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Microbial temperature dependences in soil: The belowground feedback to climate change

Tájmel, Dániel

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List of papers

I. Cruz-Paredes, C., Tájmel, D., & Rousk, J. (2021). *Can moisture affect temperature dependences of microbial growth and respiration?*. Soil Biology and Biochemistry, 156, 108223.

II. Tájmel, D., Cruz-Paredes, C., & Rousk, J. (2023). *Heat wave-induced microbial thermal trait adaptation and its reversal in the Subarctic*. Global Change Biology, 30, e17032.

III. Cruz-Paredes, C., Tájmel, D., & Rousk, J. (2023). *Variation in temperature dependences across Europe reveals the climate sensitivity of soil microbial decomposers*. Applied and Environmental Microbiology, 89(5), e02090-22.

IV. Tájmel, D., Wårlind, D., Hicks L. C., & Rousk, J. *Representing the climate-induced shift of soil microbial thermal traits in the ecosystem model LPJ-GUESS*. Manuscript.

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DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on 19th of April 2024 at 09.30 in the Blue Hall, Department of Biology, Sölvegatan 37, Lund, Sweden.

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“You have to focus on the things you can change”

– Katalin Karikó

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Abstract

Since the Industrial Revolution, human activities have elevated atmospheric CO_2 concentrations. The consequences of this include rising temperatures, shifts in precipitation patterns, and increased intensity and frequency of extreme weather events, such as heat waves and droughts. Elevated temperatures can accelerate microbial activity in soil, potentially resulting in an increased rate of soil organic matter (SOM) decomposition. This increased microbial decomposition may, in turn, lead to a release of CO_2, contributing to a positive feedback loop amplifying climate warming. To understand the microbial feedback to warming, I studied the processes leading to carbon (C) accumulation through microbial growth and CO_2 release via microbial respiration. I determined the temperature dependence of microbial growth and respiration to assess how these process rates change with altered temperatures. The results of this thesis indicate that (i) the microbial temperature dependence is not dependent on soil moisture. This validation through an empirical test is important, as most ecosystem models employ a distinct temperature dependence that operates independently of soil moisture. In addition, (ii) the temperature dependence of bacterial growth can become warm-shifted within one growing season due to a summer heat wave simulation in the field and with a similar trend for fungal growth. The warm-shifted bacterial growth temperature dependence fully recovered within a year and matched the temperature dependence at ambient conditions. These findings highlight the fast microbial responses to a heat wave and the long-lasting legacy of such extreme weather events. The results also indicate that (iii) the microbial temperature dependence varies systematically with environmental temperatures along a wide climate gradient in Europe. Microbial communities showed warm-shifted temperature dependences in warmer ecosystems and cold-shifted temperature dependences in colder areas. Finally, (iv) empirically determined microbial temperature dependences were incorporated into a dynamic vegetation model LPJ-GUESS. Specifically, separate temperature dependence for microbial growth and respiration were employed to represent C sequestration and emissions from soils in response to temperature variations. In addition, the microbial temperature dependences were allowed to adjust to the climate that they encounter. Therefore, the microbial thermal traits can become climate-specific and adjust to changes in thermal regimes.

Popular science summary

Have you ever considered the life beneath the surface of the ground? Beneath our feet lies a hidden universe of microscopic creatures – soil microorganisms. These tiny but mighty decomposer creatures, also called microbes, including bacteria and fungi, are the engineers of our ecosystems, playing an essential role in breaking down soil organic matter. When microbes grow, they use carbon from soil organic matter to build their cells. This carbon in microbial cells can remain in soils after the microbes die. However, microbes also release carbon into the atmosphere through their respiration, contributing to the greenhouse effect. Therefore, microbes may store soil carbon through microbial growth or release carbon through respiration. Like all living organisms, microbes are dependent on temperature. As temperature rises, both microbial growth and respiration increase. This is especially important in the face of climate change, as rising temperatures significantly affect microbial activity, influencing soil carbon cycling. In this thesis, I studied how microbes respond to changes in temperature by focusing on their temperature dependences. Specifically, I wanted to understand how the temperature dependence of bacterial and fungal growth and respiration is affected by soil moisture, a heat wave, and climate across a wide range of environmental temperatures.

First, I found that the temperature dependence of microbial growth and respiration was not influenced by moisture. This finding is important because models that predict the impact of climate change often separate the temperature dependence of moisture. Also, microbial growth and respiration rates decreased with lower soil moisture. However, bacterial growth was more affected than fungal growth, leading to a greater fungal dominance in dry soils. Second, I showed that a summer heat wave resulted in a shift towards microbes that thrive at high temperatures. Following the heat wave, it took a full year for the microbes to return to their natural state. Third, I found that temperature dependences varied with climate. Microbes living in cold areas preferred cold temperatures, while microbes in warmer regions preferred higher temperatures. This preference was stronger for bacterial growth than fungal growth, indicating that bacterial growth is more sensitive to changes in temperatures. Moreover, microbial growth was more sensitive than respiration. These differences in temperature sensitivities have important implications for predicting future carbon storage and losses, as well as for understanding the impact of climate warming on soil. Finally, the microbial temperature dependences were added to a model to predict the impacts of climate change on microbes and how these changes influence soil carbon cycling.

Populärvetenskaplig sammanfattning

Har du någonsin tänkt på livet under marken du står på? Under våra fötter finns ett dolt universum av mikroskopiska varelser – mikroorganismer. Dessa små men betydande mikrober, som inkluderar bakterier och svampar, är ingenjörerna I våra ekosystem och spelar en viktig roll för att bryta ner organiskt material I jorden. När mikrober växer använder de kol från organiskt material I marken för att bygga upp sina celler. Kolet I mikrobiella celler kan stanna kvar I jorden efter att mikroberna dör, vilket bidrar till att kol lagras i jorden. Mikrober bidrar också till att kol släpps ut I atmosfären genom respiration, även kallat cellandning, vilket kan bidra till ökad växthuseffekt. Därför är mikrober viktiga för att både lagra kol i marken och frigöra kol till atmosfären. Liksom alla levande organismer påverkas mikrober av olika temperaturer. När temperaturen stiger ökar både mikrobiell tillväxt och respiration. Detta är särskilt viktigt med tanke på klimatförändringarna, eftersom stigande temperaturer påverkar mikrobernas aktivitet, och på så sätt markens kolcykel. I den här avhandlingen studerade jag hur mikrober reagerar på temperaturförändringar, genom att fokusera på deras temperaturberoende. Specifikt ville jag förstå hur temperaturberoendet för bakterier och svampars tillväxt samt respiration påverkas av markens vattenhalt, en värmebölja och hur det varierar mellan olika klimat.

Först fann jag att temperaturberoendet av mikrobiell tillväxt och respiration inte påverkades av markens vattenhalt. Detta fynd är viktigt eftersom modeller som förutspår effekterna av klimatförändringar ofta separerar temperaturberoendet från markfukt. Dessutom minskade den mikrobiella tillväxten och respirationen med lägre vattenhalt, där bakteriernas tillväxt påverkades mer än svamparnas, vilket ledde till att svampar dominerade I torra jordar. För det andra visade jag att en värmebölja under sommaren resulterade I mikrober som trivs bättre vid höga temperaturer. Efter värmeböljan tog det ett helt år för mikroberna att återgå till samma temperaturberoende som innan värmeböljan. För det tredje fann jag att temperaturberoendet varierade mellan olika klimat. Mikrober som levde I kalla områden föredrog lägre temperaturer, medan mikrober I varmare områden föredrog högre temperaturer. Denna preferens var starkare för bakterier än svampar, vilket tyder på att bakterier är mer känsliga för temperaturförändringar. Dessutom var mikrobiell tillväxt känsligare än respiration. Dessa skillnader I temperaturkänslighet är viktiga för att förstå hur kol kan lagras och frigöras i framtiden, samt för att förstå hur global uppvärmning påverkar jorden. Slutligen användes de mikrobiella temperaturberoendena till en modell för att bättre förutsäga hur klimatförändringar påverkar mikrober och i sin tur markens kolcykel.

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Paper I

Cruz-Paredes, C., **Tájmel, D.**, & Rousk, J. (2021). *Can moisture affect temperature dependences of microbial growth and respiration?*. Soil Biology and Biochemistry, 156, 108223.

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Paper IV

Tájmel, D., Wårlind, D., Hicks L. C., & Rousk, J. *Representing the climate-induced shift of soil microbial thermal traits in the ecosystem model LPJ-GUESS*. Manuscript.

Author's contribution to the papers

Paper I

CCP, **DT**, and JR conceived and designed the experiment. CCP and **DT** conducted the laboratory work. CCP analyzed the data. CCP wrote the manuscript under the supervision of JR, and all authors provided comments on the manuscript draft.

Paper II

DT, CCP, and JR conceived and designed the experiment. **DT** and CCP conducted the laboratory work. CCP conducted the bioinformatics analyses. **DT** analyzed the data. **DT** wrote the manuscript under the supervision of JR, and all authors provided comments on the manuscript draft.

Paper III

CCP, **DT**, and JR conceived and designed the experiment. CCP and **DT** conducted the laboratory work. CCP analyzed the data. CCP wrote the manuscript under the supervision of JR, and all authors provided comments on the manuscript draft.

Paper IV

DT, DW, LCH, and JR conceived the study. **DT** and DW analyzed the data. DW conducted the model simulations. **DT** and DW wrote the manuscript under the supervision of JR, and all authors provided comments on the manuscript draft.

DT - Dániel Tájmel

CCP - Carla Cruz-Paredes

LCH - Lettice C. Hicks

DW - David Wårlind

JR - Johannes Rousk

Introduction

Climate change, caused by elevated CO_2 concentrations in the atmosphere, results in increased temperatures, altered precipitation patterns, reduced snow cover, and an increased intensity and frequency of weather extremes such as heat waves and droughts (IPCC, 2021). All these changes profoundly impact microbial communities inhabiting soils, which, in turn, play a key role in terrestrial ecosystems by controlling carbon (C) and nutrient cycling. This thesis focuses on the effects of temperature on soil microbial decomposers and their consequences for terrestrial C cycling.

Soils are the largest C reservoir of the terrestrial biosphere by storing between 2300 and 2800 petagrams (Pg) of soil organic carbon (SOC) (Jobbágy & Jackson, 2000; Jackson et al., 2017). The SOC content is governed by the balance between C input from plant residues, root exudation and microbial biomass, and the rate of C loss as CO_2 via plant and microbial respiration (Fig. 1) (García-Palacios et al., 2021; Liang et al., 2017). Considering the magnitude of the C exchange between soils, plants, and the atmosphere, even relatively small losses from the soil C storage can have a profound impact on atmospheric CO_2 concentrations (Friedlingstein et al., 2014; IPCC, 2021). Climate change is disturbing this balance and is anticipated to induce higher rates of plant primary productivity and microbial activity (Cavicchioli et al., 2019) (Fig. 1). However, the disproportionate increase in microbial respiration due to increased microbial activity is expected to result in a significant C release from soils (García-Palacios et al., 2021), providing a positive feedback to warming (Jansson & Hofmockel, 2020) and further exacerbating climate change. Even though this C feedback mechanism has received significant research focus in recent decades, there is no agreement on its magnitude and its regulation (Dacal et al., 2019; IPCC, 2021).

Soil microorganisms are the key decomposers responsible for breaking down soil organic matter (SOM) (Schimel & Schaeffer, 2012). During the decomposition process, microorganisms not only release C as CO_2 to the atmosphere through microbial respiration but also incorporate C into their biomass via microbial growth (Bardgett et al., 2008; Liang et al., 2017, 2019) (Fig. 1). The incorporated C in microbial biomass can remain in the soil after microbial death, with this microbial necromass potentially contributing to C accumulation with a long residence time (Camenzind et al., 2023; Liang et al., 2019). This microbial necromass C can make up to half of the SOC pool (Liang et al., 2019). One way to assess how efficiently

microorganisms utilize C is known as microbial carbon use efficiency (CUE) (Geyer et al., 2016, 2019; Manzoni et al., 2012b). The CUE can be estimated as the proportion of C that microorganisms use for growth relative to the total C used for both growth and respiration. A high CUE leads to a higher fraction of C accumulation in microbial biomass, while a low CUE leads to proportionally less C accumulation in biomass. The use of CUE, therefore, allows for an assessment of how microbial communities drive changes in C dynamics.

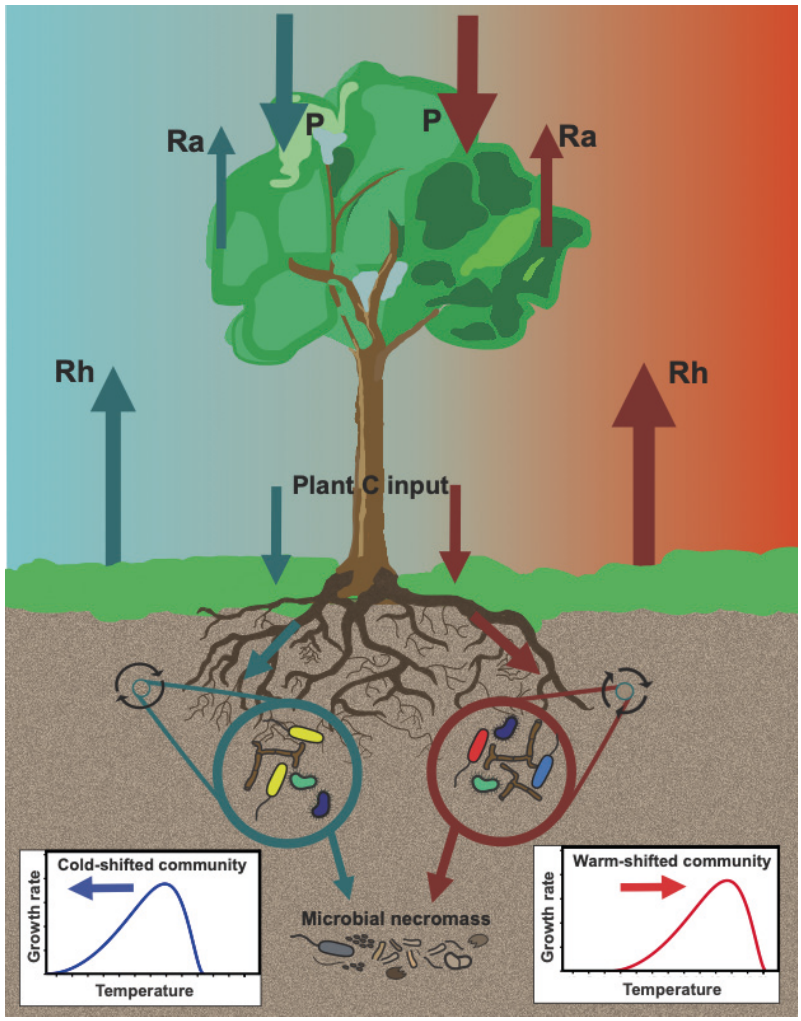


Figure 1. The change in terrestrial C movements between land and atmosphere due to climate change. The increased microbial activity at warmer temperatures is expected to result in higher soil heterotrophic respiration (Rh), leading to C losses from soil. The soil microbial community composition is also expected to change with warming. Warmer temperature can induce warm-shifted microbial temperature dependences. Photosynthesis (P), autotrophic respiration (Ra), and plant C inputs are also expected to increase due to climate change.

Temperature is a particularly important factor influencing all living organisms, including microorganisms, and strongly influences microbial respiration and growth rates, therefore affecting overall microbial decomposition (Pietikäinen et al., 2005; Bárcenas-Moreno et al., 2009; Alster et al., 2016). Given its critical role in shaping microbial activity in soil, it is important to understand the response of both microbial respiration and growth to temperature changes. However, our understanding of microbial growth and respiration temperature responses is limited, leading to uncertainties in predicting the response of SOM decomposition to temperature increase and, consequently, the potential magnitude of the predicted climate feedback (Friedlingstein et al., 2014; Sulman et al., 2018; IPCC, 2021).

Temperature can affect microbial processes, including microbial respiration and growth, directly and indirectly. The direct effect of temperature on microbial processes is the biochemical response primarily driven by enzyme kinetics (Schipper et al., 2014). However, microbial processes are affected by indirect effects of temperature, such as variations in soil moisture (Rustad et al., 2001; Carey et al., 2016; Suseela et al., 2012) and changes in substrate availability (Frey et al., 2013; Manzoni et al., 2012b; Werner et al., 2020). The combined direct and indirect effects of temperature are often termed as apparent temperature sensitivity, whereas solely the direct effect of temperature is commonly referred to as intrinsic temperature sensitivity (Davidson & Janssens, 2006). Direct and indirect effects of temperature on microbial processes are difficult to disentangle. Yet, it is crucial to isolate the direct effects and determine the intrinsic temperature sensitivity since most ecosystem models employ a distinct temperature dependence that operates independently of indirect effects (Sierra et al., 2015).

One way to assess the direct temperature effects on soil microorganisms is by determining the intrinsic microbial temperature dependence. This can be assessed through short-term laboratory assays (Kirschbaum, 1995, 2006) and has been determined in both aquatic (Decembrini et al., 2021; Kritzberg & Bååth, 2022; Mulholland et al., 2011) and soil (Pietikäinen et al., 2005; Bárcenas-Moreno et al., 2009; Donhauser et al., 2020; Rijkers et al., 2022; Rinnan et al., 2009) environments. The intrinsic microbial temperature dependence defines how the rate of a process changes with temperatures. For example, microbial growth is zero at a minimum temperature (T_{min}). As the temperature increases, microbial growth accelerates until it reaches an optimum temperature (T_{opt}), where the growth rate peaks. Beyond this T_{opt}, the growth rate decreases until it reaches the maximal temperature (T_{max}), where microbial growth rates are zero again (Fig. 3). A microbial community can adjust its temperature dependence to the local environmental conditions that they encounter, resulting in changes in T_{min}, T_{opt}, and T_{max} (Bååth, 2018). For instance, it has been shown that the temperature dependence of microbial growth is cold-shifted in colder and warm-shifted in warmer ecosystems along environmental gradients (Nottingham et al., 2019; Rinnan et al., 2009) (Fig. 1). A shift in the temperature dependence for microbial growth has also been seen due to chronic warming of soil

in the field (Nottingham et al., 2022; Rousk et al., 2012), but not when warming was only administered in winter (Birgander et al., 2018). Moreover, laboratory experiments have demonstrated that the temperature dependence can be experimentally shifted only when the microbial community is exposed to temperatures exceeding the T_{opt} (Bárcenas-Moreno et al., 2009; Birgander et al., 2013). Together, these findings suggest that the exposure of a microbial community to temperatures above the T_{opt} determines the microbial temperature dependence shifts.

Aims and objectives of the thesis

The aim of this thesis was to elucidate how soil microbial communities respond to warming and the consequences for C cycling. Specifically, this study addresses the following objectives:

- To test a common ecosystem model assumption: Is the temperature response of microbial growth and respiration independent of soil moisture? (**Paper I)**
- To investigate whether experimental warming during the summer could shift the temperature dependences of microbial growth and respiration and how such changes persist. (**Paper II**)
- To assess how environmental temperature determines the temperature dependences of microbial growth and respiration across a wide climate gradient in Europe. (**Paper III**)
- To incorporate climate-specific microbial temperature dependences determined in **Paper II** and **Paper III** into a dynamic vegetation model (DVM). (**Paper IV**)

Overview

I used various approaches to study microbial responses to warming: a soil incubation experiment under laboratory conditions (**Paper I**, Fig. 2a), a field warming experiment in a subarctic ecosystem (**Paper II**, Fig. 2b), and a climate gradient across Europe (**Paper III**, Fig. 2c). In **Paper I**, the soil incubation experiment was used to simulate and study the effects of varying moisture conditions on microbial temperature dependences. The controlled laboratory conditions allowed for the precise manipulation of soil moisture and temperature. In **Paper II**, a heat wave was simulated by subjecting soils to increased temperatures for two summer months using infrared (IR) heaters. By deploying heating systems in the field, the temperature treatments could be controlled in a natural setting. In **Paper III**, the microbial temperature dependences were investigated along a wide European climate gradient covering ecosystem types from the Subarctic to the Mediterranean. In **Paper IV**, the temperature dependences defined in **Paper II** were employed, combined with the survey of the latitudinal climate gradient across Europe assessed in **Paper III**, to model how climate-specific microbial thermal responses affect the European scale C budget (Fig. 2e).

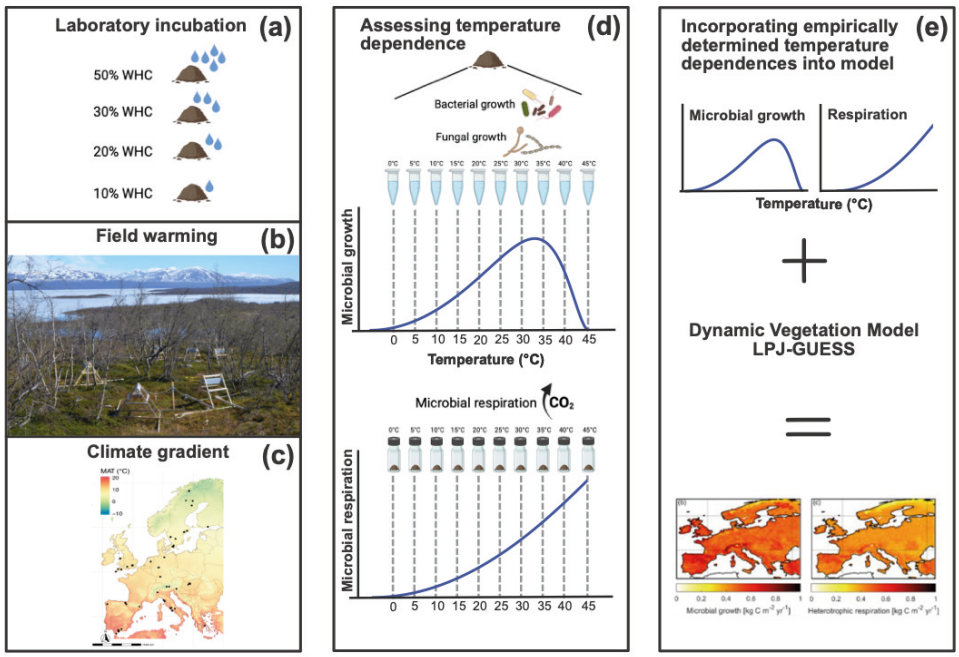


Figure 2. Overview of the different approaches used to study microbial temperature dependences in this thesis. (a) A laboratory experiment was used to test if the temperature response of microbial growth and respiration are independent of soil moisture by adjusting the soil water content to different moisture levels and then assessing the microbial temperature dependences (**Paper I**); (b) a field warming experiment used to assess the effect of a summer heat wave on microbial temperature dependences (**Paper II**); (c) a survey along a climate gradient in Europe was used to test the climate sensitivity of microbial temperature dependences (**Paper III**). (d) The temperature dependence of bacterial growth, fungal growth, and microbial respiration were assessed by short-term laboratory incubation at 10 temperatures (between 0 and 45°C) and then modeled with the *Ratkowsky* square root model (see more details in section 4.1 and Box 1). (e) Temperature dependences from **Paper II** and **Paper III** were used to improve the representation of microbial decomposers across Europe in a Dynamic Vegetation Model (DVM) LPJ-GUESS (**Paper IV**). Panel (a) and (d) created with BioRender.com.

Soil microbial decomposers under climate change

Heterotrophic microorganisms drive the decomposition of SOM (Eliasson et al., 2005). The two main groups of decomposers in soil are bacteria and fungi (Waring et al., 2013). Even though both groups decompose SOM, they differ in various aspects, including their cell structure, function, and ecological roles. Bacteria are single-cell microorganisms (Silhavy et al., 2010) known for their ability to rapidly reproduce and efficiently metabolize a wide range of simple molecules, such as sugars (Boer et al., 2005). In contrast, fungi are known for their cellular structure, which consists of a network of hyphae, collectively forming a mycelium (Nagy et al., 2020). While fungi are commonly thought to break down more complex polymers like cellulose and lignin (Romaní et al., 2006), they can also decompose simpler compounds (Khosravi et al., 2015). In this thesis, the growth of both bacteria and fungi communities were studied as proxies for potential contributors to C sequestration in soil (Liang et al., 2017). Furthermore, total microbial respiration (representing the contribution from both bacterial and fungal decomposers) was assessed as a driver of CO_2 emissions from soils.

Temperature is one of the most important abiotic factors influencing both bacterial and fungal activity (Pietikäinen et al., 2005). While many studies assess the temperature response of soil respiration, far fewer consider microbial growth. However, it is crucial to recognize that both microbial respiration and growth exhibit a strong temperature sensitivity (Pietikäinen et al., 2005; Bárcenas-Moreno et al., 2009; Alster et al., 2016). For example, with increasing temperatures, microorganisms increase their metabolic activity (Dijkstra et al., 2011), can take up nutrients faster (Zhang et al., 2019), and reproduce and mineralize C more rapidly (Wang et al., 2021). The temperature response can be different between soil bacteria and fungi. For example, fungi tend to have a higher community-level T_{opt}, and therefore potentially outcompete bacteria at higher temperatures (**Paper I**, **Paper II**, **Paper III**). A higher T_{opt} of fungal growth also implies greater tolerance to higher temperatures compared to bacterial growth. The difference in temperature tolerance of bacterial and fungal decomposers can also have an impact on the fungal-to-bacterial growth ratio, and therefore on their relative contribution to decomposition. For example, in **Paper II**, the highest fungal-to-bacterial growth ratio was found at

low (0-5°C) and high (40-45°C) laboratory incubation temperatures, indicating a greater fungal dominance.

In addition to temperature, water also plays a crucial role in shaping the microbial dynamics in soils, as it operates as an essential resource, acting as a solvent and functioning as a medium for transportation (Schimel, 2018). Soil microorganisms rely on water for their fundamental life processes, such as growth, respiration, reproduction, and survival (Manzoni et al., 2012a; Schimel, 2018). For instance, the substrates that serve as energy sources for microorganisms are often water-soluble (Bailey et al., 2017). Thus, water also serves as a transport medium for both microorganisms and substrates within the soil (Beven & Germann, 2013). Both microbial growth and respiration are highly sensitive to moisture (Leizeaga et al., 2021; Manzoni et al., 2012a). When there is no water present, microbial rates drop to zero. As the soil water content increases, both microbial growth and respiration increase until the optimal moisture level reaches approximately 50-60% water holding capacity (WHC). Increasing the moisture level beyond the optimum may reduce oxygen levels in soil and lead to anaerobic conditions that result in a decline in microbial activity (Jansson & Hofmockel, 2020). Fungi and bacteria respond differently to soils drying. Similarly to temperature, fungi are thought to have a higher tolerance to drier soil conditions than bacteria (Manzoni et al., 2012a). This is because fungal networks allow fungi to explore and redistribute water from a larger soil volume (Guhr et al., 2015). Also, bacteria are more sensitive to drying due to thinner cell walls (Schimel et al., 2007) and the lack of ability to move, escape, or allocate resources from other reservoirs (Kaisermann et al., 2015). In **Paper I**, soil samples were incubated at four decreasing moisture levels (from 50% WHC to 10% WHC). With lower soil moisture, both bacterial growth and fungal growth rates decreased. However, fungi could maintain a higher growth rate at lower moisture levels, resulting in an increased fungal-to-bacterial growth ratio. Similarly, in **Paper II**, the heat wave simulation in the field led to significantly drier soils, resulting in a higher fungal-to-bacterial growth ratio in the warmed plots. When the soil moisture was subsequently adjusted to optimal level (50% WHC), the fungal-to-bacterial growth ratio adjusted to match those of soils from the control plots, eliminating the differences caused by drying. In line with these findings, de Vries et al. (2018) and Ullah et al. (2021) found that drought impacts soil bacteria more than fungi. All these findings suggest that fungi are more drought-resistant and may cope better with drier soil conditions due to climate warming.

In addition to temperature and moisture, other environmental factors are changing due to climate warming and thus influence microbial activity in soils (Classen et al., 2015). For example, an increase in atmospheric CO_2 levels can increase the primary productivity of plants, resulting in increased plant-derived C input (Pritchard, 2011) (Fig. 1). This leads to more decomposable material for soil microbial communities, potentially increasing microbial growth (Yuan et al., 2022) (Fig. 1). On the contrary, long-term warming is also thought to be associated with increased microbial

activity, resulting in a depletion of the labile, readily available substrates, necessitating the microbial community to degrade more stable organic matter compounds (Melillo et al., 2002; Conant et al., 2011; Frey et al., 2013), potentially leading to decreased microbial activity (Sullivan et al., 2020). This complex interplay between drivers highlights the multifaceted nature of climate change impacts on microbial communities.

Microbial temperature dependences

Understanding the microbial temperature dependence is fundamental to disentangle the complexities of ecosystem functioning. Most soil C models rely on the temperature dependence of ecosystem processes such as microbial respiration and growth (Bååth, 2018). Employing temperature dependences that capture these microbial processes can help forecast the influence of climate change-induced temperature increases on soil C dynamics. In this chapter, I discuss three commonly used models to study temperature dependences of microbial respiration and growth. I also use empirical data to assess and compare the model fits among these models.

Models used to assess the microbial temperature dependence

The most commonly used approach to determine the temperature sensitivity is Q_{10}, which describes how much microbial rates change with a 10°C increase in temperature. This is typically based on the *Arrhenius* model (1889) (Box 1, eqn 1), which was initially intended to describe reaction rates in physical chemistry. However, in recent years, the *Arrhenius* model has been a subject of debate for modeling microbial rate changes such as respiration. Alster et al. (2020) argued that the *Arrhenius* model is not suitable to model microbial temperature dependences for at least two reasons: (i) it does not consider the temperature sensitivity of microbial enzyme catalysis. Therefore, it ignores some biological aspects of the reaction; (ii) it assumes a continuous increase in biological reaction rates and does not capture the peak and decline above the T_{opt} of microbial processes. Despite this, most C models still use the *Arrhenius* model and assume a constant Q_{10} for respiration (Q_{10}=2-3) (Davidson & Janssens, 2006; García-Palacios et al., 2021). While this assumption may be reasonable in some cases, we know that the Q_{10} is not constant with increases in temperature as it increases towards lower temperatures and decreases with higher temperatures (Kirschbaum, 1995; Bååth, 2018; Nottingham et al., 2019; Alster et al., 2020). For example, Bååth (2018) compared Q_{10} values for respiration across climates, and based on that, lower Q_{10} values were found for higher temperature ranges (between 15 and 25°C). In cold environments, $Q_{10(5\text{-}15)}$ reached 2.3, while $Q_{10(15\text{-}25)}$ dropped to as low as 1.8 for a higher temperature

interval. Similarly, in tropical environments, $Q_{10(5\text{-}15)}$ reached 9.0, whereas the $Q_{10(15\text{-}25)}$ for the higher temperature interval was 1.8.

Box 1. Determining the temperature responses

Arrhenius equation is used in most soil C models to predict temperature sensitivity of microbial rates. Arrhenius proposed a theory to explain the temperature dependence of chemical reaction rates in the 19th century, following:

$$ln(k) = lnA - EA/RT \,, \quad (1)$$

where k = biological rate, A = constant, E_A = activation energy for the studied reaction, R = universal gas constant, T = temperature (in Kelvin).

Ratkowsky model also called square-root model, is used in microbiology and ecology to describe the relationship between the growth rate of a microorganism or species and temperature, following:

$$R^{1/2} = a\,(T - T_{min})x\,(1 - e^{b(T-Tmax)}) \,, \quad (2)$$

where R = microbial rate, a and b = slope parameters, T = temperature (in Celsius), T_{min} and T_{max} = minimum and maximum temperature

Simplified Ratkowsky model is commonly used for describing microbial process rates between T_{min} and temperatures lower than the optimum temperature (T_{opt}):

$$R^{1/2} = a\,(T - T_{min}) \,, \quad (3)$$

where parameters are the same as in eqn 2.

Macromolecular Rate Theory (MMRT) is a relatively new model that accounts both physical and biological reaction rates with temperature change, following:

$$ln(k) = ln\left(\frac{k_B T}{h}\right) - \frac{\Delta H^{\ddagger}_{T_0} + \Delta C^{\ddagger}_P (T - T_0)}{RT} + \frac{\Delta S^{\ddagger}_{T_0} + \Delta C^{\ddagger}_P (lnT - lnT_0)}{R} \,, \quad (4)$$

where k = rate constant, kB = Boltzmann's constant, h = Planck's constant, R = the universal gas constant, T = temperature (in Kelvin), H = enthalpy, S = entropy, C_P = heat capacity, and ‡ indicates that it is the transition state.

Another model for capturing microbial responses to temperature variations was proposed by *Rakowsky* (1983), widely known as the 'square-root' equation (Box 1, eqn 2) (Ratkowsky et al., 1983). Although initially designed for pure bacterial cultures, this model has been continuously applied in diverse applications: food microbiology (Juneja et al., 2009), lake sediment studies (Bell & Ahlgren, 1987), aquatic systems (Li & Dickie, 1987), as well as in soil systems (Pietikäinen et al., 2005; Rinnan et al., 2009). The *Ratkowsky* is an empirical model that shows a negatively skewed distribution pattern for microbial growth (Fig. 3). For microbial respiration, a simplified version of the *Ratkowsky* model (Box 1, eqn 3) can be employed, as respiration rates tend to increase at high temperatures where microbial growth rates already decline. With this model, useful indices, such as minimum temperature (T_{min}), optimum temperature (T_{opt}), and maximum temperature (T_{max}) can be determined to characterize the distributions of microbial temperature traits (Fig. 3). A lower T_{min} indicates a community with a better ability to thrive at low

temperatures, while a higher T_{min} indicates a community with greater capacity to grow at higher temperatures. Among all indices (T_{min}, T_{opt}, T_{max}), T_{min} can be determined with the highest precision (Fig. 3). The T_{min} can also be determined for both microbial growth and respiration, and therefore the temperature dependence of both processes with the same index can be assessed. Consequently, T_{min} is often used to characterize the microbial temperature dependence and its shift (Bååth, 2018).

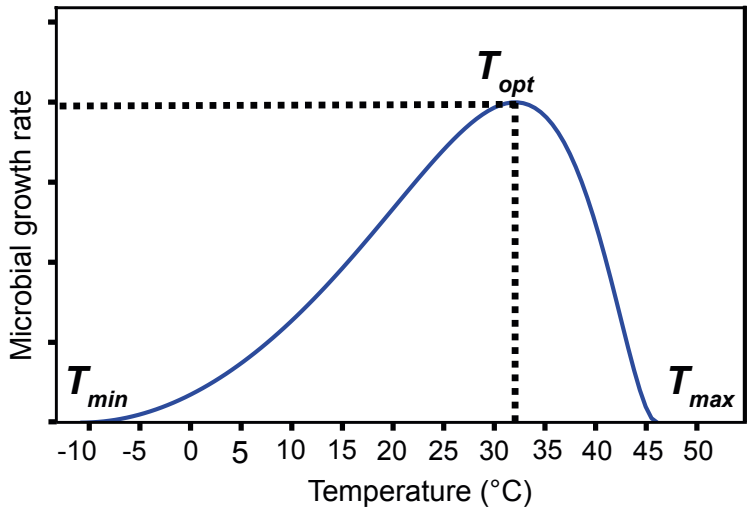


Figure 3. Schematic representation of microbial growth temperature dependence modeled with *Ratkowsky* model. T_{min} = minimum temperature, T_{opt} = optimum temperature, T_{max} = maximum temperature.

Recently, another model, the Macromolecular Rate Theory (*MMRT*) (Box 1, eqn 4), has been proposed (Hobbs et al., 2013; Alster et al., 2020) which is based on the theory of thermodynamics of microbiological processes. *MMRT* relies on the fact that large macromolecules, such as enzymes are involved in biological reactions; this is the origin of its name. Enzymes have a large heat capacity, meaning more energy is required to raise their temperature compared to smaller molecules (Alster et al., 2020). The *MMRT* model incorporates this biological aspect, accounting for enzymes with large heat capacity, resulting in temperature-dependent activation energy of biochemical reactions (Hobbs et al., 2013). Similarly to the *Ratkowsky* model, the *MMRT* model can also capture the maximal process rates at T_{opt}, and a decline in rates beyond that temperature.

In this thesis, the *Ratkowsky* model was employed to model bacterial and fungal growth (between 0°C and 45°C) (Box 1, eqn 2), and microbial respiration (typically between 0°C and 25°C) (Box 1, eqn 3). Previous studies used different temperature ranges to determine microbial temperature dependences. Similarly to **Paper I**, **Paper II**, and **Paper III**, studies determined the entire temperature dependence

curve for bacterial growth (Bárcenas-Moreno et al., 2009; Birgander et al., 2013, 2018; Pietikäinen et al., 2005; Rijkers et al., 2022; Rinnan et al., 2009) and fungal growth (Birgander et al., 2018; Pietikäinen et al., 2005). However, other studies focused only on the increasing part of the curve, below the T_{opt} of microbial growth as this temperature range can be used to determine T_{min}, which is often used to characterize the microbial temperature dependence. For that, the simplified version of the *Ratkowsky* model has been used for both microbial growth (Nottingham et al., 2019) and respiration (Li et al., 2021) (Box 1, eqn 3). The *MMRT* model (Alster et al., 2016, 2023; Robinson et al., 2017) has primarily been used to determine temperature dependence of microbial respiration, covering incubation temperatures from 2°C up to 60°C.

Model comparison using empirical measurements

In this chapter, the three different models, *Ratkowsky*, *Arrhenius*, and *MMRT* were compared. For that, I used empirically determined microbial growth and respiration measurements for two different soil types: subarctic soils (**Paper II**; Fig. 4) and temperate soils (Lund, preliminary data; Fig. 6). All three different models were fitted to the empirical measurements to determine which model best describe the data. This fitting process was done using a non-linear least-square curve fitting, and the goodness of fit was assessed using a chi-squared test (χ^2) and the corresponding p-values (Table 1). High p-values indicate a better model fit, while low p-values indicate a higher model deviation from the empirical data. To validate how well the models describe the data, the model residuals were also assessed (residuals for Fig. 4 are shown in Fig. 5, and residuals for Fig. 6 are shown in Fig. 7). For the model comparison, two different temperature ranges were used. Below the T_{opt} of microbial growth, both respiration and growth increase with higher temperatures. However, beyond the T_{opt} of growth, respiration and growth are decoupled (**Paper I**, **Paper II**, **Paper III**, Pietikäinen et al., 2005; Birgander et al., 2013). While growth rates decrease, indicating a disruption in growth at high temperatures, respiration rates continue to increase. This suggests that the increased respiration is not derived from growth related microbial functioning. The increase in respiration rates at high temperatures may be caused by the continued enzyme activity even after microbial death (Ramsay et al., 1983).

Fig. 4a and 4b show the respiration rates and curve fits with each model for temperature ranges between 0°C and 25°C and 0°C and 40°C for subarctic soils, respectively. In Fig. 4a, *Arrhenius* described the data best (p=0.96), then *MMRT* (p=0.94), and *Ratkowsky* (p=0.86) model (Table 1). In Fig. 4b, for the extended temperature range, *MMRT* (p=1.00) and *Arrhenius* (p=0.99) model showed a similarly good fit, followed by *Ratkowsky* (p=0.41). For the *Ratkowsky*, the lower goodness of fit was caused by the more pronounced deviations in the high-

temperature region above 30°C, while for *Arrhenius* occurred above 35°C (Fig. 4b). As seen in the plot of residuals, the *Ratkowsky* model systematically underestimated the data (Fig. 5b). Therefore, the *MMRT* model appears as the most suitable for explaining the respiration rate data across the entire temperature range (Fig. 4b). Consequently, while all models performed reasonably well for the respiration rates within the shorter temperature range, the *MMRT* and *Arrhenius* model showed better fit than the *Ratkowsky* model for the entire temperature range.

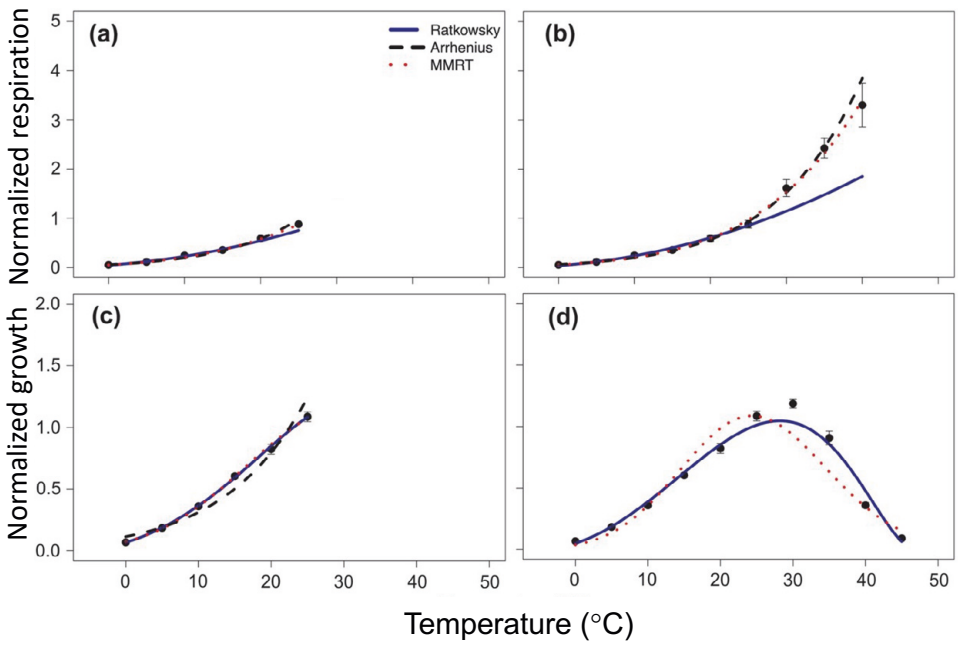


Figure 4. Temperature dependences of microbial growth and respiration with three different model fits for subarctic soil. *Arrhenius*: black dashed line, *Ratkowsky*: blue solid line, and *MMRT*: red dashed line. Filled circles represent data points used for the model fits. (a) Normalized respiration temperature dependence fitted between 0°C and 25°C. (b) Normalized respiration temperature dependence modeled between 0°C and 40°C. (c) Normalized microbial growth temperature dependence modeled between 0°C and 25°C. (d) Normalized microbial growth temperature dependence modeled between 0°C and 45°C. The data used for the respiration and bacterial temperature dependences are from **Paper II**, determined in soils from control plots in August 2020.

Fig. 4c and 4d illustrate the microbial growth rates, and the curve fits with each model for temperature ranges of 0°C to 25°C and 0°C to 45°C, respectively. In contrast to respiration rates, the *Arrhenius* model failed already to explain the microbial growth data between 0°C and 25°C temperature range (Fig. 5c; Table 1). Given the inability of the *Arrhenius* model to capture declining growth rates above the T_{opt}, it was excluded from the fit in Fig. 4d. In Fig. 4c, both the *Ratkowsky* (p=1.00) and *MMRT* (p=0.97) models effectively described the data for the temperature range between 0°C and 25°C, with a better bit for Ratkowsky.

However, for the entire temperature range, *MMRT* could not capture the pronounced negative skewed pattern of the data (Fig. 4d). As seen in the residuals plot, the *MMRT* model strongly underestimated the data at temperatures of 30°C and 35°C, while the *Ratkowsky* model underestimated the data at 30°C (Fig. 5d). Overall, for the microbial growth rates within shorter temperature ranges, both *Ratkowsky* and *MMRT* performed well, but the *Ratkowsky* (p=0.34) model showed a better fit than *MMRT* (p=0.08) for the entire temperature range (Fig. 4d).

The microbial temperature responses in soils from temperate climate (Fig. 6) were similar to those in subarctic soils (Fig. 4). This similarity is reflected in comparable model curve fits. Generally, the models showed better fits for the subarctic soils, largely owing to the higher variability among the Abisko measurements, which afforded the models greater flexibility in their fit. For respiration rates, *MMRT* showed the best fit for both the sorter (Fig. 6a; Fig. 7a; p=0.35) and entire (Fig. 6b; Fig. 7b; p=0.33) temperature ranges. For microbial growth, similarly to the subarctic soils, *Ratkowsky* model resulted in the best fit for both the shorter (Fig. 6c; p=0.95) and extended (Fig. 6d; p=0.59) temperature range.

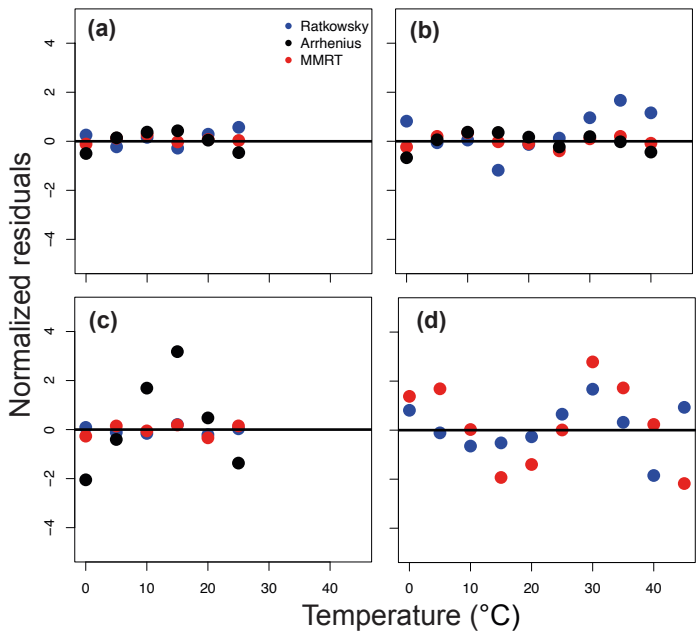


Figure 5. Normalized residual plots show how far the predicted values by *Ratkowsky*, *Arrhenius*, and *MMRT* model deviate from empirically determined measurements in Fig. 4. The residuals are determined by the difference between the empirical measurement value and the predicted value by the model and divided by the standard deviation of the empirical measurement. Residuals for (a) Fig. 4a model fit; (b) Fig. 4b model fit; (c) Fig. 4c model fit; (d) Fig. 4d model fit.

In summary, at a lower temperature range (0-25°C) all tested models provided a reasonably good fit for respiration rates in subarctic soils. However, the *MMRT* model appears as the most suitable for explaining the respiration rate data across the entire temperature range (0-45°C) for both subarctic and temperate soils. For microbial growth, both the *Ratkowsky* and *MMRT* model gave a reasonable fit for the data for the lower temperature range (0-25°C). However, *Ratkowsky* exhibited the best fit for the entire temperature range for both soil types. With the *Ratkowsky* model, useful indices, such as T_{min}, T_{opt}, and T_{max} can be determined to describe the microbial temperature dependence (see discussion in section 4.1). For this reason, in this thesis, the *Ratkowsky* model was employed to describe microbial respiration within the lower temperature range and for microbial growth across the entire temperature range. However, it must be kept in mind that for modeling the temperature dependence of respiration, especially at higher temperature intervals (25-40°C), where *Arrhenius* or *Ratkowsky* could not capture the empirical measurements well, *MMRT* would likely provide a better model fit.

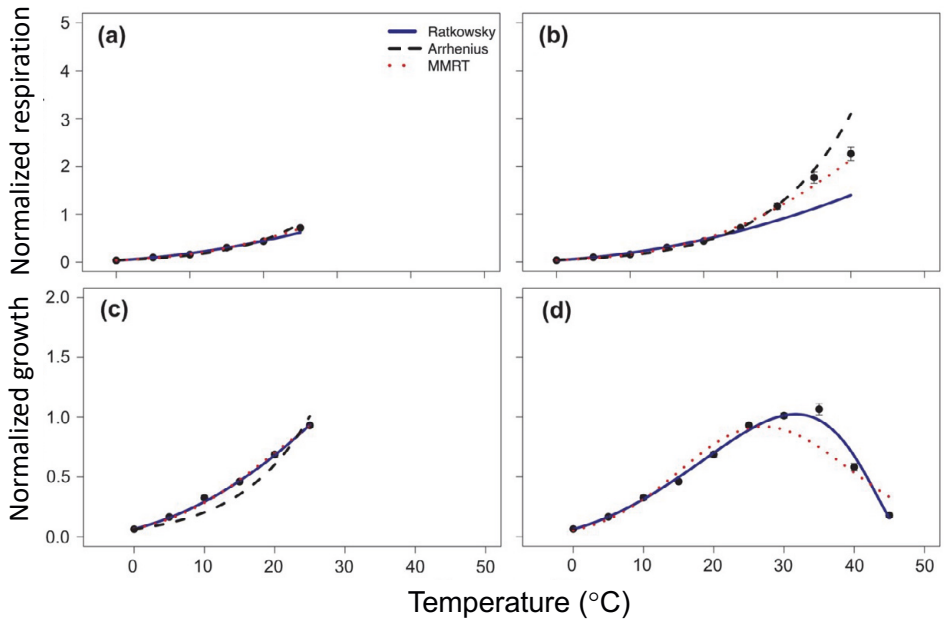


Figure 6. Temperature dependences of microbial growth and respiration with three different model fits for temperate soil (data from the warming experiment in Lund)**.** *Arrhenius*: black dashed line, *Ratkowsky*: blue solid line, and *MMRT*: red dashed line. Filled circles represent data points used for the model fits. (a) Normalized respiration temperature dependence fitted between 0°C and 25°C. (b) Normalized respiration temperature dependence modeled between 0°C and 40°C. (c) Normalized microbial growth temperature dependence modeled between 0°C and 25°C. (d) Normalized microbial growth temperature dependence modeled between 0°C and 45°C. The data used for the respiration and bacterial temperature dependences are from the warming experiment in Lund, determined in soils from control plots in September 2020.

It is important to note that even during the summer when temperatures peaked in Abisko and Lund, the highest recorded soil temperatures were approximately 9°C in Abisko and 22°C in Lund (at -8cm depth in 2020). These soil temperatures were significantly lower than those high incubation temperatures (Fig. 4b, 4d, 6b, 6d). Therefore, the shorter temperature ranges shown (Fig. 4a, 4c, 6a, 6c) are more common temperatures that microorganisms encounter in these ecosystems. Another important aspect is the reduction in soil moisture due to evaporation as soil temperatures rise (Kerridge et al., 2013). Decrease in soil moisture was observed both in the subarctic and temperate soils in the summer and resulted in reduced microbial activity (**Paper II**, Lund warming experiment). Consequently, even though microorganisms could still exhibit increasing growth and respiration at soil temperatures around 25°C and 30°C, they are likely to be limited by available water in the field.

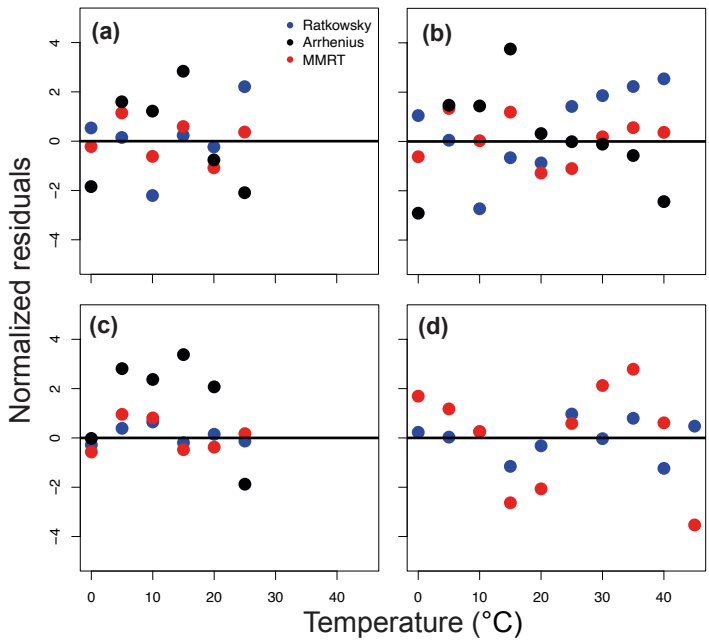


Figure 7. Normalized residual plots show how far the predicted values by *Ratkowsky*, *Arrhenius*, and *MMRT* model deviate from empirically determined measurements in Fig. 6. The residuals are determined by the difference between the empirical measurement value and the predicted value by the model and divided by the standard deviation of the empirical measurement. Residuals for (a) Fig. 6a model fit; (b) Fig. 6b model fit; (c) Fig. 6c model fit; (d) Fig. 6d model fit.

Table 1. The chi-squared test (χ^2) values and the corresponding p-values in parentheses for subarctic and temperate soils modeled by *Ratkowsky*, *Arrhenius*, and *MMRT*. High p-values indicate a better model fit and *vice versa*.

	Ratkowsky	*Arrhenius*	*MMRT*
		Subarctic soil	
Fig. 4a	1.31 (0.86)	0.59 (0.96)	0.39 (0.94)
Fig. 4b	7.19 (0.41)	1.00 (0.99)	0.45 (1.00)
Fig. 4c	0.12 (1.00)	17.5 (0.002)	0.26 (0.97)
Fig. 4d	6.81 (0.34)	NA	12.7 (0.08)
		Temperate soil	
Fig. 6a	5.28 (0.26)	16.1 (0.003)	3.27 (0.35)
Fig. 6b	26.6 (0.00)	33.2 (0.00)	6.93 (0.33)
Fig. 6c	0.71 (0.95)	29.2 (0.00)	2.26 (0.52)
Fig. 6d	4.65 (0.59)	NA	28.5 (0.00)

The microbial temperature dependence is independent of soil moisture

Even though temperature and moisture are both considered important factors regulating microbial activity in soils, there is a disagreement regarding the effect of moisture on microbial temperature dependence. In an empirical study, Gabriel & Kellman (2014) identified the temperature sensitivity of soil respiration to be independent of moisture. Conversely, Craine & Gelderman (2011) observed a moisture effect on the temperature sensitivity of soil respiration. To test the potential effect of moisture on microbial temperature dependences, the temperature dependences of bacterial growth, fungal growth, and respiration were examined across different moisture levels (**Paper I**). Soil samples were adjusted to four moisture levels (10%, 20%, 30%, and 50% WHC) ranging from dry conditions to optimal moisture levels (see discussion in section 3). Subsequently, bacterial growth, fungal growth, and respiration rates were assessed at 10 different temperatures, ranging from 0°C to 45°C. Results indicate that microbial rates decreased overall with lower moisture levels due to soil drying. Yet, these variations in moisture levels did not influence microbial temperature dependences. More explicitly, there were no detectable differences in the T_{min}, T_{opt}, and T_{max} at the different moisture levels. In a similar experiment, Schipper et al. (2019) aimed to evaluate the interaction between moisture and temperature responses. They incubated soil samples at five different moisture levels between 20% and 80% WHC and measured microbial respiration rates across a temperature gradient between 2°C and 60°C. Applying the *MMRT* model, they observed no changes in the temperature dependence parameters of their model, which is in accordance with our results. Since the microbial temperature dependences are independent of moisture, one might expect that the moisture dependence is also unaffected by temperature. In **Paper I**, the experimental design also allowed us to test this hypothesis by studying microbial growth and respiration rates under decreasing moisture across temperatures (between 0°C and 45°C). Microbial growth and respiration rates decreased with decreasing moisture at all temperature incubations. No significant impact of temperature on microbial drought sensitivity was found, assessed by IC_{50}, which indicates the soil moisture level at which microbial growth and respiration are reduced by half. These results suggest that the microbial temperature and

microbial moisture dependence operate independently of each other, which validates widely used but rarely tested assumptions employed in soil C models (Sierra et al., 2015).

The microbial temperature dependence shift and its reversal

Microbial temperature dependence shifts play a crucial role by directly influencing microbial growth, respiration, and thus the decomposition of SOM. For example, a community with a cold-shifted temperature dependence exhibits higher rates at colder temperatures. In contrast, a warm-shifted community shows lower rates at cold temperatures but has a competitive advantage at high temperatures (Fig. 8a). Recognizing these microbial thermal shifts becomes particularly important in the context of climate change (**Paper IV**, Allison et al., 2010; Dacal et al., 2019; García-Palacios et al., 2021), where changes in temperature patterns can impact the microbial temperature dependences and potentially lead to shifts.

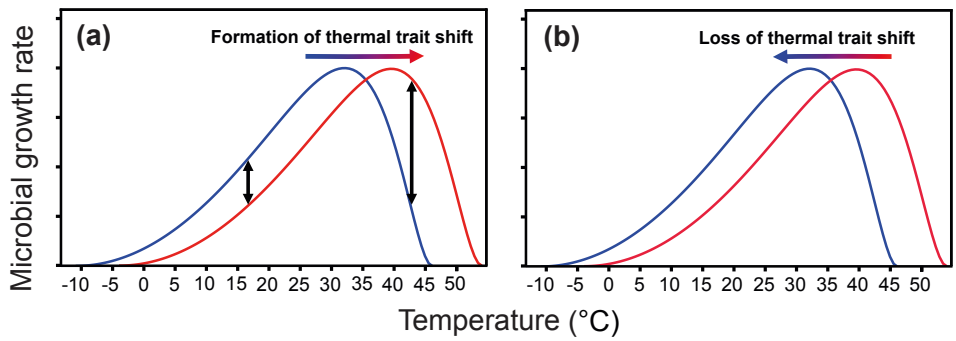


Figure 8. Schematic representation of microbial growth temperature dependences with *Ratkowsky* model curve fit illustrating cold-shifted microbial growth with blue color, and warm-shifted microbial growth with red color. (a) The warm-shift in microbial temperature dependence. Black arrows indicated the community's advantages at low and high temperatures. (b) The reversal of warm-shifted temperature dependence to cold-shifted temperature dependence.

Three mechanisms have been proposed that can result in a shift in temperature dependences, including (i) physiological changes; (ii) changes in community composition; or (iii) evolutionary adaptation through genetic changes (Bárcenas-Moreno et al., 2009). Allison, 2023 also suggested that these three mechanisms are important ways for microorganisms to adjust to drought and can lead to shifts in microbial moisture responses. Physiological changes may involve alterations in cell membrane structure or enzyme expression, which occur on the scale of days and

weeks, resulting in changes in thermal traits (Bradford, 2013). Over time, the environmental conditions may favor the survival and growth of microorganisms that cope better with the new thermal regime. This can lead to changes in the microbial community composition, where the less temperature-tolerant taxa may struggle to cope with the higher temperatures, and the composition of the community gradually changes towards warm-tolerant microorganisms. It has been suggested that this community shift can occur over periods ranging from weeks to months (Donhauser et al., 2020; Oliverio et al., 2017). Thermal trait changes can also occur through evolutionary adaptation. However, evolutionary adaptation requires hundreds and thousands of generations to occur (Mongold et al., 1996). In the natural environment, bacterial turnover, leading to a new generation, can take 15-20 days (Bååth, 1998), while for fungi it can take 1-6 months (Rousk & Bååth, 2011). Therefore, the evolutionary adaptation necessary for temperature dependence shift would likely span several years.

The direction of temperature change can also be an important aspect. Warmer temperatures may lead to faster microbial turnover compared to cooler temperatures (Hagerty et al., 2014). Consequently, faster microbial turnover can lead to quicker changes in microbial thermal traits, resulting in shifts in microbial temperature dependences. This may help explain why there is a stronger change in microbial temperature dependence towards warming compared to colder temperatures (Bárcenas-Moreno et al., 2009; Birgander et al., 2013; Nottingham et al., 2021).

The microbial temperature dependence shift

A decade ago, a debate arose regarding the importance of microbial thermal adjustment for microbial respiration (Bradford et al., 2008; Hartley et al., 2008). The debate centered on the observation that microbial respiration increased in response to soil warming in the field. However, this initial increase in respiration rates dissipated over time, eventually returning to ambient levels (Melillo et al., 2002). Bradford et al. (2008) argued that the reduced respiration rates are caused by the physiological adjustment of the microbial community, a shift in the microbial respiration temperature responses, interpreted as thermal acclimation. More recent studies also suggest that soil microbial respiration adjusts to the changing thermal regimes in global drylands (Dacal et al., 2019), covering different biomes (Bradford et al., 2019) and along a geothermal gradient (Alster et al., 2023). In the experiments of Dacal et al. (2019) and Bradford et al. (2019), the microbial respiration rates were regressed against the MAT, and they found that soil microbial respiration rates were greater for cooler than for warmer sites. This finding can potentially be translated into cold-shifted temperature dependences of respiration in cooler sites and warm-shifted at warmer sites, similar to that found across Europe (**Paper III**). On the other hand, Hartley et al. (2008) and Karhu et al. (2014) argued that the reduced microbial

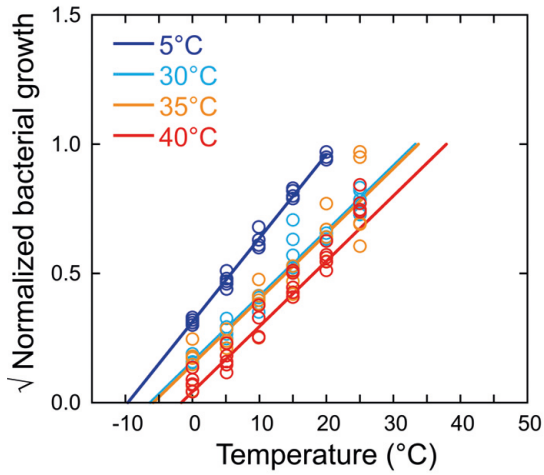
respiration rates are due to substrate depletion as an indirect effect of warmer temperatures and that no microbial thermal acclimation occurred. This disagreement regarding the cause of the decreased respiration rates with higher temperatures partly arises from the fact that microbial processes are influenced by both direct and indirect effects of temperature change. Indeed, changes in substrate quality or composition can affect microbial respiration (Hernández & Hobbie, 2010). However, studies that assessed the intrinsic microbial temperature dependences to avoid indirect effects in soils after field warming (Nottingham et al., 2022; Rousk et al., 2012), or laboratory incubations (Bárcenas-Moreno et al., 2009; Birgander et al., 2013; Donhauser et al., 2020; Rijkers et al., 2022) have shown that microbial communities can indeed shift their temperature dependences to elevated temperatures.

In this thesis, to avoid the indirect effects of temperature changes, I targeted the intrinsic temperature dependences. To accomplish this, I used short soil incubations to measure microbial growth and respiration rates (e.g., 2h for bacterial growth, 4h for fungal growth, and 18h for respiration at 20°C). This method ensures that changes in growth or respiration rates due to altered conditions are minimized (Rousk & Bååth, 2011), allowing for the measurement of the direct effect of temperature (**Paper I**, **Paper II**, and **Paper III**). Additionally, the length of the incubation times was adjusted to the incubation temperatures to yield a similar level of microbial activity across temperatures ranging from 0°C to 45°C and minimizing differences in indirect effects such as variations in substrate availability. Specifically, we kept longer incubation times for lower temperatures and decreasing incubation times with increasing temperatures.

Understanding the temperature responses of different microbial processes is crucial since changes in bacterial growth, fungal growth, and respiration due to temperature increase can affect soil C storage and C emissions from soils. In **Paper III**, along a European climate gradient, the temperature dependence of bacterial growth showed the strongest response to mean annual temperature (MAT), followed by fungal growth and respiration. This means that the temperature dependence of bacterial growth is more responsive to changes in environmental temperatures compared to fungal growth and respiration. Variances in the temperature dependences of bacterial and fungal growth were found to be linked to differences in microbial community composition. These correlations suggest that microbial thermal traits adjust to the climate and likely result from variations in microbial community composition along the climate gradient in Europe (**Paper III**). Previous research suggest that fungi generally exhibit greater resistance to environmental changes, such as variations in soil moisture (**Paper I**; Evans & Wallenstein, 2012; Manzoni et al., 2012a), pH (Rousk et al., 2009), soil salinity (Rath et al., 2016; Wichern et al., 2006) compared to bacteria. This resistance is likely due to their ability to adjust their physiology in response to changing environmental conditions. Furthermore, the shift in the temperature dependence of bacterial and fungal growth were more

responsive than the temperature dependence of respiration. Microbial respiration might be less responsive, given that it is a broader microbial function, and can increase due to microbial growth and physiological stress (Schimel et al., 2007). These differences in shifts in temperature dependences have important implications for soil C cycling and for understanding how microorganisms adjust the processes they regulate in response to temperature changes. For example, a more pronounced warm shift in the temperature dependence of microbial growth compared to the temperature dependence of respiration may result in lower microbial growth rates and higher respiration rates at low temperatures. Consequently, a great microbial growth shift may lead to increased C losses through respiration compared to conditions before the warm shift occurred.

Important aspects to consider are (i) the temperature range that induces shifts in microbial temperature dependences and (ii) the speed at which these shifts occur. To investigate these aspects, I conducted a laboratory experiment using arctic soils and field experiments both in subarctic and temperate ecosystems. Arctic and subarctic soils store the greatest amount of C in terrestrial ecosystems (Jackson et al., 2017; Crowther et al., 2019), and these ecosystems are particularly vulnerable to climate change because they experience a disproportionate temperature increase compared to others (Rantanen et al., 2022; Wieder et al., 2019). Therefore, it is important to understand how soil microbial communities in these cold ecosystems respond to temperature change. In the laboratory, the arctic soil samples from Greenland were incubated at different temperatures for a month to test how temperatures, including incubations at 5°C, 30°C, 35°C, and 40°C affect the temperature dependence of bacterial growth. These soil incubation temperatures were lower, similar, and higher than the initial T_{opt} of bacterial growth, determined to be 29.9°C. Previous experiments suggest that the microbial temperature dependences are shaped by temperatures that surpass the T_{opt} of microbial growth (Bárcenas-Moreno et al., 2009; Birgander et al., 2013). However, subjecting arctic soil samples to these extreme temperatures for a month is not a realistic simulation of climate warming. Still, this experimental design allowed me to test the temperatures that are likely to induce shifts in microbial temperature dependences. As a result of the laboratory incubation, the temperature dependence of bacterial growth warm shifted (increased T_{min}) with increasing incubation temperatures (Fig. 9). Therefore, these results are in line with studies that suggest that T_{opt} acts as a tipping point and above this temperature the microbial temperature dependence quickly adjusts to the new thermal regime (Bárcenas-Moreno et al., 2009; Birgander et al., 2013; Donhauser et al., 2020). Increasing the incubation temperature to 40°C resulted in the most pronounced shift in the temperature dependence (Fig. 9). Donhauser et al. 2020 applied a similar soil incubation experiment and found that the incubation above the bacterial growth T_{opt} resulted in changes in the community composition, promoting heat-tolerant, stress-resistant, and fast-growing bacteria in alpine soils.



Incubation temperature	T_{min}
5°C	-9.6 ± 0.33
30°C	-6.3 ± 0.42
35°C	-5.8 ± 0.56
40°C	-1.7 ± 0.40

Figure 9. Normalized temperature dependence of bacterial growth and T_{min} values (°C) in Greenlandic soils. The temperature dependence of bacterial growth was determined after one month of incubation at four different temperatures (5°C, 30°C, 35°C, and 40°C). Data represent all the data points (n=5) in the figure. In the table, data represent mean values ± 1SE (n=5). For the curve fit, the simplified *Ratkowsky* model was employed for the data measured between 0°C and 25°C (Box 1, eqn 3).

In the field, where the temperatures fluctuate and cannot be fully controlled, it is more challenging to increase the temperature and detect the microbial temperature dependence shifts. To address this challenge, I employed soil warming and simulated heat waves in a subarctic (**Paper II**, Abisko) and in a temperate ecosystem (Fig. 10, Lund) using an IR heating system. In the subarctic experiment, the temperature dependence was determined at the start and end of the heat wave simulation (**Paper II**). Consequently, the experiment did not allow for disentangling when the temperature dependence shift occurred within those two months. To complement this experiment, I conducted another experiment simultaneously, where I sampled soils approximately every 2-3 weeks during a heat wave simulation in a temperate ecosystem (Fig. 10b, c, d, e). No detectable change was observed as long as the soil temperature was under the bacterial T_{opt} (Fig. 10a, b, c). However, when the temperature rose above the T_{opt} of bacterial growth, the temperature dependence warm shifted within three weeks (difference between Fig. 10c and d), and this shift persisted after two weeks (Fig. 10e).

In another experiment, Nottingham et al. (2021) translocated soil samples along a tropical climate gradient and studied microbial communities' adjustment to the new thermal regime. They found that the thermal adjustment of the microbial community was more pronounced in warmer environments compared to colder climates, which suggests higher microbial turnover facilitating faster thermal adjustment to warmer temperatures. To test this, I assessed bacterial turnover time in the temperate soils (Lund warming experiment; Fig. 10) and investigated the link with the observed

shifts in the temperature dependence of bacterial growth. To estimate the bacterial turnover time, the bacterial biomass was divided by bacterial growth rates (Fig. 10h). I found that bacterial turnover time increased with warming due to the decreased bacterial growth likely caused by a reduction in soil moisture as an indirect effect of warming (between 20-07-2020 and 04-08-2020). However, in the warmed plots, bacterial turnover time decreased fourfold due to rainfall events, resulting in faster turnover (between 04-08-2020 and 30-08-2020; Fig. 10h). This coincided with the warm shift in temperature dependence of bacterial growth (Fig. 10d). Therefore, it is likely that this faster bacterial community with shorter turnover time drove the shift in temperature dependence.

To understand how temperature legacy shapes the microbial temperature dependences, it is necessary to link the shift in the temperature dependence to environmental temperatures. Studies suggested that a 1°C increase in MAT increases the T_{min} of bacterial growth between 0.2°C and 0.3°C (a right shift of the temperature dependence curve) (**Paper III**; Nottingham et al., 2019; Rinnan et al., 2009; Rousk et al., 2012). However, since the warmest months likely shape the microbial thermal traits, MAT might not be a strong predictor for changes in microbial temperature dependence. To determine what environmental temperature had given rise to the temperature variation along a European climate gradient, the microbial temperature dependences were regressed against both summer and winter temperatures (**Paper III**). The results indicate stronger microbial thermal responses to summer than winter temperatures. In laboratory studies that linked temperature change to T_{min} change, a stronger relationship was found when soils were exposed to temperatures higher than T_{opt} of microbial growth. That is, a 1°C increase in temperature increases the T_{min} of bacterial growth by 0.8°C (Bárcenas-Moreno et al., 2009; Birgander et al., 2013). In line with these findings, the T_{min} increased by 0.7°C and 0.8°C for bacterial and fungal growth, respectively, with a 1°C increase in summer temperatures (**Paper II**). It is important to consider soil water content in the context of shifts in microbial thermal traits. High soil temperatures without available water for the microbial community are unlikely to result in a shift in microbial temperature dependence. However, when water is present and the temperature is sufficiently high, the microbial community is likely to adjust to the elevated temperatures within weeks (Fig. 10). In summary, instead of using MAT, a better predictor for the shift in microbial temperature dependence to environmental temperature might be the highest temperatures of the year when there is available water for microorganisms.

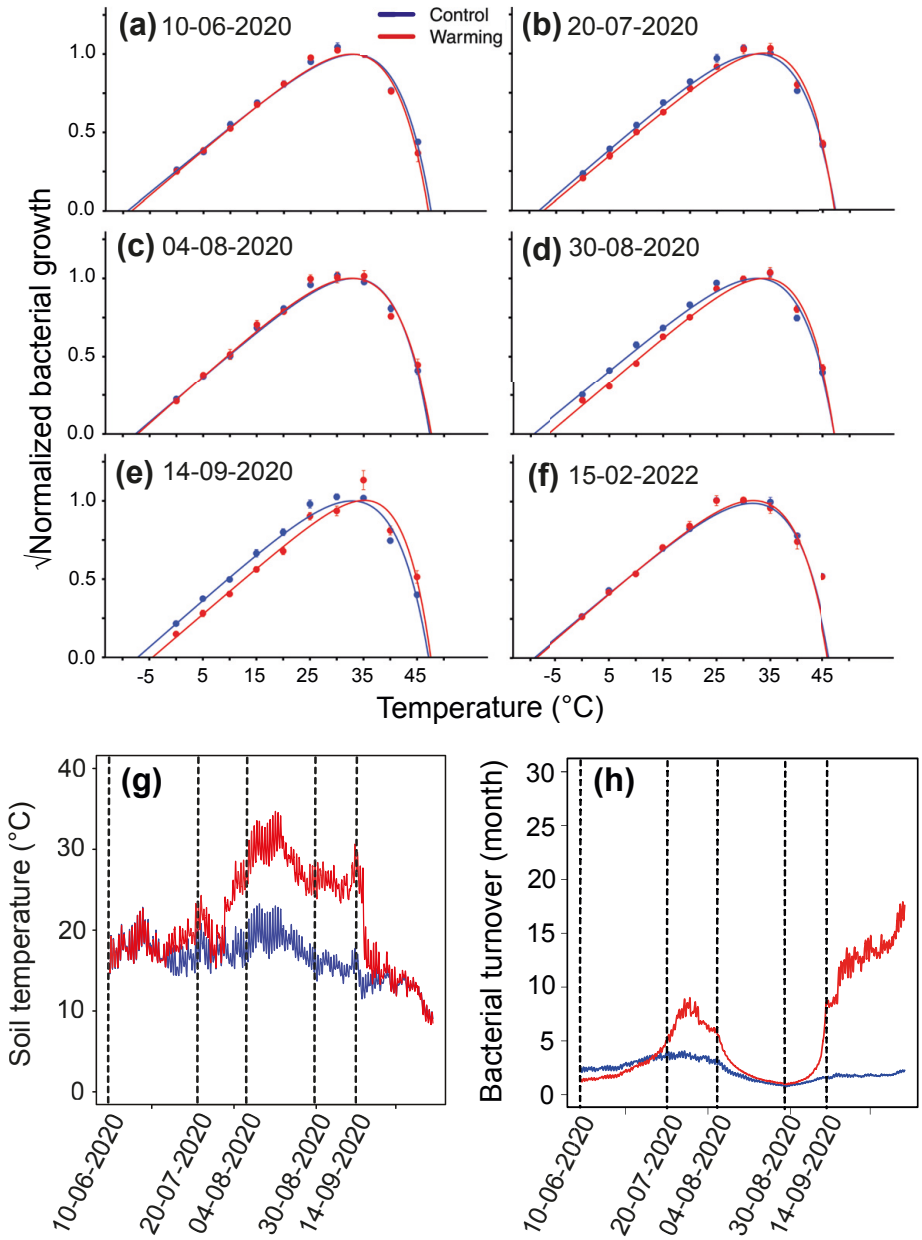


Figure 10. The response of normalized bacterial growth temperature dependences to summer heat wave simulation in Lund, Sweden. The bacterial growth temperature dependences are determined at six different sampling times. Bacterial temperature dependence determined (a) before the heat wave simulation (10-06-2020); during the heat wave simulation (b) 20-07-2020; (c) 04-08-2020; (d) 30-08-2020; (e) 14-09-2020; and 1.5 years after the heat wave simulation (15-02-2022). Panel (g) shows the mean soil temperature (°C) measured in control (n=6) and warmed (n=6) plots. For panel (a) – (f), the *Ratkowsky* model was employed for cure fitting (Box 1, eqn 2).

The microbial temperature dependence reversal after a shift

An approach to study the environmental legacy is through experimental manipulation, applying an initial temperature stressor to the microbial community and observing its responses after removing it (Fig. 8b). In **Paper II**, I not only investigated how the microbial community adjusts its temperature dependence to a summer heat wave in the Subarctic but also studied how long it takes for this shift to dissipate. After simulating a summer heat wave, the warming treatments were removed, leaving all plots (warming and control) at ambient conditions. I then sampled and determined the microbial temperature dependences 10 and 12 months after the warming treatment ended. For temperature dependence of bacterial growth, the T_{min} increased by 2.1°C with warming. After 10 months at ambient temperature, which mostly covered winter, the T_{min} difference between warming and control plots decreased to 1.2°C, although the difference was not statistically significant anymore. After a whole year, the warm-shifted bacterial community restored its temperature dependence to match the ambient conditions. Therefore, in the case of bacterial growth, the long and cold winter had a less significant impact on the temperature dependence adjustment than the short but warm summer (2 months) when the bacterial turnover rates were likely the highest. In line with these results, Nottingham et al. (2021) showed that most of the bacterial thermal traits adjust to the new environmental temperature within 2 years. For fungal growth, due to the heat wave simulation, the T_{min} tended to increase by 2.2°C with warming, and the difference decreased to 0.8 °C in 10 months at ambient winter temperature (**Paper II**). This means that, most of the differences caused by the summer heat wave dissipated within the winter months, suggesting faster fungal recovery compared to bacterial. This is interesting because one might expect slower thermal trait shift during winter due to reduced microbial turnover time resulting from cold temperatures. Schadt et al. (2003) measured both soil bacterial and fungal biomass in the winter. They found that the total microbial biomass was larger in the winter than in the summer, and the fungal dominance was stronger in cold soils. This can be explained by differences in substrate use between the seasons. In the summer, soil microbial communities primarily rely on plant root exudates (Lipson et al., 2002) that are decomposable for both bacteria and fungi. In contrast, in the winter, microorganisms predominantly decompose more complex polymers such as cellulose derived from dead plant material, primarily decomposed by fungi (Lipson et al., 2002). Therefore, these differences in substrate availability can favor a more active fungal community in cold soils relative to bacterial community. The higher fungal activity in the winter, therefore, can potentially result in faster fungal thermal trait changes. However, further research is needed to validate these results and assess the speed at which fungal growth temperature dependence can shift and how long the shift persists.

To improve the representation of microbial thermal traits in the ecosystem model LPJ-GUESS

Ecosystem models, such as Dynamic Vegetation Models (DVMs), are crucial for providing projections of how climate change will impact the terrestrial C cycling (Ahlström et al., 2015; Sitch et al., 2008). DVMs rely on microbial temperature dependence to determine the temperature sensitivity of the terrestrial C cycling. In existing DVMs, a universal temperature dependence is employed for all microbial processes across ecosystems and climatic conditions (Wieder et al., 2015). However, empirical evidence demonstrated that different microbial processes show distinct temperature responses. In particular, the temperature dependences of microbial respiration and microbial growth are different from each other (**Paper I**, **Paper II**, **Paper III**). The thermal traits that define the temperature dependences are climate-specific (**Paper III**) and are subject to change in response to temperature alteration (**Paper II**). To address these points and to improve the representation of microbial thermal traits and their adjustment to temperature change, the temperature dependences were incorporated for microbial growth and respiration from **Paper II**, and **Paper III** into a process-based DVM, LPJ-GUESS (Lund-Potsdam-Jena General Ecosystem Simulator) (**Paper IV**) according to the steps shown in Box 2.

LPJ-GUESS is known for its ability to integrate complex ecological processes, including vegetation dynamics, ecosystem biogeochemistry, and climate interactions (Smith et al., 2001, 2014). The model was chosen for its capacity to incorporate microbial processes, including microbial growth and respiration. Moreover, LPJ-GUESS allowed us to determine the environmental temperature under which the microbial community has formed. With that, a microbial community could be simulated that is formed in different climate conditions, and therefore, it becomes climate-specific. Furthermore, the microbial community is allowed to change with subsequent temperature variation. This is especially important in the context of climate change, where the microbial community is expected to change, adjust to new climate regimes, and exhibit different responses under varying climatic conditions (**Paper II**, **Paper III**, Alster et al., 2023; Dacal et al., 2019).

Two important parameters were tested in the new dynamic model scheme: the climate sensitivity of the microbial community and the microbial resistance (**Paper IV**). Climate sensitivity refers to the responsiveness of microbial temperature dependence to temperature change. Low climate sensitivity indicates a less responsive community, whereas high sensitivity indicates a greater microbial response to temperature change. Microbial resistance to change refers to how much turnover of the microbial community is required for shifts in the microbial temperature dependence. To test the sensitivity of these parameters, different levels of climate sensitivity and microbial resistance were used, and two different European sites were compared. One site is of a subarctic climate characterized by short cool summer and long cold winter, and the other site has a continental climate with warm summers and relatively cold winters. Model simulations suggest that changing the microbial resistance strongly affected the microbial thermal traits. When the microbial community was characterized by greater resistance, the temperature dependence became less responsive in both subarctic ecosystems and those in continental Europe. This suggests that changes in microbial resistance can have a large impact on microbial temperature dependences. Changes in climate sensitivity had a more pronounced effect on the subarctic compared to the continental ecosystems. While microbial temperature dependence in the Subarctic responded to all tested levels of climate sensitivity, no differences were observed between different climate sensitivity settings in the continental site. Therefore, the model simulation suggests a more climate-sensitive microbial community in high-latitude ecosystems in Europe. This finding is particularly important in the context of climate change, as these high-latitude regions are projected to experience disproportional temperature increases and climate extremes (Rantanen et al., 2022; Wieder et al., 2019).

To forecast the impact of climate change on soil and vegetation C dynamics model simulations were conducted throughout the 21st century. The results suggest that, with the new dynamic scheme, overall soil C sequestration increases, but soil C in high-latitude regions decreases. Minor variations in vegetation C were observed, except for a large impact on vegetation C in high-latitude European regions, accompanied by shifts in vegetation composition. These findings underscore the importance of directing greater attention towards accurately predicting both below- and aboveground C dynamics in high-latitude ecosystems.

Box 2. Steps to improve the representation of microbial thermal traits in LPJ-GUESS

1. Determine the temperature dependences of microbial respiration and growth separately in an empirical study (**Paper II**).
2. Assess the climate-specific microbial growth and respiration temperature dependences in an empirical study across Europe (**Paper III**).
3. The LPJ-GUESS model allowed us to determine the soil temperature under which the microbial community formed in the model. This is a useful model feature since with this we can allow the microbial community to be temperature-specific.
4. Determine the climate sensitivity of microbial temperature dependences by regressing the climate-specific microbial temperature dependences (step 2) against the average environmental temperature under which the microbial community formed (step 3).
5. By using separate microbial growth and respiration temperature dependences (step 1) and combining them with the climate sensitivity (step 4), we allowed the microbial community to be climate-specific and respond to temperature change (**Paper IV)**.

Synthesis and future perspectives

In this thesis, I studied the temperature dependences of microbial growth and respiration to better understand how soil microorganisms respond to temperature change and the consequences for terrestrial C cycling. **Paper II** showed that a heat wave simulation during the warmest part of the year in a subarctic soil strongly affected the temperature dependence of microbial growth. Specifically, the temperature dependence of bacterial growth shifted towards warmer temperatures within a growing season and with a similar tendency for fungal growth. The impact of a heat wave on microbial growth was also tested in temperate soil, confirming that the temperature dependence of bacterial growth warm-shifted within a few weeks. **Paper II** showed that after the heat wave ended, the temperature dependence of bacterial growth gradually adjusted to ambient conditions within a year. The results also indicate that temperature dependence of bacterial growth was more sensitive to temperature increases induced by a heat wave (**Paper II**) or environmental temperature legacy (**Paper III**) compared to fungal growth. Furthermore, the shift in the temperature dependence of bacterial and fungal growth were more responsive to both heat wave (**Paper II**) and environmental legacies (**Paper III**) than respiration. The results of **Paper I** and **Paper II** showed that soil moisture had a significant impact on microbial growth and respiration, with microbial rates decreasing at lower moisture levels. However, bacterial growth was more sensitive to decreasing moisture compared to fungal growth, resulting in a more rapid decline. This led to an increased fungal-to-bacterial growth ratio in drier soils, that suggests fungal dominance. Despite the strong influence of moisture on microbial rates, it did not affect the microbial temperature dependences (**Paper I**). Thus, the temperature dependence of microbial growth and respiration were not dependent of soil moisture. Finally, to improve the model predictions of ecosystem C budget on a continental scale in Europe, the representation of microbial temperature dependences was improved in a process-based DVM, LPJ-GUESS. This was done by incorporating empirically determined climate-specific temperature dependences into LPJ-GUESS (**Paper IV**). With this new model scheme, the microbial community was allowed to adjust to temperature changes, that enabled a dynamic representation of the microbial community. Subsequently, this new dynamic scheme was employed to forecast the impact of climate change on soil and vegetation C dynamics in Europe. The dynamic model scheme resulted in an overall increase in soil C sequestration, however, both soil and vegetation C in high-latitude ecosystems decreased.

Much research is still needed to understand how temperature governs soil microorganisms and decomposition processes under climate change. In **Paper II** and the Lund warming experiment (Fig. 10), the focus was on investigating a singular summer heat wave. However, given the projected increase in frequency and intensity of heat waves, it becomes imperative to extend our study to multiple heat waves. Investigating microbial temperature dependences in response to recurrent heat waves through cycles could provide crucial insights into how the legacy of initial heat waves shapes microbial communities and influences their ability to cope with subsequent episodes of extreme temperatures. For example, a repeated number of drying and rewetting cycles resulted in faster microbial growth recovery to subsequent drying and rewetting cycles (Brangarí et al., 2021; Leizeaga et al., 2022). This approach could be applied to test how repeated heat wave cycles affect the microbial temperature dependences. Such testing could be conducted through microcosm experiments, exposing soil samples to repeated heat wave cycles, or in the field by subjecting soils to heat wave cycles with field warming, as conducted in **Paper II** for one heat wave. The laboratory setting offers controlled temperatures and soil moistures and incubation duration, as conducted for the Greenlandic soils (Fig. 9). In order to experimentally force the community to become warm-shifted, soils should be incubated at temperatures higher than the microbial growth T_{opt} (as illustrated in Fig. 9) across 3-4 cycles heat wave simulations. Based on my findings, I expect that after a short heat wave simulation in the laboratory (2-4 weeks), the microbial temperature dependence would become warm-shifted, with the strongest shift for bacterial growth than fungal growth, and respiration showing the most resistance. I would also expect that if the microbial temperature dependence adjusts to the first cycle of the heat wave simulations, the microbial community would likely exhibit similarly warm-shifted temperature dependences in the subsequent cycles. This could result in competitive advantages at high temperatures compared to the temperature dependences of the community at control temperature conditions (Fig. 8a). However, this laboratory setting has limitations, for example, the soil samples are artificially isolated, the plants are removed, and the indirect factors associated with temperature increases are manipulated, such as lower soil moisture content. Therefore, to complement the laboratory experiment, heat wave simulations should be conducted in the field as well to assess how heat wave cycles affect microbial temperature dependence through complex, interacting ecosystem processes, as demonstrated in **Paper II**.

This thesis specifically focuses on soil microbial processes. However, plants are a crucial part of the terrestrial C cycle. Plants influence ecosystem processes, impacting nutrient cycling, litter quality, and quantity (DeAngelis et al., 2019). Results from a meta-analysis indicate that plant productivity, and consequently C storage increases with warming, which is particularly important in tundra compared to other ecosystems (Rustad et al., 2001). While warming is expected to accelerate SOC losses via microbial decomposition (Crowther et al., 2016), studies across

various ecosystems reveal that plant-derived C inputs could potentially offset C losses driven by microbial respiration (Lu et al., 2013). Similarly, Melillo et al. (2011) found that a 7-year soil warming experiment resulted in C losses via microbial respiration but stimulated C gains in deciduous forests by increasing microbial nitrogen mineralization, which supported higher plant productivity. However, a 26-year soil warming experiment at the same site resulted in a more complex pattern, with an overall net C loss from soils (Melillo et al., 2017). A global time series spanning a decade reported that plant productivity could not fully compensate for warming-induced heterotrophic respiration losses (Naidu & Bagchi, 2021). To get a better understanding, the temperature dependence of plant communities could be tested by measuring CO_2 uptake at a range of temperatures in the field. For example, IR heaters could be set to temperatures between 5°C and 40°C with 5-degree intervals, similar to the temperature range used for incubating soil samples. CO_2 fluxes could then be measured using bright and dark chambers. The bright chambers would determine CO_2 uptake at different temperatures, revealing the temperature dependence of plant photosynthesis, while the dark chambers would exclude photosynthesis, allowing measurement of soil respiration. In addition, in **Paper II** and the Lund warming experiment, the heat wave simulation negatively impacted the vegetation, resulting in decreased plant productivity. An upcoming project could investigate the impact of heat waves on changes in vegetation composition. After the heat wave, it took a year for the microbial temperature dependence to recover in subarctic soils (**Paper II**). It would be interesting to study the recovery of plant communities alongside microbial temperature dependences following heat waves. This could be achieved through continuous vegetation inventory coupled with *in situ* CO_2 measurements to provide a more comprehensive understanding of the soil-plant-microbial temperature responses and ecosystem recovery after such heat waves.

In **Paper IV**, empirically determined temperature dependences were incorporated into LPJ-GUESS to forecast the impact of climate change on soil and vegetation C. While this model change provided valuable insights, its limitation to a continental scale restricted future projections to Europe alone. For better predictions of the global C cycle, it is necessary to upscale the model to a global scale to enable an assessment of interactions among various ecosystems and climates. While there is a lot of empirical research on the temperature dependences of microbial respiration, studies investigating both microbial growth and respiration together are relatively scarce. The diversity of experimental methods of available surveys makes direct comparison challenging. Outside of Europe, a few studies determined microbial temperature dependences using a similar assessment as presented in this thesis. Thus, these studies could be used to upscale the model simulations in **Paper IV**. For example, Nottingham et al. (2022) assessed the temperature dependence of both microbial growth and respiration in tropical soils in Central America, while Li et al. (2021) investigated the temperature dependence of microbial respiration across China. Other studies assessed the temperature dependence of microbial growth in

the tropics (Nottingham et al., 2019), in sub- and high-arctic regions (Rijkers et al., 2023), along an Antarctic climate gradient (Rinnan et al., 2009), and in desert soil in North America (van Gestel et al., 2013). However, this list also highlights a lack of measurements in South America, Africa, Australia, and across Asia.

Soil sampling close to the Zackenberg Research Station in Greenland, June 2023 (photo by Sara Winterfeldt).

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