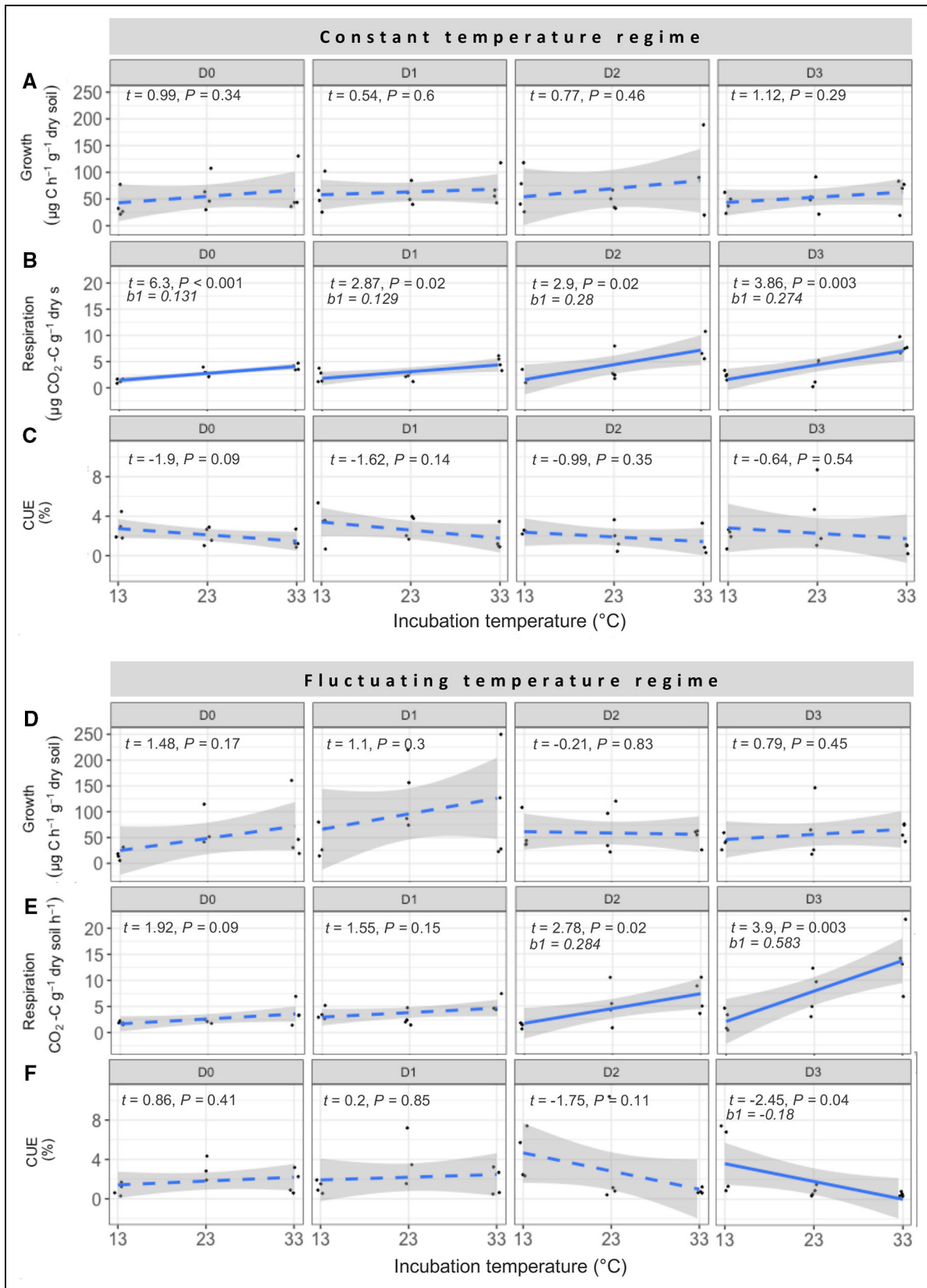


Figure 3. Relationship between C-cycling processes and temperature within the different diversity levels for the constant (A, B, and C) and fluctuating (D, E, and F) temperature regimes. Linear mixed effect models were used to evaluate the impact of short-term temperature changes on respiration, growth, and carbon use efficiency (CUE). Linear curves were fitted when the result is significant or dashed line if not significant.

duration as we evaluated microbial physiology response to temperature after 23 days. Future studies could evaluate how longer incubation durations shapes communities and influences their response to temperature.

Altogether these results show the complexity of microbial physiology response to temperature. Considering that we observe diverging results of carbon cycling processes in a relatively simple model soil system, it highlights the need to evaluate various ecosystem functions simultaneously when evaluating the relationship between diversity and ecosystem processes in complex natural soils if we aim to have a deeper understanding on how C-cycling in soils may change following environmental and anthropogenic perturbations. Even though we experimentally tested our hypothesis in a simple model soil system, our results point toward the same direction as results by Xu et al. (2021). They investigated the importance of microbial diversity in natural soil systems regarding the sensitivity of soil organic carbon (SOC) to warming and found that microbial diversity plays an important role in determining if SOC is further decomposed with warming. Moreover, Yang et al. (2022) show that multiple anthropogenic pressures can modify communities and soil functioning and highlights the importance of incorporating multifactor experimental approaches considering that about 98% of studies still evaluate a single, or two factors only (Rillig et al., 2019). Here we used a 3 multifactor experimental approach (dilution levels × temperature regime × temperature response of C-cycling functions) to unravel how microbial-controlled C-cycling functions may shift in response to changes in their environment. Altogether, our results highlight that successive changes (complexity loss associated with temperature increases) can result in distinct responses of growth and respiration, 2 important processes for understanding the fate of SOC in soils.

Data accessibility statement

All data and codes used in this study can be obtained in the Open Science Framework Project (<https://osf.io/3b24f/>) and from the authors upon request.

Supplemental files

The supplemental files for this article can be found as follows:

- Supplementary Text.docx
- Supplementary Figures 1–3. docx
- Supplementary Tables 1–5. docx

Acknowledgments

The authors would like to thank the Laine Lab team members for the supportive discussions and Prof. Dr. Owen Petchey for being a great statistics teacher.

Funding

Funding for this project was provided by the Academy of Finland (STN Multa; 327222) to A-LL. This work was also conducted with support from the University of Zurich to LADH, PAN, and A-LL (STWF-23-018).

Competing interests

The authors declare no competing interests.

Author contributions

Designed the study: NR, LADH.

Performed the laboratory experiments: NR, LADH, SL, VL.

Performed the data analysis: NR.

Wrote the first draft of the article: NR.

Contributed to finalize the manuscript: All authors.

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How to cite this article: Rohner, N, Lepori, S, Loaiza, V, Sebag, D, Verrecchia, E, Nelson, DB, Kahmen, A, Niklaus, PA, Laine, A-L, Domeignoz-Horta, LA. 2024. Erosion of community complexity increases temperature-dependency of microbial respiration, but not growth, in short-term incubations. *Elementa: Science of the Anthropocene* 12(1). DOI: <https://doi.org/10.1525/elementa.2023.00100>

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Knowledge Domain: Ecology and Earth Systems

Published: February 21, 2024 **Accepted:** January 4, 2024 **Submitted:** July 7, 2023

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