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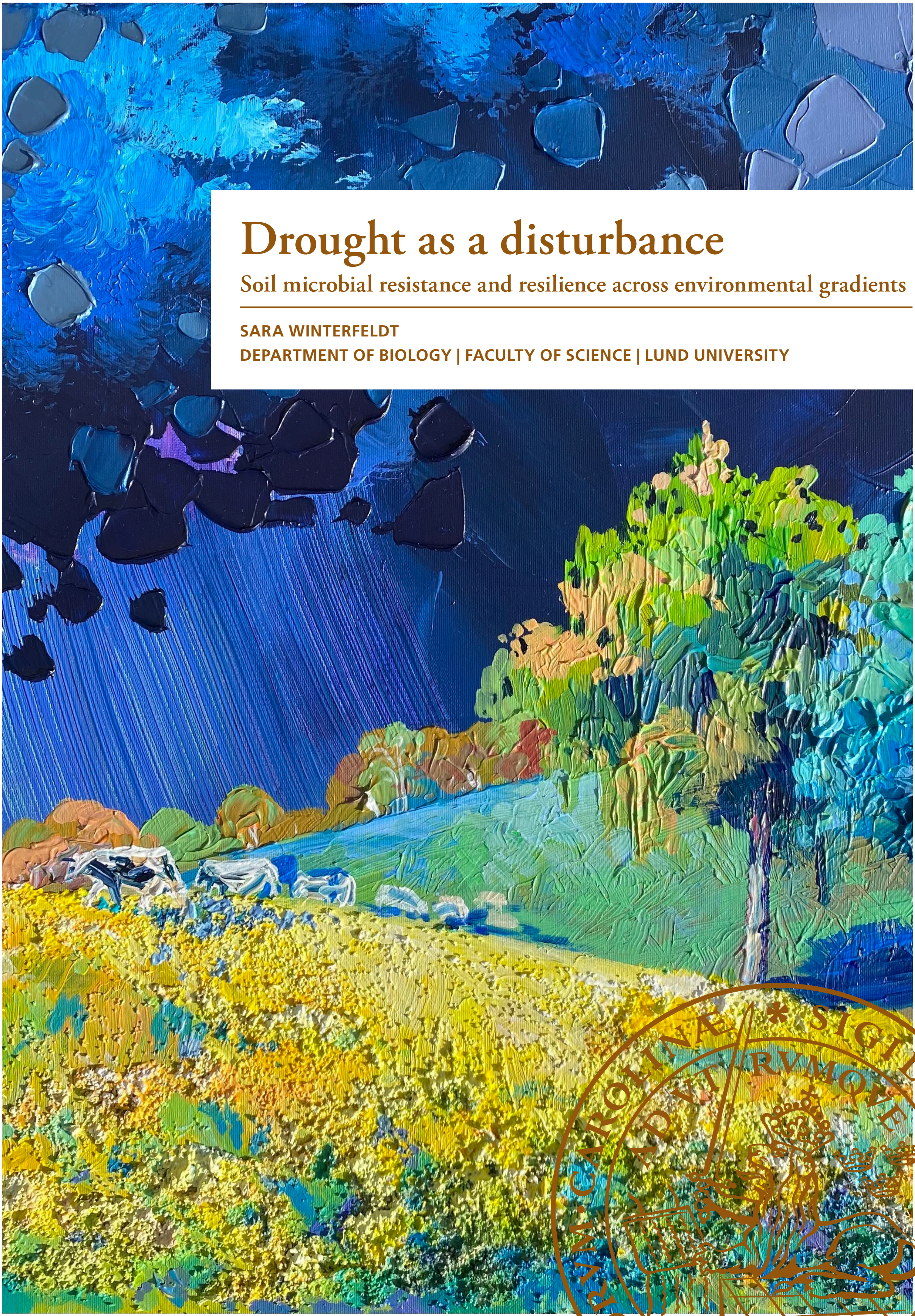

Drought as a disturbance

Soil microbial resistance and resilience across environmental gradients

SARA WINTERFELDT

DEPARTMENT OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY

Drought as a disturbance: Soil microbial resistance and resilience across environmental gradients

Drought as a disturbance

Soil microbial resistance and resilience across environmental gradients

Sara Winterfeldt

LUND UNIVERSITY

DOCTORAL DISSERTATION

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Key words: climate change, drought, microbial ecology, microbial growth, resilience, resistance, respiration, rewetting

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"How can I stand on the ground every day and not feel its power?"

- William Bryant Logan

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Abstract

The ecosystem response to disturbances is a central topic in ecology, and there is growing awareness of the impacts of human-driven climate change on ecosystem stability to disturbances. Terrestrial ecosystems are increasingly exposed to more drought and rainfall events as climate change intensifies. In soils, bacteria and fungi play a key role in ecosystem functioning, yet their responses to drought disturbances are not fully understood. In this thesis, I investigated the drought stability of microbial growth and respiration, focusing on resistance (the ability to withstand drought) and resilience (the ability to recover after drought). I used different environmental gradients including geographical gradients and field manipulation experiments to test how different factors including drought exposure history, soil properties, and plant diversity shape microbial responses to drought. I found that historical drought exposure increased bacterial drought resistance and resilience, suggesting that bacteria are more sensitive to drought in wetter climates, where drought is perceived as a more severe disturbance. Fungal growth was consistently both more resistant and resilient than bacterial growth. Interestingly, microbial carbon use efficiency (the partitioning between carbon used for growth and that released via respiration) after rewetting did not vary with climate. Other environmental factors also influenced microbial drought responses. Plant diversity had a positive effect on microbial resistance and resilience to drought. This might be due to increased access to plant-derived carbon at higher plant diversity, which could support microbial strategies to cope with drought. Surprisingly, other components of stability were unaffected by plant diversity. In contrast, lower soil pH reduced the resistance and resilience to drought, whereas soil texture, tillage, and increased temperature had negligible effects. Taken together, my findings show that climatic differences in drought exposure had a stronger effect than plant diversity in shaping microbial responses to drought. Identifying the environmental drivers of microbial growth and respiration stability improves our ability to predict microbial responses to future drought disturbances.

Popular science summary

Soils are among Earth's most complex ecosystems. Hidden beneath our feet, the soil is remarkably diverse and contains a majority of life on the planet. In the belowground world, two microbial groups dominate: bacteria and fungi. A single gram of soil contains billions of bacterial cells and hundreds of meters of fungal hyphae. Even though microbes are tiny, they play a key role in ecosystem functions. They break down organic matter, recycle nutrients, and influence whether soils release or store carbon. Microbial growth transforms carbon into forms that can stay in the soil, while they also release carbon dioxide into the air through respiration, contributing to greenhouse gas emissions. If microbes can use carbon more efficient for growth, more carbon will stay in the soil.

Water is essential for all life, including soil microbes. This is especially important under climate change, as droughts and rainfalls are becoming more severe. When soils dry, the activity of microbes is reduced. Microbes that remain active in dry soils are more drought resistant. After a drought, the first rainfall makes microbes release a lot of carbon dioxide into the air, but their growth is slow. Microbes that recover growth faster, are more resilient. In my thesis, I studied how microbes respond to drought across different climates and environments. Here are the key findings from my work:

- Bacteria in soils from dry climates were more drought resistant and recovered faster after drought compared to those in wetter climates. In contrast, fungi were generally both more resistant and resilient across all climates and environments.
- Higher diversity of plants increased both the ability of microbes to tolerate drought and the ability to recover after the drought ended.
- Other factors also shaped how microbes respond to drought and rainfall. For example, acidic soils reduced the resistance and resilience after drought, while factors such as soil texture, tillage, and high temperatures had small effects.
- The efficiency microbes use carbon after rainfall did not change with climate. In other words, microbes that recovered faster after rainfall released a similar proportion of carbon dioxide into the air as more sensitive microbes.

This thesis is part of a greater journey to understand how drought and rainfall affect microbial life. To fully unravel how microbes and their processes respond to drought, we need to identify key environmental factors and determine how different environments and disturbances interact with drought. This will help us better predict how soil microbes will respond to future droughts under climate change and if carbon will stay or be released from the soil.

Populärvetenskaplig sammanfattning

Marken är bland de mest komplexa ekosystemen på jorden. Gömda under våra fötter finns en stor del av allt liv på vår planet. I denna underjordiska värld dominerar två grupper av mikrober: bakterier och svampar. Ett enda gram jord kan innehålla miljarder bakterier och hundratals meter av svampmycel. Trots att mikrober är osynliga för ögat har de en nyckelroll i våra ekosystem. De bryter ner organiskt material, återvinner näringsämnen och påverkar om marken lagrar eller släpper ut kol. När mikrober växer omvandlar de kol som kan stanna i marken, samtidigt släpper de också ut koldioxid från marken genom respiration (”andning”), vilket bidrar till utsläpp av växthusgaser. Om mikrober använder kol mer effektivt till att växa, mer kol kan stanna i marken.

Vatten är nödvändigt för allt liv, inklusive mikrober. Det är extra viktigt under pågående klimatförändring, då perioder av torka och regn blir allt längre och intensivare. När marken torkar minskar mikrober sin aktivitet. Mikrober som kan vara aktiva under torka är mer resistenta. Första regnet efter torka gör att mikrober respirerar stora mängder koldioxid från marken som släpps ut i luften, men deras tillväxt är långsam. De som kan återhämta sig genom att växa snabbare efter regn är mer resilienta. I denna avhandling har jag studerat hur mikrober reagerar på torka och regn i olika klimat och miljöer. Här är några slutsatser från mitt arbete:

- Bakterier i torra klimat är mer torktåliga och återhämtade sig snabbare efter en torka jämfört med bakterier från mer fuktiga klimat. I motsats, svampar var mycket resistenta och resilienta i alla klimat och miljöer.
- Högre diversitet av växter ökade både mikrobers förmåga att tolerera torka och deras förmåga att återhämta sig efter regn.
- Andra faktorer kan också påverka hur mikrober reagerar på torka och regn. Till exempel, sura jordar minskade deras resistens och resiliens, medan faktorer som markens struktur, plöjning och högre temperaturer hade små effekter.
- Effektiviteten som mikrober använde kol efter regn berodde inte på olika klimat. Med andra ord, mikrober som kan att växa snabbare efter torka släppte ut lika mycket kol till luften som mer torkkänsliga mikrober.

Denna avhandling är del av en större resa för att förstå effekterna av hur torka och regn påverkar mikrober. För att fullt ut förstå hur mikrober och deras processer reagerar på torka behöver vi identifiera viktiga miljöförhållanden och förstå hur olika miljöer interagerar med torka. Detta kan hjälpa oss att bättre förutsäga hur mikrober reagerar på framtida perioder av torka i ett förändrat klimat och om kol kommer släppas ut eller stanna i marken.

List of papers

Paper I

Tang, Y., **Winterfeldt, S.**, Brangarí, A.C., Hicks, L.C. & Rousk, J. (2023). Higher resistance and resilience of bacterial growth to drought in grasslands with historically lower precipitation. Soil Biology and Biochemistry 177, 108889.

Paper II

Winterfeldt, S., Cruz-Paredes, C., Rousk, J. & Leizeaga, A. (2024). Microbial resistance and resilience to drought across a European climate gradient. Soil Biology and Biochemistry 199, 109574.

Paper III

Winterfeldt, S., Bardgett, R.D., Brangarí, A.C., Eisenhauer, N., Hicks, L.C., Liu, S. & Rousk, J. Plant diversity increases microbial resistance to drought and soil carbon accumulation. Manuscript (in review).

Paper IV

Winterfeldt, S., Bardgett, R.D., Brangarí, A.C., Eisenhauer, N., Hicks, L.C., Liu, S. & Rousk, J. Influence of plant diversity on microbial provisioning of ecosystem stability following drought. Manuscript.

Author contributions

Paper I

SW, ACB, LCH and JR planned and designed the experiment. ACB, LCH and JR sampled soils. YT and SW conducted the lab work. YT analysed the data. YT wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Paper II

SW, AL and JR planned and designed the experiment. SW conducted the lab work. CCP conducted the DNA extraction and bioinformatics analyses. SW analysed the data. SW wrote the manuscript under supervision of AL and JR. All authors provided comments on the manuscript draft and approved the final manuscript.

Paper III

SW, ACB, LCH, NE and JR planned and designed the experiment. SW, ACB, SL, NE, and JR carried out the soil sampling. SW and SL conducted the lab experiment. SW analysed the data. RDB, NE and JR acquired the funding. SW wrote the manuscript supervised by JR, ACB and LCH. All authors contributed to the draft and approved the final manuscript.

Paper IV

SW, ACB, LCH, NE and JR planned and designed the experiment. SW, ACB, SL, NE, and JR carried out the soil sampling. SW and SL conducted the lab experiment. SW analysed the data. RDB, NE and JR acquired the funding. SW wrote the manuscript supervised by JR, ACB and LCH. All authors provided comments on the manuscript draft.

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Introduction

Over the last century, ecologists have been interested in understanding how ecosystems respond to disturbances, and this topic has become central to our understanding of ecology (Newman et al., 2024). During this time, views have shifted from considering disturbances as interruptions in successional development of plant community equilibrium (Clements, 1916), to an understanding that disturbances are important and often essential for regulating ecosystem processes, community dynamics, and biodiversity (Newman et al., 2024; Sousa, 1984; White & Pickett, 1985). Disturbances are commonly defined as events that are distinct in space and time, and can cause losses of biomass, changes in community composition, and alterations in biogeochemical cycles (Grime, 1979; Sousa, 1984; White & Pickett, 1985). Broadly, disturbances can be anything from a single tree falling to create a gap in the forest, to a major fire, flood, or drought event across whole landscapes. More recently, scientists have focused on the importance of ecosystem responses to disturbances in the face of anthropogenic climate change, such as droughts (Newman et al., 2024). Disturbances are closely related to stability, which describes the ability for an ecosystem to remain the same and return to its previous state after a disturbance (van Meerbeek et al., 2021). Stability most commonly consists of two components: the ability to withstand a disturbance, that is, resistance, and the ability to recover after a disturbance, that is, resilience and these concepts have become a major focus of ecological research (Philippot et al., 2021; Shade et al., 2012). In this thesis, I focused on stability of soil microbial communities to drought disturbances. Understanding the drivers of stability, including resistance and resilience, is crucial for predicting how microbial communities and their functions will respond to drought disturbances.

The microbial role in the terrestrial carbon cycle

In soils, fungi and bacteria are the key players, and their activity drives many soil functions and biogeochemical cycles (Bardgett et al., 2008; Bradford et al., 2013; Tecon & Or, 2017). Microbial communities are essential for the turnover and cycling of nutrients, which determines ecosystem processes such as plant productivity, climate regulation, and decomposition (Bardgett & van der Putten, 2014). At the same time, soil holds the largest carbon stock in terrestrial ecosystems (Batjes, 1996; Le Quéré et al., 2018). Hence, changes in soil carbon could impact the climate. The terrestrial carbon cycle is largely regulated by microbial activity (Gougoulias et al., 2014; Schimel

& Schaeffer, 2012). In other words, microbial growth results in a build-up of microbial biomass and transforms carbon into more stable forms (Liang et al., 2017; Six et al., 2006), whereas microbial respiration contributes to the majority of carbon released from the soil to the atmosphere (Kim et al., 2012; Liang et al., 2017).

The microbial use of carbon for respiration and growth might depend on their ability to resist and recover from drought, which can contribute to positive or negative climate change feedbacks (Bardgett et al., 2008; Brangarí et al., 2021). Rewetting dry soil is known to induce a large pulse of respiration, called the Birch effect (Birch, 1958). The Birch effect is relevant at the ecosystem scale and can result in considerable losses of carbon from the soil (Barnard et al., 2020; Jarvis et al., 2007; Kim et al., 2012; Rousk & Brangarí, 2022). Rewetting increases resource availability via several processes that can fuel microbial growth and respiration through (1) physical disruption of soil aggregates releasing previously inaccessible resources (Denef et al., 2001; Kaiser et al., 2015; Navarro-García et al., 2012), (2) enzymatic activity carried out by damaged microbial cells (Brangarí et al., 2021; Fraser et al., 2016) and (3) a build-up of microbial residues such as necromass and solutes that accumulated during drought (Blazewicz et al., 2014; Fierer & Schimel, 2003; Kieft et al., 1987; Warren & Manzoni, 2023). The efficiency with which microorganisms use this carbon for growth compared to the total carbon uptake including growth and respiration (i.e., microbial carbon use efficiency) plays an important role in the soil carbon budget (Manzoni et al., 2012a).

Impact of drought disturbances on soil microorganisms

Why is it interesting to study soil microbial communities under drought disturbances?

Terrestrial ecosystems are experiencing more frequent and intense droughts (Chiang et al., 2021; Trenberth et al., 2014). Climate change alters drought cycles by both extending the duration of each cycle, resulting in more severe droughts, and by increasing the frequency of these cycles, resulting in more drying and rewetting events (Madakumbura et al., 2019).

Drought and rewetting are always linked in terrestrial ecosystems. Therefore, it can be considered as two combined disturbances. As climate change intensifies, one challenge for soil microorganisms is to both withstand drought and to recover from rewetting. As soils dry, soil microorganisms must retain water within their cells to avoid desiccation (Schimel, 2018; Wood, 2015). To survive, microorganisms can accumulate solutes within the cell such as osmolytes, produce extracellular polymeric substrates outside of the cell to retain water (Or et al., 2007; Roberson & Firestone, 1992; Warren, 2014, 2016), or they can become dormant to avoid stressful conditions (Jones & Lennon, 2010; Schimel, 2018). Not only do microorganisms have to cope with drought, but they also have to survive the large changes in water potential when the drought ends with rewetting. Microorganisms must rapidly release solutes to avoid cell lysis either by transporting solutes out through the cell membrane or by metabolising them (Malik & Bouskill, 2022; Schimel et al., 2007; Warren, 2014).

Water is essential for all life on Earth. All organisms, including soil microorganisms, require water for survival and growth. The lack of water, by drought, affects microorganisms in several ways. In soil, water serves as a transportation medium that enables them to move and access resources (Schimel, 2018; Tecon & Or, 2017). Water is also essential for resource acquisition because most resources microorganisms use are water-soluble (Schimel, 2018; Tecon & Or, 2017). As the soil dries, microbial access to soluble resources becomes limited, and thus their activity is also reduced (Manzoni et al., 2012b; Metze et al., 2023). Consequently, water availability is one of the primary factors regulating microbial communities and their processes (Sierra et al., 2015).

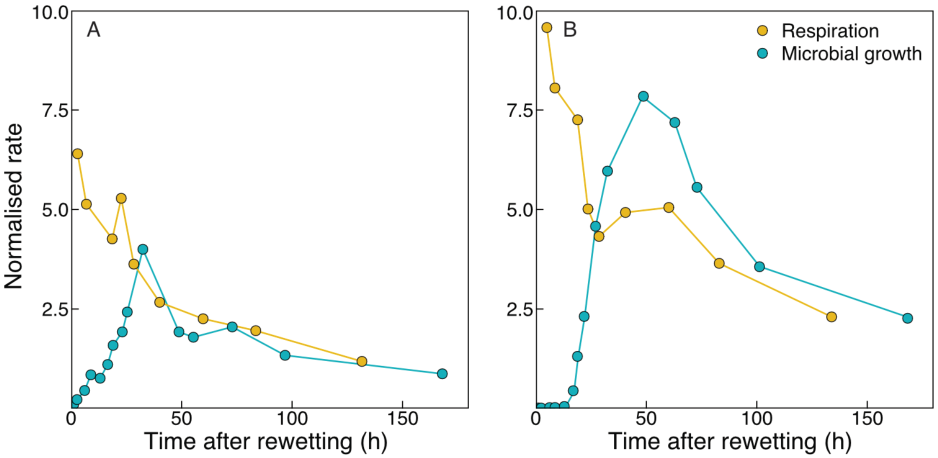

Figure 1. Different microbial growth and respiration patterns upon rewetting
(A) Microbial growth begins immediately following a linear response, which usually corresponds to a lower respiration pulse and faster growth recovery. (B) Microbial growth exhibits a lag period of no growth before exponential increase, corresponding to a larger respiration pulse and slower growth recovery. Growth and respiration rates are normalised to the rates of an undisturbed control soil.

No drought lasts forever. Eventually it will rain. Rewetting triggers fascinating dynamics of microbial activity in short time periods, often ranging from hours up to a few days (Göransson et al., 2013). Immediately after rewetting, there is a pulse of soil respiration (Barnard et al., 2020; Jarvis et al., 2007; Kim et al., 2012). Although many studies have assessed soil respiration after rewetting, far fewer have focused on microbial growth. Surprisingly, growth rates are remarkably low after rewetting, despite high rates of respiration. As such, after rewetting respiration and microbial growth are uncoupled (Blazewicz et al., 2014; Brangarí et al., 2020; Göransson et al., 2013; Iovieno & Bååth, 2008; Figure 1). The low growth rates may be due to either low survival after rewetting (Van Gestel et al., 1993) or that dormant microorganisms need time to become active (Iovieno & Bååth, 2008). A microbial community that starts growing immediately after rewetting, usually corresponds with a lower respiration pulse and generally recovers growth faster than a community with an initial lag period of no growth (Figure 1).

What can influence microbial responses to drought disturbances?

The history of drought exposure can influence how microbial communities respond to a subsequent drought event through shifts in the community composition and physiological traits (Allison, 2023; Evans & Wallenstein, 2014; Bardgett & Caruso, 2020). Drought can also affect microbial communities through interactions with the soil environment (Bardgett & Caruso, 2020; Philippot et al., 2021) (Figure 2).

Microbial communities that have already experienced drying and rewetting might be more resistant and resilient than those that have not experienced drought (Evans et al., 2022; Müller & Bahn, 2022). Higher drought exposure both in rain-exclusion field experiments (de Nijs et al., 2019; Evans & Wallenstein, 2012; Göransson et al., 2013) and in laboratory drying and rewetting cycles have demonstrated a shift towards faster microbial growth recovery and lower respiration rates (Cordero et al., 2023; de Nijs et al., 2019; Evans & Wallenstein, 2012; Leizeaga et al., 2022; Meisner et al., 2015). However, laboratory rewetting cycles did not consistently change microbial biomass (Evans & Wallenstein, 2012; Sawada et al., 2017). Furthermore, higher exposure to drying and rewetting events can induce a shift in microbial community composition towards taxa that perform better under drought (Barnard et al., 2015; Delgado-Baquerizo et al., 2017; Evans et al., 2014; Evans & Wallenstein, 2014; Metze et al., 2023; Ochoa-Hueso et al., 2018) and induce changes in extracellular enzyme activities (Bastida et al., 2017; Bouskill et al., 2016).

Microbial responses to drought disturbances may also depend on other environmental factors including differences in plant communities and soil properties (Figure 2). For example, plant communities are known to shape microbial community composition and influence their capacity to resist and recover from drought (Bardgett & Caruso, 2020; Müller & Bahn, 2022; Oram et al., 2023). Plants provide varying resource quality and quantity that microbial communities utilise, where easily available resources, such as root exudates, can support microbial strategies to cope with drought (Bennett et al., 2020; Eisenhauer et al., 2017; Lange et al., 2015; Xi et al., 2023).

Additionally, soil pH is known to be a strong regulator of microbial activity and community composition (Cowan et al., 2022; Delgado-Baquerizo & Eldridge, 2019; Fierer & Jackson, 2006; Rousk et al., 2010; Zhou et al., 2020). More acidic environments can reduce microbial recovery after rewetting (Li et al., 2023), possibly as soil microorganisms need to maintain both proton gradients and osmotic potential across the cell membrane (Lund et al., 2020). Moreover, soils rich in organic matter or with higher clay content can retain water more, enhancing moisture availability during drought. However, this can also make microbial communities more sensitive once the soil eventually dries out (Bardgett & Caruso, 2020; Fierer et al., 2003; Kaiser et al., 2015). Further, many factors are connected and influence each other. For example, both plant communities and drought history can modify the soil environment, including changes in soil pH and the quantity and quality of organic matter (Bardgett & Caruso, 2020; Malik et al., 2018).

In summary, the impact of drought on microbial communities may depend on both drought disturbance history and the soil environment they are exposed to, as well as the interaction between these (Figure 2). Therefore, to fully understand microbial resistance and resilience to drought disturbances, it is essential to consider how microbial responses vary across different environments with different plant communities and soil properties.

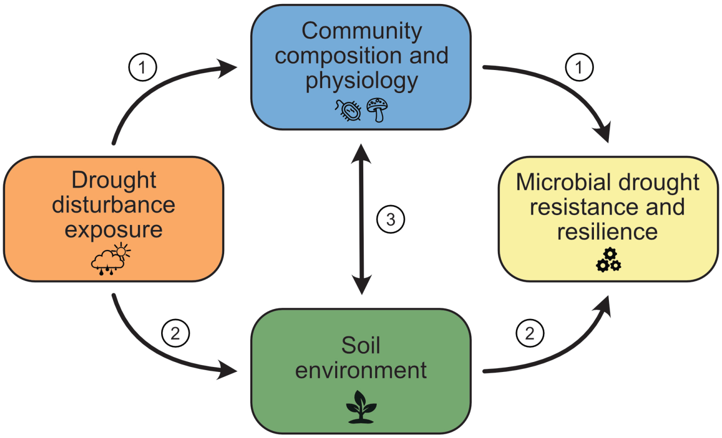

Figure 2. Drought disturbances can shape microbial drought resistance and resilience through multiple pathways

Differences in drought disturbance exposure can shape the microbial community composition and physiological traits, thereby affecting their resistance and resilience (path 1). Drought disturbances can also affect and interact with the soil environment, which can alter microbial drought resistance and resilience (path 2). The soil environment can also shift the microbial community composition, while microbial communities, in turn, can modify their surrounding environment (path 3).

Aim and objectives

The aim of this thesis was to identify how microbial responses to drought disturbances were shaped by differences in historical drought exposure across climates and by differences in the soil environment, including plant communities and soil properties. To achieve this, I determined microbial growth and respiration stability to drought by assessing resistance (i.e., tolerance to drought) and resilience (i.e., recovery after rewetting). I addressed the following objectives:

- Determined how historical drought exposure influences microbial drought resistance and resilience (**paper I**, **paper II**, **paper III**, **paper IV**).
- Identified whether additional environmental factors can shape microbial functional stability (**paper II**, **paper III**, **paper IV**).
- Resolved whether differences in microbial responses after rewetting affect the soil carbon balance (**paper I**, **paper III**).
- Investigated the link between microbial community composition and functional responses to drought disturbances (**paper I**, **paper II**).

Concepts and study design

Defining resistance and resilience

To understand how microbial communities respond to drought disturbances, different approaches can be used. One approach is to use stability, which most commonly includes the components resistance and resilience (Bardgett & Caruso, 2020; Griffiths & Philippot, 2013; Philippot et al., 2021; Shade et al., 2012). In this thesis, I focused on the stability of microbial growth and respiration. By measuring the functional response of active microorganisms, we can predict shifts in community-level traits linked to drought (Hicks et al., 2022a).

Microbial communities can withstand drought by maintaining their activity at lower moisture levels i.e., resistance. In this thesis, I defined resistance as the soil moisture level when microbial rates were inhibited by 50% (Figure 3A). This is based on dose-response curves which describe when a concentration, or in this case level of soil moisture, reduces a process by 50%, called inhibitory concentration (IC_{50}). The IC_{50} value was used to estimate microbial drought resistance, where lower IC_{50} values indicate higher drought resistance and vice versa, higher IC_{50} values indicate lower drought resistance. Furthermore, microbial communities can recover back towards their original state when the drought ends with rewetting i.e., resilience. Here, I defined resilience as the time taken for microbial growth to recover back to pre-disturbance rates of an undisturbed control soil (Figure 3B). However, in several samples microbial communities shifted their baseline after rewetting and did not fully recover back to the control, which has been widely observed (Müller & Bahn, 2022). To overcome this, I estimated resilience as the time when growth reached 50% of the control. This level is arbitrary, as any level of recovery can be chosen, but it enables a quantitative comparison between different soil samples. Shorter recovery times indicates a higher drought resilience and conversely longer recovery times a lower resilience. These definitions were used in **paper I**, **paper II** and **paper III** (Figure 3). In **paper IV**, a different definition of stability for growth and respiration was adapted to evaluate different aspects of stability within a multidimensional stability framework. The six stability components included resistance, resilience, compensatory recovery, final recovery, temporal stability and overall stability (see "*Multiple aspects of stability in response to plant diversity*"). In this thesis, I used the definition of drought resistance as the moisture level when microbial growth was inhibited by 50% and drought resilience as the time taken for microbial growth rates to recover back to 50% of pre-disturbance levels (Figure 3), if not otherwise stated.

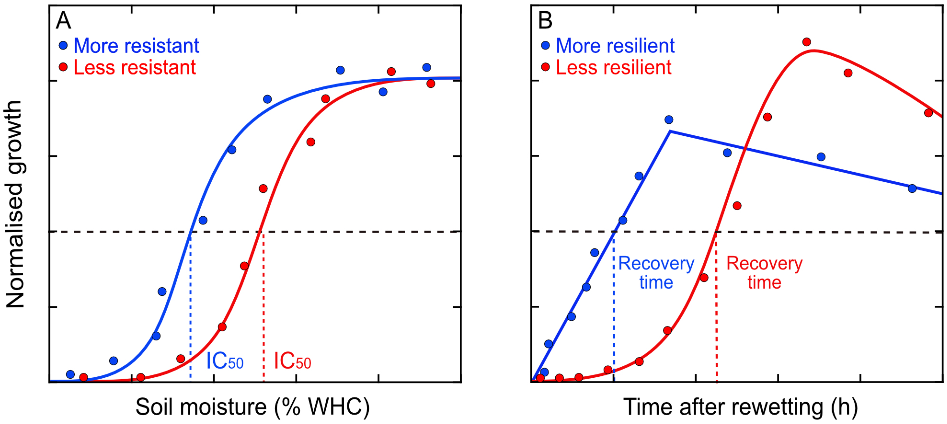

Figure 3. Conceptual illustration of how microbial drought resistance and resilience has been assessed in this thesis

(A) Microbial drought resistance was estimated as the soil moisture when growth was reduced by 50% (IC_{50}, black dashed line). The blue curve represents a more drought resistant community (lower IC_{50}), that can maintain growth at lower soil moisture (% water holding capacity, WHC), while the red curve shows a less resistant community (higher IC_{50}). (B) Microbial drought resilience was estimated as the time taken for growth to recover back to 50% of pre-disturbance rates (black dashed line). The blue curve represents a more resilient community (faster recovery time), compared to the red curve that shows a less resilient community (slower recovery time).

Experimental setups

I have used a combination of geographical gradients (**paper I** and **paper II**) and field manipulation experiments (**paper I**, **paper III** and **paper IV**) to understand how drought disturbances affect microbial communities (Figure 4). Geographical gradients resemble more natural, but at the same time more complex conditions with several interacting factors. Manipulation field experiments instead offer more controlled settings that allow the investigation of specific factors. In **paper I**, a grassland precipitation gradient across Sweden was used to investigate how differences in mean annual precipitation affected microbial communities. Precipitation was the main factor varying across this gradient. In **paper I**, we used five sites with field rain exclusion shelters to test the effect of reduced precipitation. All sites across the precipitation gradient were also sampled two times for a separate experiment investigating the effect of a soil tillage disturbance (not included in a paper). In **paper II**, I used a climate gradient across Europe to investigate whether climate history and soil properties (e.g., pH, organic matter, and soil texture) determined microbial drought resistance and resilience. To achieve this, sites were selected to represent a broad range of different climates and soil properties. Differences in climate reflect differences in drought exposure along the two gradients, where drier sites have higher drought exposure than wetter sites. To quantify how dry each site was, I used an aridity index, which allows for comparison across different climates and experiments. The aridity index is calculated as the ratio of precipitation to potential evapotranspiration, where lower values indicate drier climates. In this context, drylands are defined as having an aridity index below 0.65 (Maestre et al., 2015), whereas humid climates have values above this threshold. All soils in **paper I** and most soils in **paper II** were located in humid climates (Figure 4).

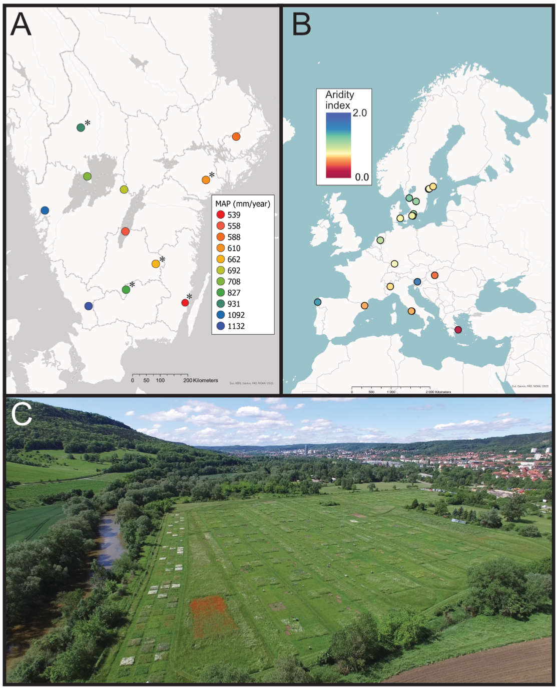

Figure 4. Overview of the different study systems used to assess microbial responses to drought (A) Precipitation gradient across Sweden, stars * represent sites sampled in **paper I**. All sites across the precipitation gradient were sampled in a separate experiment. (B) Climate gradient across Europe estimating climate as aridity index (**paper II**). (C) Plant diversity field experiment at the Jena Experiment (**paper III** and **paper IV**). Maps were produced in ArcGIS Pro (ESRI). Photo credit: the Jena Experiment.

In **paper III**, I used a long-term plant diversity experiment, the Jena Experiment, consisting of a gradient of plant species richness from monocultures up to 60 species mixtures, to investigate the effects of plant diversity on microbial resistance to drought. In **paper IV**, the same plant diversity experiment, the Jena Experiment, was used to assess how plant diversity affected several different stability components after a drought disturbance. Additionally, in both **paper III** and **paper IV**, two different soil depths were included. The topsoil experiences a higher frequency of drought and rewetting events compared to the subsoil, which allowed the investigation of how differences in drought exposure shape microbial responses to drought. Lastly, I also carried out an experiment to test whether warming affects microbial drought resistance by incubating soils from Greenland at different temperatures (not included in a paper).

Environmental legacy effects describe how the effects of historical conditions can persist in microbial communities and influence their responses to following environmental changes (Canarini et al., 2021; Evans et al., 2022; Hawkes et al., 2017; Müller & Bahn, 2022). In this thesis, I investigated how previous conditions shape microbial community responses following a drought disturbance (Figure 2). In particular, I focused on assessing microbial growth and respiration, as these serve as sensitive indicators of how microbial communities perceive changes in the environment. Throughout my experiments, microbial responses to drought were assessed in the same way using microcosms which allowed for high control of the soil moisture during the experimental period. Using the same drought and rewetting exposure allows us to directly compare microbial responses between samples from different ecosystems and environments. In each experiment, soils were first dried to estimate microbial drought resistance by measure microbial growth and respiration rates at different soil moisture levels from optimal moisture (approximately 50% water holding capacity, WHC) down to air-dried (2-6% WHC) (Figure 3A). Then, the air-dried soil samples were rewetted back to 50% WHC to assess microbial resilience to drought. To capture the dynamic response patterns (Figure 1; Figure 3B), I measured microbial growth and respiration at high time resolution up to one week after rewetting (Brangarí et al., 2022; Göransson et al., 2013; Iovieno & Bååth, 2008).

Main findings

In this chapter, I tested how drought exposure history and a range of additional environmental factors, including plant diversity and soil properties, influenced microbial responses to drought. I also examined the effects of other soil disturbances, investigated the microbial carbon use after drought and assessed whether there are links between microbial community composition and function. Finally, I compared the effect sizes to better understand which factors drive resistance and resilience to drought. The results are primarily from my four papers, but also includes insights from other projects carried out during my PhD to place these findings in a broader context.

Effects of drought history on microbial drought responses

Bacterial resistance and resilience to drought depend on climate

The climate across ecosystems can influence the drought history, where drier climates are exposed to more frequent and intense drought events compared to wetter climates. How do differences in historical drought exposure across climates influence microbial responses to drought disturbances? In both **paper I** and **paper II**, from the Swedish precipitation gradient and the European climate gradient, respectively, we observed increased resistance and resilience of bacterial growth in soils from drier ends of the gradients. In contrast, fungal growth did not exhibit any trend across the gradients (see "*Fungi and bacteria respond differently to drought disturbances*"). In another study across Europe, the resistance and resilience of microbial community composition to drought were lower from wetter climates than in those from drier climates (Knight et al., 2024). Wetter climates that have experienced less severe drought events also showed a larger reduction in microbial biomass when exposed to rewetting than those from drier climates (Sawada et al., 2017). Additionally, respiration was more sensitive to drought at sites with historically wetter conditions (Hawkes et al., 2017). Together, these findings indicate that a history of higher drought exposure can select for microbial communities with increased resistance and resilience (Evans et al., 2022; Figure 2).

The effects of drought on microbial communities have often been studied in drylands, as these ecosystems regularly experience prolonged drought periods (Maestre et al., 2015; Maisnam et al., 2023), and it has been found that shifts in microbial community composition, diversity, and function depend on aridity on a global scale (Delgado-

Baquerizo et al., 2017; Maestre et al., 2015). However, humid regions have received less attention, despite predictions that many humid areas will experience more severe drought and rainfall events (Christensen et al., 2007). Studies across dryland gradients revealed that neither resistance and resilience of microbial growth and respiration (Leizeaga et al., 2021), nor community composition (Dacal et al., 2022) were affected by differences in drought history. Additionally, respiration and extracellular enzyme activity showed similar responses to drying and rewetting across a semi-arid precipitation gradient (Tiemann & Billings, 2011). Microbial communities in drier climates may already be adjusted to frequent drought events, resulting in a higher proportion of drought-tolerant taxa that are better at coping with drought. Thus, the effects of drought may be less pronounced in dryland ecosystems than in more humid areas (Dacal et al., 2022). The sites from **paper I** and **paper II** were mostly from humid climates, where bacterial communities perceive drought as a more severe disturbance as illustrated by lower drought tolerance and longer recovery times. In other words, bacterial communities in wetter climates are generally more sensitive to drought disturbances than those in drier climates.

In **paper I**, we also investigated the effect of rain exclusion shelters, but the microbial resistance and resilience were comparable to those in the control soils across the precipitation gradient. The rain shelters reduced precipitation by 19% on average. However, in **paper I**, an effect size of around 30% was estimated to be required to detect changes in resistance and resilience, which could explain the lack of different responses to drought. These results suggest that there could be a threshold for inducing differences in resistance and resilience. Consistent with this, rainfall manipulation experiments in humid sites with a reduction of more than 30% precipitation have found a shift in microbial resilience (de Nijs et al., 2019; Göransson et al., 2013), suggesting that this threshold might be valid in humid ecosystems. This threshold may be different in dryland ecosystems. In drylands, a 35% reduction in rainfall resulted in no change in microbial resistance and resilience to drought (Dacal et al., 2022), and a 25% reduction did not change microbial growth recovery (Hicks et al., 2025). Whereas with a rainfall reduction of 40%, there was a shift from growth allocation to drought tolerant strategies (Malik et al., 2020b). It is possible that in humid climates, microbial communities are less used to drought and hence, a smaller reduction in rainfall is needed to detect differences in resistance and resilience compared to dry climates.

Are the observed patterns of bacterial growth resistance and resilience to drought in relation to the aridity index in **paper I** and **paper II** consistent? To test this, I combined data from these two papers with resistance from the topsoil (0-10 cm) in **paper III** and resilience in the topsoil (estimated as recovery time) from **paper IV**. In addition, I used other experiments carried out during my PhD. These include the control soils from two samplings along the Swedish precipitation gradient in August 2021 and 2023 and a drought resistance experiment with soils from Greenland at ambient temperature (see

"*Exposure to other disturbances may affect microbial drought responses*"). By integrating the results, I could assess whether the patterns in **paper I** and **paper II** remain on a larger scale. Altogether, both bacterial resistance and resilience increased as the climate became drier (Figure 5). Thus, climate (estimated as aridity index) appears to determine both bacterial resistance and resilience to drought.

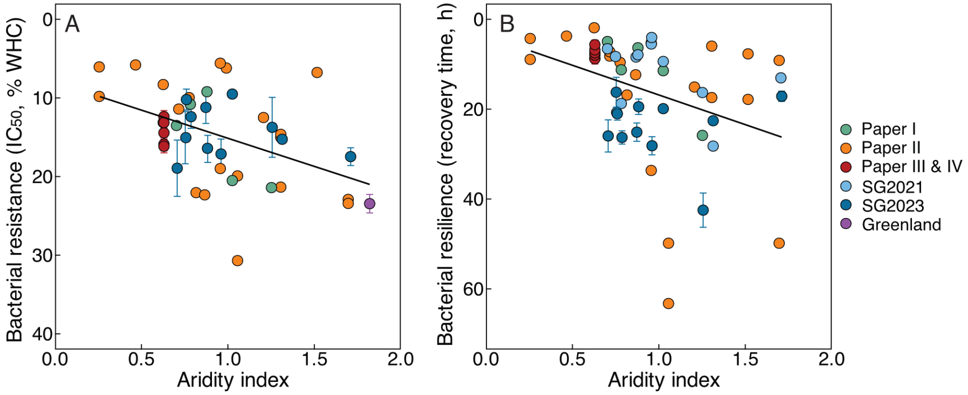

Figure 5. Bacterial growth stability to drought decreases in wetter climates
Bacterial growth stability to drought from my different PhD projects. (A) Bacterial drought resistance (ability to withstand drought) estimated as the soil moisture when bacterial growth rates were reduced by 50%. (B) Bacterial drought resilience (recovery time after rewetting) estimated as the time it takes for bacterial growth to reach 50% of an undisturbed control soil. Higher aridity index indicates more humid climates. SG = Swedish precipitation gradient sampled in August year 2021 (for resilience) and 2023 (for resistance and resilience). Samples from Greenland included estimates of drought resistance.

Other intriguing insights also emerge when these results are combined. First, there are differences in bacterial drought responses between the years across the Swedish precipitation gradient when comparing **paper I** with the sampling in August 2021 and 2023 (see "*Differences in drought resistance and resilience across years*"). Second, the patterns of bacterial resistance and resilience to drought remains quite variable to the aridity index, suggesting that other factors may interact with drought and influence their responses (see "*Impact of other factors on microbial resistance and resilience to drought*" and "*Plant diversity effects on microbial responses to drought*"). Third, the variable patterns of resistance and resilience may also reflect that the aridity index is a relatively insensitive measure of short-term or seasonal fluctuations in soil moisture. These fluctuations, including recent drought or rainfall events, may have a stronger influence on microbial drought responses (Wang et al., 2022; Yuste et al., 2014). Therefore, drought intensity or frequency could be better predictors of microbial resistance and resilience to drought. For instance, temperature traits across the same European climate gradient as in **paper II** were better explained by the warmest month of the year rather than by the mean annual temperature (Cruz-Paredes et al., 2023).

Moreover, soil moisture below 30% WHC has been shown to alter microbial growth recovery after rewetting in soils from both the UK and Greenland, while above this level rewetting had no effect on growth (Meisner et al., 2017). One might assume that time periods below this moisture level could induce shifts in microbial drought resistance and resilience. Hence, one appropriate metric could be the time the moisture is below 30% WHC or the number of rewetting events that fluctuate below this moisture level. However, identifying an appropriate measure of drought exposure requires a better understanding of whether this threshold is valid in other ecosystems. Despite these limitations, the aridity index is valuable for assessing the influence of long-term climate patterns on microbial communities and evaluating potential changes over time under climate change.

In this thesis, I covered climates across the continental scale in Europe that included mostly humid sites. To better understand global patterns of microbial drought resistance and resilience, a natural next step would be to expand the gradients and include more ecosystems. Drylands are one of the ecosystem types that could be included. Globally, drylands are estimated to cover 45% of the land surface (Prăvălie, 2016) and are expected to expand by 11-23% by the year 2100 (Huang et al., 2016). As drylands expand, understanding microbial responses to drought is becoming increasingly important in these systems. Another key ecosystem is the Arctic, which is experiencing one of the most rapid changes in climate, with temperatures increasing at nearly twice the global rate, and at the same time it holds the largest soil carbon stock (Jansson & Hofmockel, 2020). Thus, shifts in microbial communities and functions due to drought disturbances in the Arctic could impact carbon emissions from the soil and consequently the global carbon cycle. Knowledge about tropical ecosystems is also limited regarding microbial responses to drought, and although tropical areas tend to be humid throughout the year, the variation in precipitation is expected to increase (Chiang et al., 2021; Trenberth et al., 2014). By extending the range of ecosystems studied, it may be possible to identify global patterns of microbial growth resistance and resilience.

Soil depth influences microbial functional stability to drought

Microbial communities and their functions vary with depth along the soil profile, driven by differences in resources, water availability, and temperature (Engelhardt et al., 2018; Peng et al., 2025; Tecon & Or, 2017). For example, the quality and quantity of soil organic matter are higher in the topsoil compared to the subsoil (Eisenhauer et al., 2017; Lange et al., 2023; Mellado-Vázquez et al., 2016; **paper III**). Interestingly, microbial communities that are separated by only 10-20 cm in depth can be as different from each other as between sites (Eilers et al., 2012). In line with this, in **paper III** at the Jena Experiment, we found that small changes in depth between the topsoil (0-10 cm) and subsoil (10-30 cm) had on average one third higher microbial growth and two times higher microbial respiration and microbial biomass in the topsoil (**paper III**). Differences in soil depth can influence drought exposure history, as the topsoil is exposed to more frequent moisture fluctuations due to higher rates of evaporation, water uptake from roots, and precipitation than deeper soil layers. Similarly as along the geographical gradients (Figure 5), we expected that a higher frequency of drought exposure would select for microbial communities with higher drought resistance and resilience in the topsoil compared to deeper soil layers (Brangarí et al., 2022). According to these expectations, in **paper III** and **paper IV** there was a significant difference in stability with soil depth. Microbial growth resistance was lower in the subsoil across all plant diversity treatments with a mean IC_{50} value of 12.8% WHC in the topsoil and 15.1% WHC in the subsoil (**paper III**). A similar pattern was observed for microbial growth resilience, with a mean recovery time of 7.2 h in the topsoil and 9.5 h in the subsoil, using data from **paper IV** (Figure 6). Further, different aspects of stability measured for both growth and respiration in **paper IV** (see "*Multiple aspects of stability in response to plant diversity*") were lower in the subsoil than in the topsoil. Taken together, these lines of evidence suggest that soil depth is a strong determinant of microbial functional stability to drought, likely due to differences in drought history that shape microbial community composition (Figure 2).

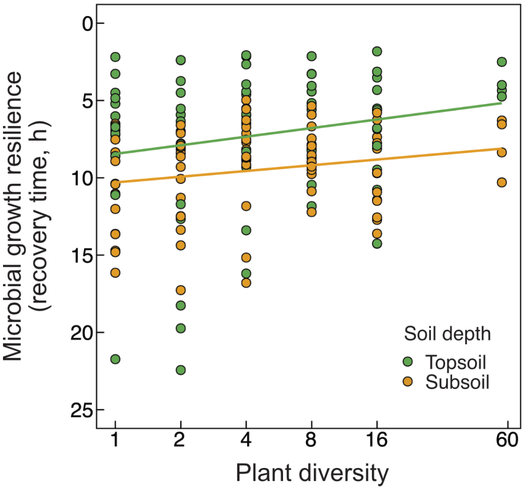

Figure 6. Microbial growth resilience was higher in the topsoil and increased with plant diversity The effect of soil depth on microbial growth resilience to drought in relation to plant species diversity treatments (from monocultures to 60 plant species mixtures). Green colour represents the topsoil (0-10 cm) and orange colour represents the subsoil (10-30 cm). Resilience was estimated as the time taken for microbial growth to recover to 50% of an undisturbed control soil using data from **paper IV**.

Differences in drought resistance and resilience across years

The first sampling along the precipitation gradient in Sweden was conducted in May 2021 to assess resistance and resilience and included five sites (**paper I**; Figure 4). All sites across the gradient were also sampled in August 2021 to assess drought resilience and in August 2023 to assess both drought resistance and resilience. Comparing the results from these three sampling times revealed some interesting differences.

First, the drought resilience in May 2021 from **paper I** and in August 2021 showed relatively consistent recovery times (Figure 5). The lack of differences in bacterial growth resilience between the two time points suggests that the difference in precipitation between spring and summer might not have been sufficient to induce changes in bacterial drought resilience. In contrast, bacterial drought resilience varied between the years. Samples from 2021 were more resilient than those from 2023 (Figure 5). One possible explanation could be differences in drought exposure between the relatively dry summer of 2021 compared to the more wet summer of 2023, particularly during the two months prior to sampling (Figure 7). A moisture level above 30% WHC has been shown to not induce differences in bacterial recovery times (Meisner et al., 2017; **paper I**). In both the summer of 2022 and 2023, the soil moisture was above this threshold for the majority of the time, implying that the microbial community was rather adjusted to moist conditions and therefore showed longer recovery times. There is evidence that one summer drought can induce large shifts in microbial community composition (Wang et al., 2022) and extracellular enzyme activities (Bouskill et al., 2016). As such, it could be assumed that bacterial drought responses also can shift quite rapidly, for example during a drier spring or a wet summer leading to different responses between the two years. Whereas, some studies have shown that it can take several years for the microbial community composition to adjust to small increases in precipitation within the normal climatic variability (Bell et al., 2014; Cruz-Martínez et al., 2009). Therefore, it is possible that larger short-term differences in precipitation is needed to shift microbial drought responses. Indeed, bacterial community composition was mainly determined by short-term more intense drought events rather than long-term but less intense droughts (Yuste et al., 2014).

Second, bacterial drought resistance showed less consistent patterns between 2021 and 2023 (Figure 5). This is interesting because one might expect similar shifts in resistance and resilience. Long-term drought can result in more gradual changes in microbial physiology and composition, while short-term rewetting can induce faster microbial turnover and shifts in community composition (Blazewicz et al., 2020; Inamine et al., 2022; Koch et al., 2018). Indeed, rewetting caused larger shifts in soil microbial community composition than reduced precipitation (Wang et al., 2022) and summer drought during 18 years increased growth resilience but not resistance (de Nijs et al., 2019). This suggests that rewetting could be the driving force shaping microbial resilience by causing more rapid shifts of soil microbial community composition than drought. Consequently, changes in drought resistance may take longer than resilience.

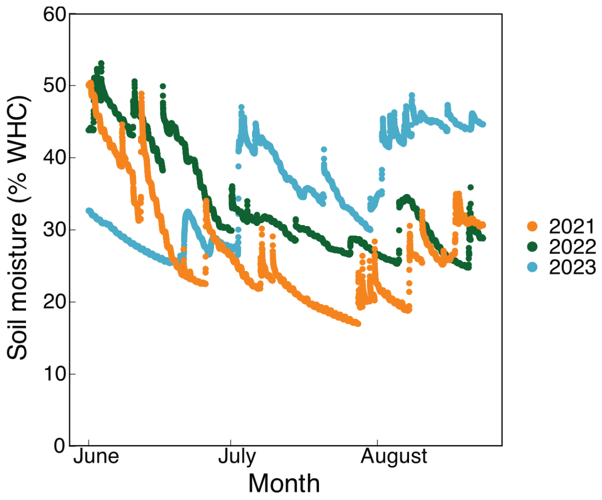

Figure 7. Soil moisture differences during the summer of 2021, 2022, and 2023
Soil moisture as % water holding capacity (WHC) during summer 2021, 2022, and 2023 at the 558 mm/year mean annual precipitation site across the Swedish precipitation gradient (see figure 4).

Together, these results raise several questions: How much time do microbial communities need to adjust to differences in soil moisture? What drought intensity is needed to induce a shift in microbial community responses? How long does the effect of drought persist? How much can the responses to drought vary between years or seasons? In a future study it would be interesting to monitor microbial responses across different seasons, to assess whether recent weather events can explain potential shifts in resistance and resilience. Tracking microbial responses over seasons could also reveal how long a shift in resistance and resilience remain during the year.

Plant diversity effects on microbial responses to drought

Plant diversity can shape microbial resistance and resilience

The impact of biodiversity on ecosystem functions has been studied systematically during the last decades and multiple studies have reported positive effects of diversity on ecosystem functions (Eisenhauer et al., 2024; Lange et al., 2023; Tilman et al., 2014). For instance, higher plant diversity has been shown to enhance aboveground primary production, as well as belowground microbial biomass and respiration rates (Chen et al., 2019; Eisenhauer et al., 2010, 2013; Prommer et al., 2020; Zheng et al., 2024). As a result, plant diversity can influence microbial processes regulating decomposition and soil carbon cycling (Fornara & Tilman, 2008; Hooper et al., 2012; Lange et al., 2015). A growing number of studies have also demonstrated a positive relationship between plant diversity and stability (Craven et al., 2018; Eisenhauer et al., 2024; Gross et al., 2014; Tilman et al., 2006). For example, higher plant diversity has been shown to buffer the effects of drought disturbances by enhancing the tolerance and recovery of plant primary production (Isbell et al., 2015; Tilman et al., 2014; Tilman & Downing, 1994; Wagg et al., 2017). This raises the question of whether plant diversity can also influence microbial functional stability to drought.

In **paper III** and **paper IV**, we tested if plant diversity can modulate microbial responses to drought. We found that higher plant diversity had a positive effect on both microbial growth resistance (**paper III**) and resilience (data from **paper IV**; Figure 6). There are several possible explanations for these patterns. First, plants are the primary contributors of carbon entering the soil, and higher plant diversity increases root biomass and, in turn, the amount of carbon input via root exudates (Eisenhauer et al., 2013; Mueller et al., 2013; Ravenek et al., 2014). This carbon may support microbial communities with strategies to cope with drought. In line with this, increased carbon availability has been associated with greater microbial tolerance to drought (Bennett et al., 2020; Li et al., 2022; Xi et al., 2023). Additionally, in **paper III**, we found evidence that microbial communities use a larger proportion of plant-derived carbon at higher plant diversity. Together, these findings suggest that plant diversity can promote microbial resistance and resilience to drought by improving access to carbon resources. Second, plant diversity may enhance microbial functional stability by promoting a more heterogeneous soil environment, which can support higher microbial diversity (Eisenhauer et al., 2018; Lange et al., 2015). The likelihood that some taxa can maintain activity during drought disturbances increases with higher microbial diversity (Loreau et al., 2021). Consistent with this, microbial diversity has been shown to be important for maintaining soil functions (Bardgett & van der Putten, 2014; Peng et al., 2025; Wagg et al., 2014; Yang et al., 2022) and may therefore contribute to higher drought resistance and resilience. Our preliminary results show that bacterial evenness increased with higher plant diversity, while the total number of taxa remained unchanged (Figure 8). These results are similar to those reported by de Souza et al. (2024), Li et al. (2022) and Zhou et al. (2020), suggesting that plant diversity can support a more even distribution of microbial taxa rather than higher richness. Additionally, uneven microbial communities were also found to be less resistant to salinity disturbances (Wittebolle et al., 2009). Together, this suggest that evenness can play a role in enhancing drought stability.

To further explore the role of plant diversity, a valuable next step would be to test whether the positive effects on microbial resistance and resilience also occur in systems with living plants, using either field or greenhouse experiments. Additionally, it is not known if the effect of plant diversity extends to natural grasslands and forests, and whether plant diversity can also buffer microbial responses to other disturbances, such as heatwaves.

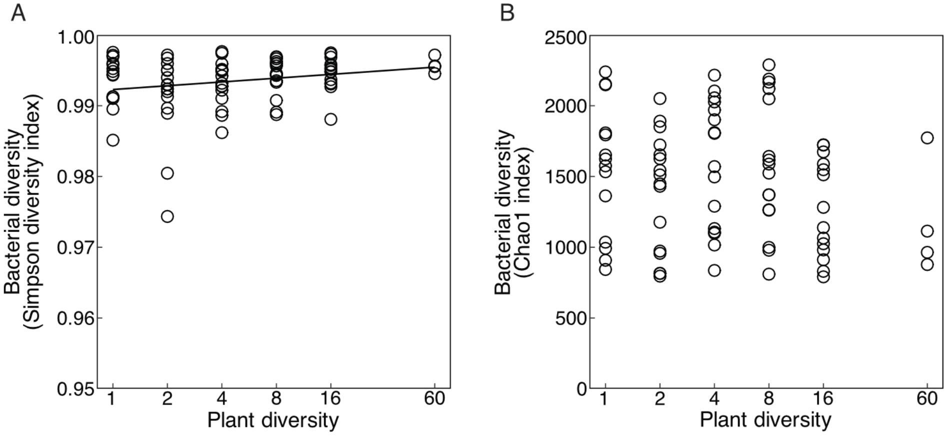

Figure 8. Relationship between bacterial diversity indices and plant diversity
(A) Simpson index (accounting for both number of taxa and their evenness) and (B) Chao1 index (estimate the total number of taxa particularly accounting for rare species). Data from Shangshi Liu.

Multiple aspects of stability in response to plant diversity

Stability is central to understand the ecosystem ability to resist or recover from disturbances (Kéfi et al., 2019). Most studies have focused on a single aspect of stability in response to disturbances, commonly resistance or resilience (Donohue et al., 2016). However, single aspects might not fully explain the ecosystem response to a disturbance (Hillebrand et al., 2018). One approach to estimate the overall ecosystem impact of a disturbance is to assess multiple aspects of stability. In the proposed framework by Hillebrand et al. (2018) and Urrutia-Cordero et al. (2022), multiple functional stability components were evaluated. The advantage of this framework is the ability to compare different stability components across disturbances and assess relationships between them. Adapting this framework, in **paper IV**, we investigated whether plant diversity affected multiple microbial functional stability aspects after rewetting. The stability components tested were resistance, resilience, compensatory recovery, final recovery, temporal stability and overall stability (Figure 9). Surprisingly, in **paper IV**, compensatory recovery and temporal stability of growth were reduced at higher plant diversity, while the other stability components for growth were unaffected by plant diversity. In this paper we also assessed the stability of respiration, which were all unaffected by plant diversity.

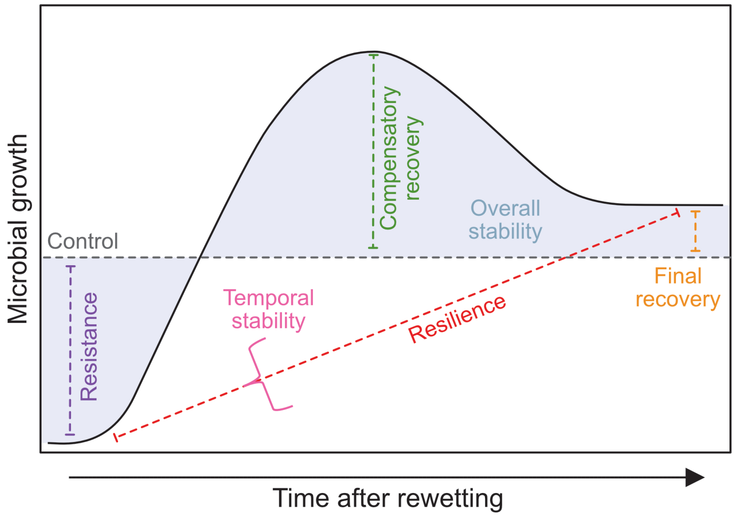

Figure 9. Conceptual representation of the six stability components used to asses microbial growth responses to drying and rewetting in paper IV
Resistance was defined as the difference between the drought disturbed and control treatment at the initial measurement point. Final recovery was the degree of recovery at the end of the experiment. Compensatory recovery was the difference between the maximum growth and control. Resilience was defined as the rate of recovery, and estimated as the slope of the curve between the first and last measurement. Temporal stability was calculated as the standard deviation of the residuals around the resilience curve. Overall stability was measured as the area of the curve deviating from the control over the measured time period.

Why do different growth stability measurements differ in their response to plant diversity? The choice of stability metric and how they are defined might affect the outcome of the results (Kéfi et al., 2019; Renes et al., 2020). For instance, the lack of relationship between microbial growth resistance and plant diversity in **paper IV** may be a result of air-drying the soil. This pushes microbial communities towards their physiological limits, resulting in low initial microbial growth rates across all diversity treatments. However, the ability to maintain growth at lower moisture levels still depends on plant diversity (see **paper III** and Figure 3). Moreover, in **paper IV**, growth resilience was unaffected by plant diversity, likely because most soils showed similar resistance and final recovery. This could be explained by the fact that resilience is defined by resistance and final recovery (Figure 9). However, microbial communities recovered growth back to the control faster at higher diversity (resilience as defined in this thesis; Figure 6), likely as this metric is more sensitive to capture initial changes in growth rates during the first days after rewetting (Figure 3). Further, the compensatory recovery i.e., microbial overshoot after rewetting, increased at higher plant diversity (**paper IV**). This may be due to higher carbon resource availability at higher plant diversity (Eisenhauer et al., 2013; Mueller et al., 2013; Steinauer et al., 2016), which could fuel higher microbial growth rates. A smaller overshoot in growth also reduced the deviation from the control, correlating to increased overall stability (Figure 9).

These results are also interesting given that we did not find a trade-off between microbial resistance and resilience for microbial growth in **paper IV**. Similarly, in **paper I** and **paper II** there was no trade-off in microbial growth resistance or resilience, as well as when comparing resistance (**paper III**) with resilience as recovery time defined in this thesis (Figure 3) from **paper IV**. This does not match common expectations within the field of ecology. Several studies have argued that there is a trade-off between resistance and resilience, as organisms can either optimise traits for tolerating drought or recovering after rewetting (de Vries et al., 2012; Hillebrand & Kunze, 2020; Matos et al., 2020; Orwin et al., 2006). One proposed reason is that differences in life history strategies give rise to trade-offs (Malik et al., 2020a). Slow growing microorganisms may be more resistant as they have a higher competitive ability at low resource availability, such as during drought, while fast growing microorganisms may be more resilient, as they have traits to maximise growth rates when resources are abundant, such as after rewetting (de Vries & Shade, 2013; Fierer et al., 2007; Orwin et al., 2006; Roller & Schmidt, 2015; Schimel et al., 2007). Drought resistant mechanisms like osmolyte production and spore formation, are also metabolically costly which might limit growth rates and recovery upon rewetting (Chen et al., 2021; Evans & Wallenstein, 2014; Malik et al., 2020a; Schimel et al., 2007). For instance, microbial growth rates were reduced at lower mean annual precipitation, reflecting larger investment in drought-tolerant strategies at drier sites (Foley et al., 2023). However, we did not find evidence that microbial growth exhibits a trade-off between being resistant or resilient to drought. Our results suggest that microbial taxa that have drought tolerant strategies not only survive drought, but are also ready to resume growth more quickly after rewetting. As such, if resistance is high, it requires less distance to recover back to the control. The microbial community may also consist of some taxa that have drought resistance traits, while others have resilient traits, resulting in both resistance and resilience being reflected at the community-level. For example, across British grasslands the microbial community consisted of both drought resistant and resilient taxa (Lavallee et al., 2024).

The role of plants during drought disturbances

So far, I have covered how drought history and plant diversity can influence microbial community responses to drought. However, plants have been absent from my study systems, and only their legacy effects have been considered. Naturally, this is a simplification. Plants play a crucial role in shaping microbial communities by providing resources such as root exudates and by regulating water and nutrient availability (Bardgett et al., 2014; Williams & de Vries, 2020). The amount of root exudates can increase under moderate drought, although the effects become variable under more severe drought (Preece & Peñuelas, 2016), or even decline under drought (Hou et al., 2025). Plants may buffer the effects of drought on microbial communities by providing recourses that can be used for drought tolerance strategies (Barnard et al., 2020; Canarini et al., 2017; de Vries & Shade, 2013; Karlowsky et al., 2018; Mellado-Vázquez et al., 2016). In plant-soil systems, drying and rewetting usually occur more slowly than in laboratory studies, which may give soil microorganisms time to produce osmolytes and activate strategies to deal with drought (Bouskill et al., 2016; Warren, 2016). In air-dried soils well below the permanent wilting point, plants cannot survive as their activity declines faster under water limitation than microbial activity, and as such the air-drying used in this thesis does not capture drought at an ecosystem scale (Barnard et al., 2020). When plants are present, differences in soil moisture between control and drought treatments might as a consequence be smaller (Canarini et al., 2017). Thus, including plants in our experimental systems can help resemble more realistic drought conditions.

To test the effects of plant diversity on both plant and microbial responses during drought, we set up a greenhouse pot experiment using common native Swedish grass species. In this experiment, we used two monocultures, one with a slow-growth strategy and one with a fast-growth strategy, as well as 8-species grass mixture (Figure 10). The grasses were grown for three months before being exposed to drying (down to 7% WHC) and rewetting (back to 50% WHC) during a total of four weeks. Plants with a slow-growth strategy tend to be more drought tolerant due to adaptations such as thicker leaves that can maintain function during drought, while fast-growing plants have lower resistance due to larger leaf area and water use (Oram et al., 2023; Reich, 2014; Wright et al., 2004). In line with this, the slow-growing grass in our greenhouse experiment had thicker leaves, lower leaf area, and higher root biomass compared to the fast-growing grass. Additionally, slow-growing plants might support microbial drought tolerance via continued input of root exudates, while fast-growing plants might support a higher microbial resilience via high rates of root exudation after rewetting (Oram et al., 2023; Williams & de Vries, 2020). Hence, these grasses might influence microbial communities differently during drying and rewetting. Similar to **paper III** and **paper IV**, we expected increased microbial resistance and resilience with higher grass diversity. In addition, we expected the slow-growing monoculture to increase microbial growth resistance but reduce resilience, with the opposite for the fast-growing grass.

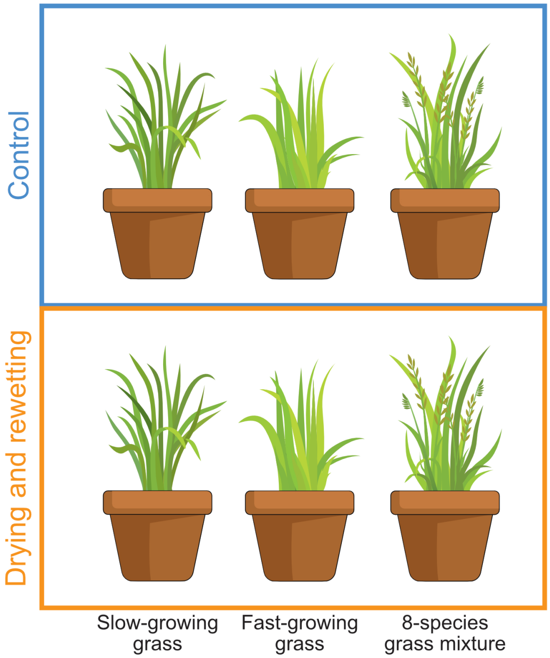

Figure 10. Experimental design of the greenhouse experiment
The greenhouse pot experiment has two grass monocultues, one with a slow-growth strategy (Schedonorus arundinaceus) and one with a fast-growth strategy (Agrostis stolonifera), and an 8-species grass mixture (Agrostis capillaris, Agrostis stolonifera, Festuca rubra, Festuca trachyphylla, Lolium perenne, Poa pratensis, Poa trivialis, Schedonorus arundinaceus). One group served as a control treatment and was kept at 50% WHC during the experimental period. The other group was exposed to a drying and rewetting event during a total of three weeks of drying (to 7% WHC) and one week of rewetting (to 50% WHC). Each treatment consisted of four replicates.

Preliminary results suggest that the grass with fast-growth strategy supported higher microbial growth resilience than the 8-species grass mixture and the slow-growing grass (Figure 11A). While respiration responses were more similar between the fast-growing grass and mixture than the grass with slow-grow strategy (Figure 11B). Another greenhouse experiment has reported variable effects on microbial resilience to drought, where plant functional groups had a stronger impact than plant species richness (Jayaramaiah et al., 2025). In addition, the positive effects of plant diversity on ecosystem stability to drought has been shown to strengthen over time during several years (Eisenhauer et al., 2010; Wagg et al., 2017, 2022). These results might explain why microbial growth resilience was unaffected by plant diversity in our greenhouse experiment. The higher microbial growth resilience with the fast-growing grass might be due to a slower recovery of the aboveground biomass than the slow-growing grass. This might reduce competition with plants for available resources, allowing microbial communities to recover growth faster. These results raise further questions about the interaction between plant and microbial communities during drought, which can be tested in a future field or greenhouse experiment. For instance, are plant functional groups more important than overall plant diversity in shaping microbial resistance and resilience? Do plant and microbial responses differ depending on drought intensity or duration? Do microbial drought responses differ in soils with plants compared to those without?

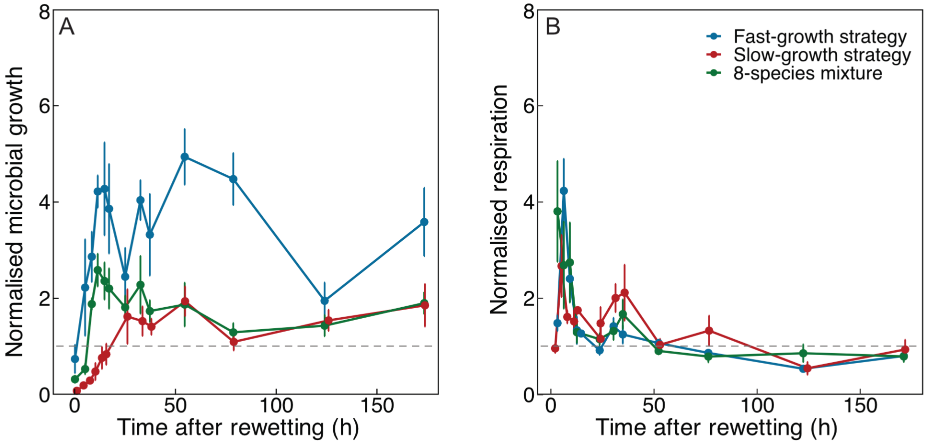

Figure 11. Microbial growth and respiration after rewetting in soils planted with different grasses
The greenhouse pot experiment measuring (A) microbial growth and (B) microbial respiration after rewetting. The experiment had two monocultures, slow-growth strategy (Schedonorus arundinaceus) and fast-growth strategy (Agrostis stolonifera), and an 8-species grass mixture (Agrostis capillaris, Agrostis stolonifera, Festuca rubra, Festuca trachyphylla, Lolium perenne, Poa pratensis, Poa trivialis, Schedonorus arundinaceus). The dashed line represents the undisturbed control.

Impact of other factors on microbial resistance and resilience to drought

Soil properties can affect drought resistance and resilience

In **paper II**, across the European climate gradient, a large proportion of the variation in drought resistance and resilience could not be attributed to differences in climate (Figure 5). This suggests that, aside from drought history, other factors may also influence the microbial drought responses (Bardgett & Caruso, 2020; Figure 2). Supporting this, we found that high soil pH coincided with high alpha diversity. This, in turn, enhanced bacterial resistance and resilience to drought. These results are consistent with Delgado-Baquerizo et al. (2017) and are in line with earlier findings showing a strong relationship between pH and microbial diversity (Delgado-Baquerizo & Eldridge, 2019; Fierer & Jackson, 2006; Zhou et al., 2020). High microbial diversity is important for maintaining soil functions by increasing the likelihood of taxa that can provide several functions (Bardgett & van der Putten, 2014; Loreau et al., 2021). In addition, physiological strategies to survive in acidic environments could lead to increased maintenance, thus lowering growth rates (Lund et al., 2020; Malik et al., 2018). Together, lower microbial diversity and acidic pH could explain a large fraction of the decrease in bacterial drought resistance and resilience in **paper II**. This implies that in ecosystems where low bacterial diversity is expected, such as boreal spruce forests with low pH, reduced bacterial resistance and resilience to drought may also be expected. In contrast, other soil properties such as soil texture and the soil C/N ratio were not important determinants of bacterial drought responses in **paper II**. Similarly, in soils across Britain, soil pH was a more important factor compared to clay content and C/N ratio (Malik et al., 2018), while in drylands carbon content plays a larger role in determining microbial responses to drought (Dacal et al., 2022; Maisnam et al., 2023).

Many environmental factors are correlated and interact with each other, making it difficult to disentangle what shapes microbial communities (Delgado-Baquerizo et al., 2017; Peng et al., 2025). For example, low pH is usually correlated with high organic matter and low carbon quality (defined as the total microbial carbon use) (**paper II**). One approach to better understand how individual factors affect microbial communities is to use controlled gradients that vary only in the factor of interest. This can be achieved using manipulation field experiments or gradients. Based on the results of **paper II**, we should first focus on how pH influences microbial drought resistance and resilience, and second, on differences in organic matter quality and quantity. In addition, a number of other factors may also interact with drought responses which have not been considered in this thesis. For instance, these could be factors that exert additional pressures on ecosystems due to human activities, including fertilisers, plastic pollution, and heavy metal contamination (Fierer et al., 2021; Yang et al., 2022). These factors might change microbial diversity and composition, and thus possibly alter their ability to cope with drought disturbances (Figure 2).

Exposure to other disturbances may affect microbial drought responses

In natural systems, microbial communities are often exposed to multiple different disturbances that can occur either at the same time or in cycles after each other. Although soils are complex systems, most studies have focused on the effects of a single disturbance (Philippot et al., 2021; Rillig et al., 2019). For instance, droughts often occur together with heatwaves (Trenberth et al., 2014). Exposure to multiple disturbances can make microbial communities more or less sensitive to another disturbance of the same or a different type (Cordero et al., 2023; Peng et al., 2025; Philippot et al., 2021; Renes et al., 2020). Investigating multiple disturbances and their interactions could improve our understanding of microbial functional stability under climate change.

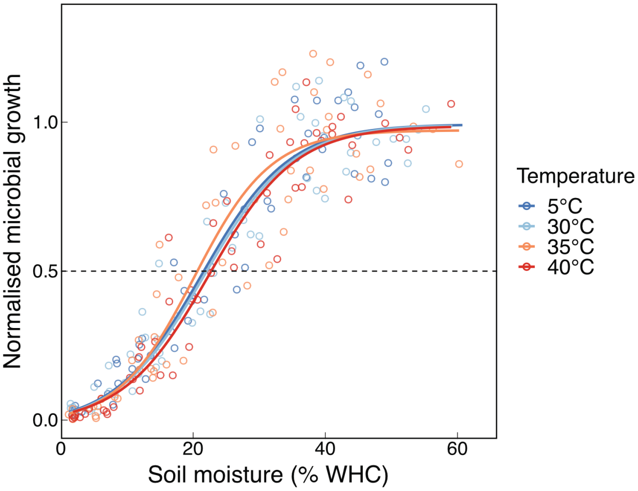

Figure 12. Higher temperature treatments did not influence microbial growth resistance
Microbial drought resistance in soils from Greenland. Soils were incubated at four different temperatures, 5°C (ambient temperature), 30°C, 35°C, and 40°C, for one month before assessing microbial resistance to drought. Drought resistance was estimated as the soil moisture when microbial growth was reduced by 50% represented by the dashed line.

To test whether increased temperatures affect microbial drought resistance, we exposed soils from Greenland to different temperatures for one month and then assessed the microbial resistance to drought. At higher incubation temperatures, there was a shift in growth towards warm-adapted communities (Tájmel, 2024). However, microbial growth resistance to drought was similar regardless of previous temperature exposure (Figure 12). This suggests that microbial community shifts that give rise to changes in thermal traits are not necessarily the same as those used to cope with drought. For example, common physiological adaptations to higher temperatures, including changes in cell membrane lipids and expression of heat shock proteins, differ from the mechanisms used to cope with drought (Griffiths & Philippot, 2013; Jansson & Hofmockel, 2020). This is in line with a study showing that protein functions affected by heat did not respond to drought (Knight et al., 2024). Additionally, another study found that the majority of actively growing taxa differed between temperature and drought treatments (Metze et al., 2023). Yet some overlap exists, microbial communities previously exposed to drought were more resistant and resilient to a subsequent heat-drought disturbance (Bérard et al., 2012). Interactions between different disturbances could be further studied by combining temperature and drought disturbances to simulate future climate conditions. The combination of higher temperatures and drought will result in faster soil drying and a more intense drought. This more intense disturbance may then result in microbial communities with lower resistance and resilience (Meisner et al., 2017).

Land use is also a key factor influencing microbial communities, driven by differences in plant inputs from roots and litter (Karlowsky et al., 2018; Malik et al., 2020b; Manzoni et al., 2012b) as well as by variation in management practices (Lavallee et al., 2024; Peng et al., 2025; Zhang et al., 2016). For instance, tilling, a common agricultural practice, disturbs the soil by mixing plant material and microbial communities from different soil layers. Tilling also disrupts soil aggregates, potentially releasing previously inaccessible resources (Denef et al., 2001; Six et al., 2000). These resource pulses caused by tilling may select for microbial communities that can quickly use available resources (Placella et al., 2012; Reischke et al., 2014) and thus recover growth faster after rewetting (Hicks et al., 2022b; Slessarev et al., 2020). Moreover, tilled agricultural soils have been shown to have faster microbial growth recovery than grasslands (Brangarí et al., 2022).

To investigate the effects of tilling, we established a field experiment where we disturbed the soil in spring (Figure 13) and compared microbial responses to drought at the end of the growing season with those in undisturbed soils along the Swedish precipitation gradient (Figure 4). I expected that microbial communities would be less sensitive to drought in tilled soils because of a combination of reasons (1) the additional resource pulse from disrupted soil aggregates might select for fast-growing microbial communities, (2) enhanced plant input through soil mixing that microorganisms can use, and (3) higher drought exposure in bare soil than in grass-covered soil leading to a shift towards more drought tolerant taxa. Surprisingly, no differences were observed in microbial growth resistance and resilience, or respiration responses between the tilled and control plots in August 2023 (Figure 13). What could explain the lack of differences in microbial responses between tilled and control plots? Preliminary results indicated that the soil moisture was similar between the control and tilled plots, suggesting that the tilled sites did not experience more drying and rewetting events, and therefore microbial communities were equally adjusted to moisture fluctuations (Brangarí et al., 2022). Moreover, I tested if resource release from soil aggregates affected microbial drought resilience. To do this, soil aggregates were disrupted by grinding soils in a laboratory experiment. However, disruption of soil aggregates did not alter microbial growth resilience or respiration after drought. This is in agreement with findings that physical soil disturbance had no effect on fungal or bacterial communities (Bennett et al., 2020), although another study found that disrupting soil aggregates can increase both microbial biomass and the respiration pulse after rewetting

(Navarro-García et al., 2012). My results suggest that the release of resources previously protected in soil aggregates did not influence microbial community responses to drought. From these results some new questions emerge: Does the timing of tillage during the season influence microbial drought responses? Does tilling frequency affect microbial responses to drought?

Figure 13. Field experiement across the Swedish precipitation gradient
(A) Tilling treatment and control plots. (B) The rotary tiller machine used to till the soil. (C) The respiration response after rewetting between the control and tilled treatment at the 692 mm/year precipitation site (see figure 4).

Microbial carbon use after rewetting

Can microbial responses to drought influence the soil carbon balance? To answer this question, I estimated the carbon use efficiency (CUE) after rewetting. Microbial CUE is defined as the ratio between carbon incorporated into biomass via growth to the total carbon uptake (Manzoni et al., 2012a; Roller & Schmidt, 2015). In other words, CUE is one way to estimate the proportion of carbon staying in soils as microbial biomass (Geyer et al., 2020; Manzoni et al., 2012a). A higher CUE indicates a greater allocation of carbon used for the production of microbial biomass compared to respiration (Liang et al., 2017), and CUE has been argued to be an important predictor of soil carbon storage (Tao et al., 2023). As soils dry, microbial activity and CUE decrease (Canarini et al., 2017; Manzoni et al., 2012b; Tiemann & Billings, 2011), since microbial communities have to allocate more resources to survival (Butcher et al., 2020; Schimel et al., 2007). One study argued that more resistant communities that maintain their activity under drought can contribute to higher soil carbon losses than less resistant communities (Allison, 2023). However, the majority of the carbon release occurs when drought ends with rewetting (Barnard et al., 2020; Kim et al., 2012), hence the CUE after rewetting is likely to dominate the soil carbon budget (Placella et al., 2012).

Several studies have found that higher microbial drought resilience correlates with a lower respiration pulse, resulting in higher CUE compared to communities with lower resilience (Brangarí et al., 2020; de Nijs et al., 2019; Leizeaga et al., 2021; Figure 1). As climatic differences in drought exposure can determine microbial resilience (Figure 5), it may also characterise CUE.

In **paper I** and **paper II**, we found different results for CUE one day after rewetting. Across the Swedish precipitation gradient (**paper I**), CUE after rewetting increased in soils from drier sites, implying that more resilient microbial communities were better at allocating carbon to growth after rewetting. This is in accordance with Tiemann & Billings (2011), who found higher CUE at drier sites across a precipitation gradient in the Great Plains. Contrary, across the European climate gradient (**paper II**) there was no difference in CUE after rewetting. How can we explain the different results of CUE in **paper I** and **paper II**? The answer likely lies in differences in soil properties that can have a stronger effect than differences in microbial growth recovery. Higher nutrient and resource availability (Manzoni et al., 2012a; Roller & Schmidt, 2015) as well as higher soil pH can increase CUE (Jones et al., 2019; Malik et al., 2018). In line with these studies, in **paper II**, CUE was strongly correlated with soil C/N ratio and soil pH, where higher pH and lower C/N ratio increased CUE. Similarly, CUE decreased at higher plant diversity after rewetting (data from **paper IV**). This may be due to reduced nitrogen availability at higher plant diversity (Guiz et al., 2016), despite higher carbon availability (see **paper III**). Indeed, induced nutrient limitation with high carbon quality has been associated with reduced CUE across sites similar to the European climate gradient in **paper II** (Cruz-Paredes & Rousk, 2024). This implies that while high carbon inputs can result in fast growth rates after rewetting, but it can only be used for growth if sufficient nutrients are available. These results suggest that carbon release after rewetting may be greater in soils where microbial communities are exposed to more stressful conditions, such as acidic pH or nutrient limitation. Therefore, under climate change, soils in these environments may have a higher potential for carbon loss following drought disturbances.

When combining data from different experiments during my PhD (see "*Bacterial growth resistance and resilience to drought depend on climate*", Figure 5), climate (estimated as aridity index) did not influence CUE at 24 h after rewetting (Figure 14). Interestingly, the CUE was generally higher at the end of the summer when comparing **paper I** sampled in May with the sampling in August in 2021. Even if bacterial growth resilience to drought did not differ (Figure 5), they might have developed strategies to use carbon more efficiently at the end of the summer (Figure 7) and hence exhibit a comparably higher CUE. Taken together, these results suggest that more resilient microbial growth does not always correspond to a higher CUE (Figure 14).

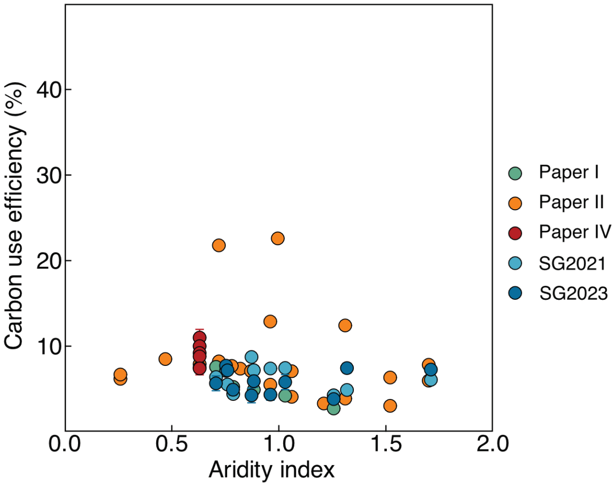

Figure 14. Microbial carbon use efficiency was uncorrelated with aridity index
Microbial carbon use efficiency (CUE) at 24 h after rewetting. Data from **paper I**, **paper II** and **paper IV**, and from the sampling at the Swedish precipitation gradient (SG) in August 2021 and 2023. A higher aridity index indicates a more humid climate, whereas a lower aridity index indicates a drier climate.

Linking microbial community composition to microbial functions

Disturbances can result in shifts in microbial community composition (Jurburg et al., 2024). One challenge in understanding the role of soil microbial communities under climate change is linking changes in composition with function (Figure 2). In **paper I**, the community composition indicated by phospholipid fatty acid (PLFA) was correlated with fungal resistance and bacterial resilience to drought, and PLFA analysis in **paper III** showed a link with microbial growth resilience. Similarly, in **paper II**, the community composition based on DNA sequencing was associated with bacterial resilience but not resistance. Other studies have linked changes in bacterial community composition to the magnitude of the respiration pulse following rewetting (Barnard et al., 2015) and to soil multifunctionality during drought (Canarini et al., 2021). In contrast, another study found no link between community composition and microbial growth recovery (Hicks et al., 2025). The results from this thesis suggest that shifts in microbial community composition can select for growth resilience (Figure 2), likely due to high mortality and turnover after rewetting (Blazewicz et al., 2020; Engelhardt et al., 2018; Koch et al., 2018), which acts as a stronger environmental pressure than drought periods (Evans et al., 2014). In line with this, rewetting caused larger shifts in microbial community composition than reduced precipitation, suggesting that rewetting events determine shifts in community composition (Wang et al., 2022).

Surprisingly, a rather small proportion of the differences in community composition could be explained by microbial drought resistance and resilience (**paper II**). One explanation could be that microbial communities are more strongly shaped by their environment. In **paper I**, the microbial community composition was correlated with soil pH. In **paper II**, the strongest drivers of microbial community composition were soil pH and organic matter, and in **paper III** the community composition changed with plant diversity and soil depth. It is therefore likely that traits to cope with these environmental conditions are stronger determinants of microbial community composition than those for drought disturbances. However, we could not distinguish whether changes in microbial growth resilience were mainly due to shifts in physiological traits or community composition. To investigate if there are shifts in microbial community composition, we can monitor how the community changes over time before and after rewetting. This also allows us to investigate resistance and resilience of the community composition and test links between compositional and functional stability.

To strengthen the link between community composition and functional responses to drought, more targeted approaches can be used. One method is stable isotope probing, which identifies only metabolically active taxa by tracking the incorporation of labelled stable isotopes, for example into DNA (Radajewski et al., 2000). However, it does not provide quantitative information about elemental fluxes. To overcome this, quantitative stable isotope probing can be used to assess growth rates of individual taxa (Hungate et al., 2015). This technique enables estimates of growth rates, mortality, and turnover, and can identify which microorganisms contribute to carbon cycling and ecosystem processes during drought disturbances (Blazewicz et al., 2020; Metze et al., 2023). In future work, we can use these approaches to investigate temporal changes in community composition after rewetting across the different environments studied in this thesis. This could help resolve if the observed differences in microbial drought resilience are driven by shifts in growing taxa and determine whether the same taxa can be both resistant and resilient.

Fungi and bacteria respond differently to drought disturbances

It is generally thought that fungi are more resistant to drought, while bacteria can recover faster when the drought ends (de Vries & Shade, 2013; Karlowsky et al., 2018; Manzoni et al., 2012b; Shade et al., 2012). In line with this, fungal community composition (Blazewicz et al., 2013; de Vries et al., 2018; Yuste et al., 2011), fungal growth rates (Leizeaga et al., 2021) and fungal-based food webs (de Vries et al., 2012) are more drought resistant than bacteria. Additionally, fungal networks are also more stable under drought than bacterial networks (de Vries et al., 2018). Whereas, some studies have found fungal community composition to be more sensitive than bacteria to drought (Boyle et al., 2024; Maisnam et al., 2023; Meisner et al., 2018). The results from **paper I**, **paper II** and **paper III** further add to the evidence that fungi are generally more drought resistant than bacteria (Figure 15). The higher fungal growth resistance may be due to their hyphal network allowing them to access water which could be an advantage in drier conditions (Guhr et al., 2015; Karlowsky et al., 2018; Yuste et al., 2011) and the thicker cell walls which can better withstand drought (Schimel et al., 2007).

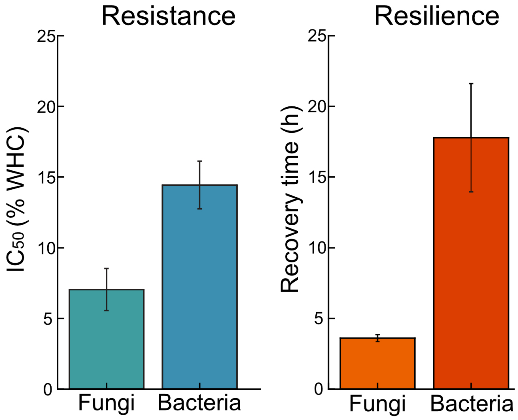

Figure 15. Fungal growth exhibited higher drought resistance and resilience than bacteria
Mean values of fungal and bacterial growth resistance and resilience to drought across the European climate gradient. Drought resistance was estimated as the soil moisture when growth rates was reduced by 50% (IC_{50}). Drought resilience was estimated as the recovery time back to 50% of an undisturbed control soil. Data from **paper II**.

Bacteria are thought be able to quickly use resources after rewetting, and therefore recover faster (Canarini et al., 2021). Conversely, in both **paper I** and **paper II** fungi recovered their growth rates faster than bacteria (Figure 15), matching previous results (Hicks et al., 2022b, 2025). In soils from the Jena Experiment, bacteria and fungi exhibited similar recovery times of around 7 h (data from **paper IV**), which is consistent with another study where fungal and bacterial growth showed a similar resilience to drought (Leizeaga et al., 2021). Generally, across my studies, fungi were both better at maintaining growth rates at low moisture levels and recovered faster when the drought ended, suggesting that fungal communities that were able to maintain growth rates at low soil moisture were also more ready to start growing following rewetting. To conclude, in this thesis I did not find a trade-off between fungal and bacterial growth responses to drought.

Neither historical drought exposure (**paper I** and **paper II**), plant diversity (**paper III** and **paper IV**) or soil properties (**paper II**) induced differences in fungal growth resistance or resilience to drought. Fungi generally have a higher physiological flexibility to adjust to different environments than bacteria. Specifically, they have a broader pH range (Rousk et al., 2010), a more flexible C/N ratio (Fierer et al., 2009), can utilise more varied carbon resources (Fierer et al., 2009; Six et al., 2006), have a wider range of optimal temperatures (Cruz-Paredes et al., 2023) and higher salt tolerance compared to bacteria (Rath et al., 2016). The lack of differences in fungal drought resistance and resilience may reflect their broad environmental tolerance, leading to similar responses across the environmental gradients used in this thesis.

Comparing the effects of different drivers on resistance and resilience

In this thesis, I tested different potential drivers of microbial drought resistance and resilience, but what factor is the strongest determinant? In a study from Tilman et al. (2012), they compared the effect of plant diversity with nutrient addition, fire, herbivory and drought on plant biomass production by combining field experiments from Cedar Creek Ecosystem Science Reserve. They found that differences in plant diversity had a larger impact on plant biomass production than the other factors tested. Inspired by this paper, I compared the response ratio for bacterial growth resistance and resilience to drought between differences in mean annual precipitation (**paper I**), climate estimated as aridity index (**paper II**), plant diversity (**paper III** and **paper IV**), soil depth (**paper III** and **paper IV**), tilling from the Swedish precipitation gradient and temperature in soils from Greenland (see "*Exposure to other disturbances may affect microbial drought responses*"). To do this, I estimated the absolute difference in resistance and resilience between the driest and wettest site, between the lowest and highest plant diversity treatment, and between the control and tilling or temperature treatment.

I found that differences in drought exposure with mean annual precipitation in **paper I** and aridity index in **paper II** had the strongest impact on bacterial growth resistance and resilience to drought (Figure 16). The effect of mean annual precipitation and aridity index was around 2 times higher than plant diversity for both resistance and resilience. Plant diversity had the second largest impact, followed by soil depth. Tilling and temperature did not impact the resistance and resilience. The effects of different factors might depend on the magnitude between them. Therefore, these comparisons should be evaluated in the context of the natural range expected in these ecosystems. For example, sites across the European climate gradient (from Sweden to Greece) largely covers the climatic variation found across the continent. Sites across the Swedish precipitation gradient also cover the ranges of differences in precipitation between the Swedish east and west coast. The plant diversity effect is within the range expected in native European grasslands compared to monoculture crops (Roscher et al., 2004; Tilman et al., 2012). As such, this dataset covers large differences that can be found within the European continent. In summary, this comparison can give an idea of the importance of different factors, where differences in drought exposure via precipitation and aridity index were the most important factors shaping how bacterial communities respond to drought disturbances.

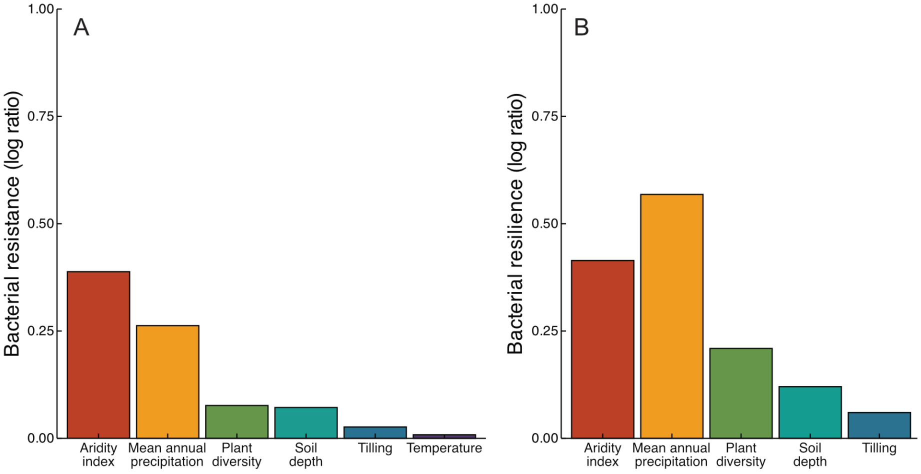

Figure 16. Differences in drought exposure had the largest effect on resistance and resilience
The absolute response ratio (log) of different potential drivers on (A) bacterial growth resistance to drought and (B) bacterial growth resilience to drought. Climatic differences in drought exposure were estimated as aridity index in **paper II** and as mean annual precipitation in **paper I**. Plant diversity was ranging from monocultures to 60 plant species richness in **paper III** and **paper IV**. Soil depth was the difference between topsoil (0-10 cm) and subsoil (10-30 cm) in **paper III** and **paper IV**. Tilling was the difference between tilling treatment and undisturbed control along the Swedish precipitation gradient sampled in August 2023. Temperature effects was estimated as the difference between the incubation temperature at 5°C and 40°C in soils from Greenland.

Conclusion

In this thesis I investigated how different factors shape microbial responses to drought disturbances. Based on my objectives, I have learned the following:

Higher drought exposure increased microbial resistance and resilience

Drought history can select for higher resistance and resilience to drought disturbances. In both **paper I** and **paper II**, I found that bacterial growth resistance and resilience to drought increased in drier climates. This suggests that bacterial responses to drought depend on the climate of origin, with more sensitive responses in soils from wetter climates where drought is perceived as a more severe disturbance (Figure 5). Climatic differences in drought exposure were the strongest factors influencing bacterial growth resistance and resilience (Figure 16). Fungal growth did not change across the gradients and was both more resistant and resilient than bacteria. Furthermore, differences in drought history between soil depths in **paper III** and **paper IV** showed that microbial communities were more sensitive to drought in deeper soil layers (Figure 6). The impact of soil depth was less pronounced than the effects of precipitation and aridity index, suggesting that deeper soil layers can also experience drought (Figure 16).

The environment can shape microbial resistance and resilience

The environment had different effects on microbial resistance and resilience to drought. Several of the tested factors influenced microbial responses to drought. In **paper II**, acidic soil pH reduced microbial diversity and was a strong determinant of bacterial growth resistance and resilience to drought. This suggests that both the soil environment and microbial diversity influence how microbial communities cope with drought. Furthermore, in **paper III** and with data from **paper IV**, plant diversity had a positive effect on microbial resistance and resilience to drought, likely due to higher resource availability. In contrast, in **paper IV** other tested stability components were mostly unaffected by plant diversity (Figure 9). Additionally, exposure to increased temperature (Figure 12) and tillage (Figure 13) did not influence microbial resistance and resilience.

Differences in drought exposure did not change carbon use efficiency after rewetting

Microbial CUE after rewetting did not vary with differences in climatic-driven drought exposure (Figure 14). This suggests that higher microbial growth resilience at drier climates does not necessarily correspond to higher CUE after rewetting. Instead, the soil environment may have a larger impact on microbial CUE after rewetting and influence the carbon budget more than the climate. For example, CUE was correlated with soil C/N ratio and soil pH in **paper II**, and with plant diversity in **paper III** and **paper IV**. However, when environmental differences were minor, microbial CUE increased at drier sites at lower mean annual precipitation (**paper I**).

Microbial community composition links to drought resilience

There was a link between community composition and growth resilience to drought in **paper I**, **paper II** and **paper III**, but not to resistance. This suggests that rewetting may be the driving force in shaping microbial community composition, likely as rewetting exert a stronger environmental pressure than drought. Our results also suggest that microbial community composition is influenced by the soil environment, for example by soil pH and organic matter. These factors may have played a more critical role in determining microbial community composition than drought disturbances alone.

In this thesis, I have contributed to answering some key questions about how microbial communities respond to drought disturbances. Based on the work in this thesis I have also identified several questions for future research:

- Are there global patterns of microbial growth stability?
- What level of drought intensity is needed to induce a shift in microbial responses to drought, and does this threshold vary between environments?
- How long does the shift in microbial resistance and resilience persist after a drought disturbance and are there seasonal differences?
- How does the combination of multiple disturbances or environmental conditions influence microbial community responses to drought?
- Does the microbial community composition change over time after rewetting?
- Which microbial taxa grow following drought, and does this depend on the environment or ecosystem?
- Can plant diversity influence microbial drought responses in other ecosystems, such as natural grasslands or forests?
- Do microbial drought responses vary among different plant-soil systems, and do these differences depend on drought intensity or duration?

The interaction between the soil environment, drought disturbances and microbial drought responses are complex, yet they present exciting opportunities for future research. This thesis, along with the questions posed above, can improve our understanding of microbial responses to drought and their role in the terrestrial carbon cycle. Lastly, with the insights gained from this thesis, I am convinced that drought is one of the most fascinating disturbances for studying microbial communities and functions.

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The author at Kobbefjord research station, Greenland

Drought as a disturbance

Welcome into the fascinating world of microbes. Have you ever wondered how life belowground is affected by drought and rainfall events? Then this thesis is for you. Here I explore if the ability of microbes to tolerate and recover from drought varies across climates, environments and disturbance types. I also resolve how microbes influence the soil carbon cycle after drought and if there is a link between microbial community composition and their functions. My thesis is part of a greater journey to understand the effects of drought on microbes and it opens doors to further exciting research to unravel the complex interplay between soil microbes, their environment and drought under climate change.

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