1 GENERAL INTRODUCTION

Stephanie D. Jurburg
Terrestrial systems are constantly confronted with environmental change at a range of scales. Periodic fluctuations in climate, gradual geologic shifts, extreme climatic events, and anthropogenic pressures such as land-use change present challenges—or perturbations—to which such systems must respond and adapt. Resolving these responses and determining the ecological properties which promote the adaptability to environmental change are two topics which lie at the roots of ecology. Darwin already proposed that species richness bolsters long-term ecosystem stability (Darwin, 1859). This proposal gave rise to research on the relationship between diversity (D) and stability of the system (S) and the mechanisms underlying the D-S relationship. A century later, the term “resilience” was introduced in the scientific literature, but it was given two different definitions. In 1973, Holling distinguished between ecological resilience, defined as the amount of pressure a system can withstand before shifting to an alternative state and engineering resilience, defined as the speed of return to the original state following a perturbation (Holling, 1973). The former term has since then been operationalized and redefined (see Table 1 for definitions) in many different ways (Hodgson et al., 2015), as discussed in the following sections. Research into the D-S relationship and the resilience of ecological systems has become central to ecology (Hooper et al., 2005), and is still active (Deng, 2012; Hodgson et al., 2015).

In particular, the study of ecological resilience in the soil microbial system (defined as encompassing Bacteria, Archaea and Fungi in this thesis) is in its infancy. While the importance of soil microbiota to function of the ecosystem has been recognized for over a century (Beijerinck, 1901), the importance of microbial community structure is still debated (Nemergut et al., 2014), as the high diversity and rapid turnover rates in soil are expected to result in a remarkably adaptive system (Finlay et al., 1997). The recent revolution in high-throughput sequencing has shifted microbial ecology research efforts away from cultivation-based methods. As these technologies allow for a more complete and dynamic view of soil microbial communities, and the importance of microbial community structure to ecosystem functioning becomes clear (Bardgett & van der Putten, 2014; B. Griffiths, Bonkowski, Roy, & Ritz, 2001; B. Griffiths et al., 2000; Wagg, Bender, Widmer, & van der Heijden, 2014; Wittebolle et al., 2009), the framework for understanding microbial community recovery is shifting from an engineering resilience perspective to
an ecological resilience perspective. We use the definition of ecological resilience outlined by Hodgson and colleagues, who describe resilience in terms of resistance—the degree to which the system is impacted immediately after disturbance—and recovery, which captures the endogenous processes that bring the system to equilibrium (Hodgson et al., 2015).

It is expected that many terrestrial ecosystems on Earth will be faced with increasing magnitude and frequency of disturbances as a result of climate change and anthropogenic pressures in the near future (Díaz et al., 2006; Donat et al., 2016; IPCC 2007, 2007; Millenium Ecosystem Assessment, 2005). It is likely that the soil microbiota will be affected. Given the crucial role of the soil microbiota in sustaining and regulating nutrient cycles (Philippot et al., 2013; Rustad et al., 2011; Schimel, 1995), understanding how soil ecosystems recover from disturbances is now extremely relevant.

Table 1. Definitions of key ecological concepts

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
<th>Reference</th>
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<tr>
<td>Disturbance</td>
<td>an event that alters the (soil) environment and has possible repercussions for the local (microbial) community, or an event that directly alters that community</td>
<td>(Hylke, 1985)</td>
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<tr>
<td>Resistance</td>
<td>the degree to which the community is altered immediately after disturbance.</td>
<td>(Hodgson, McDonald, &amp; Hosken, 2015)</td>
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<tr>
<td>Ecological resilience</td>
<td>the process of recovery following disturbance, described by resistance and recovery</td>
<td>(Hodgson et al., 2015)</td>
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<td>Engineering resilience</td>
<td>the rate at which a system returns to a steady state following disturbance</td>
<td>(Holling, 1973)</td>
</tr>
<tr>
<td>Microbial interactions</td>
<td>the dependence of one population’s growth or survival on the abundance of the other population. They be negative or positive (i.e., competition or cooperation), as well as direct or indirect (i.e., antibiotic warfare or competition for resources).</td>
<td>(Widder et al., 2016)</td>
</tr>
<tr>
<td>Disturbance legacy</td>
<td>biotic and abiotic conditions created by prior environments that persist when the environment changes</td>
<td>(Hawkes and Keitt, 2013)</td>
</tr>
<tr>
<td>Succession</td>
<td>succession, the sequence of species replacements through which ecosystems form and develop over time</td>
<td>(Odum, 1989)</td>
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**RESILIENCE OF SOIL MICROBIAL COMMUNITIES: AN EVOLVING CONCEPT**

Soil resilience was initially proposed as a key feature of behavior of the system under stress in 1994 (Blum, 1994). It was suggested as a key component of long-term soil quality soon after that (Seybold et al., 1999), but the methods for measuring soil resilience were not yet specified. Experimental work explicitly testing the effect of microbial diversity on the recovery of soil function and microbial community structure was reported a year later (Griffiths et al., 2000). The authors employed chloroform fumigations of increasing duration to create soils with varying microbial diversity levels, and measured functional and compositional parameters of the resulting communities as well as their ability to decompose grass material following transient (heat) and persistent perturbations (copper contamination, B. Griffiths et al., 2000). The results indicated a negative or null relationship between the tested functions (i.e. decomposition rate, microbial growth rate on added nutrients) and diversity, but a positive relationship between the levels of phylogenetically-conserved functions (i.e. methane oxidation) and diversity. Most importantly, the authors reported a generally positive relationship between diversity and resistance, defined in this case as the degree of immediate change following the perturbation, as well as between diversity and resilience, defined as the time of return to pre-disturbance conditions. These findings unveil some of the complexity of microbial recovery, dispelling the notion that the inexhaustible diversity found in these systems and the rapid growth rates of their members make soil microbial systems limitlessly resilient (Finlay et al., 1997). If not all functions are equally redundant, might there be a threshold of minimum diversity below which the most uncommon functions start to collapse? And if these functions are important for the community itself, might this collapse trigger a feedback mechanism, affecting the rest of the community? A range of experiments, reviewed in Chapter 2, have revealed that microbial function generally tends to increase with increasing richness and evenness (Awasthi et al., 2014; Bell et al., 2005; Salles et al., 2012, 2009; Wittebolle et al., 2009).

Studies of how disturbance triggers the responses in the soil microbial community have been largely lacking, however. This has been due to both technical and conceptual limitations. The technical limitations arose, until recent years, from a general lack of refined methodologies for assessing whole microbial communities without culturing: most of the older studies that assessed soil microbial community compositions employed methods such as PCR-DGGE, PCR-T-RFLP and PLFA, yielding rather rough estimates of microbial community compositions (Hirsch et al., 2010). Identifying and monitoring individual populations over time (particularly in the highly diverse soil system)
was time-consuming, cost-prohibitive or impossible. However, with the advent of high-throughput sequencing and sequence analysis methods, it has become possible to obtain community census data comparable to the datasets routinely used to study macro-ecological systems (Prosser, 2015).

The conceptual limitations stem from the continued usage of the engineering resilience concept (Griffiths and Philippot, 2012), which quantifies resistance and resilience. Resistance has been measured by comparing undisturbed soils (as controls) to soils which have been recently disturbed (Figure 1, A). Resilience has been quantified in various ways, but it generally compares the soils at the end of the experiment to the soils immediately after disturbance, using the control soils as reference (Orwin and Wardle, 2004), in order to determine how rapidly the soil tends to return towards its pre-disturbance state after disturbance. The engineering resilience concept, however, has several drawbacks. First, it is most fit for measuring single parameters, such as respiration, nitrification and community richness, and is thus more appropriate for the assessment of functional parameters than multivariate community structure, even though the latter may be as ecologically relevant as functional parameters in soil (Balser & Firestone, 2005; Bardgett & van der Putten, 2014; Wagg et al., 2014). As assessing community structure becomes increasingly popular, multivariate metrics of community resilience are necessary (Figure 1). Second, the application of the engineering resilience concept to soil assumes that microbial systems behave like an elastic, that is, they will tend to return to the pre-disturbance state without deviations. However, recent meta-analyses have shown that soil microbial communities often don’t return to their pre-disturbance state (in terms of both composition and function) within experimental periods ranging from days to years (Allison and Martiny, 2008; Shade et al., 2012). This indicates that the soil microbiota may tend towards novel states following a disturbance. Several studies also indicate that the process of microbial recovery is highly deterministic (i.e. non-random) and may occur in stages (Placella et al., 2012; Song et al., 2015), suggesting that throughout recovery the trajectory of the microbial community may exhibit deviations. Finally, the finding that communities exhibit thresholds of ‘allowed’ disturbance frequency, beyond which they shift to a completely unpredictable conformation (Kim et al., 2013), implies that whether the community tends to return towards its pre-disturbance conformation is

![Figure 1](image-url)

**Figure 1. Resilience of a hypothetical community.** A. A classical depiction of the engineering resilience concept. The community-wide parameter—here, total community—is measured in the soil prior to disturbance. The soil is then disturbed (orange), and measured at least once after disturbance in order to quantify resistance, and once thereafter, to quantify resilience. B. The response of the community to disturbance over time is dependent on the community members’ individual tolerance ranges (I). Once the system is disturbed (orange), populations which are not tolerant to these environmental conditions might disappear from the community (II). Once the disturbance ceases, the community’s composition has changed (III). The community may continue to change after the disturbance through regrowth or immigration, as new populations arise to occupy the available niches (IV). C. As these changes progress, dominance patterns may change greatly. D. The engineering resilience concept does not apply to community data as, at a population level, complex dynamics may result from the disturbance, more similar to succession than to an elastic.
dependent on the intensity and frequency of disturbance. The mechanistic explanations for these phenomena are standing questions in microbial ecology, including why communities don’t always recover, why—despite the diversity and rapid growth rate of bacteria—the patterns observed are generally deterministic and which factors trigger phase-like shifts in community composition.

The increased emphasis on microbial community structure in soil has thus resulted in an increasingly complex view of soil microbiomes. As more insight into the drivers of microbial community structure and its influence in ecosystem services are obtained, the engineering resilience concept has become far too simplistic for soil microbial communities (Barnard et al., 2013; Kim et al., 2013; Moroenyane et al., 2016). Throughout this thesis, we take advantage of high-throughput sequencing technology, and use it to focus on microbial community structure. We apply an ecological resilience concept to analyze the temporal pattern of recovery of microbial community composition following disturbance. Several questions arise. Is there a linear relationship between disturbance intensity and resistance of the microbial community? Is the recovery of soil microbial communities similar to that observed in macro-ecological communities? How does the recovering community respond to further perturbation, and what effect does this repeated perturbation have on the interactions within the community?

SOIL DISTURBANCE AND THE MICROBIAL COMMUNITY

Throughout this thesis, I define a disturbance as an event that alters the soil environment and has possible repercussions for the local microbial community, or directly alters that community (Rykiel, 1985). I use the terms disturbance, stress and perturbation interchangeably. I focus on the responses of the microbial communities to transient perturbations, that is, disturbances which have a definite end (i.e., moisture pulses, heat and cold shocks), as opposed to long-term perturbations (i.e., metal pollution, persistent changes in pH), since in the latter the environment is permanently changed and gradual community adaptation plays a central role. Short-term disturbances, on the other hand, result in transiently open niche spaces and an ephemeral increase in available nutrients due to cell mortality. In the latter case the environment is presumed to be relatively similar to the pre-disturbance environment after the cessation of the disturbance. Throughout this thesis, I focus on the short-term (~1 month) dynamics in the microbial communities following pulse disturbances, including short-lived heat and cold shocks, drying and flooding events.

The effects of a disturbance are, theoretically, not evenly distributed among community members. Microbes have growth optima which are defined along an infinite number of axes of environmental variables that constrain the organism’s theoretical niche. Stress on an organism occurs when one or more of these environmental variables change(s) beyond the organism’s optimum (Figure 1, B), creating physiological challenges or threatening its function or survival (Schimel et al. 2007). One strategy for survival is inherent resistance, in which populations possess mechanisms for tolerating the physiological challenges, as is the case with endospore production among members of the Firmicutes, which promotes resistance to heat and other stressors. An alternative strategy is acclimation, in which tolerance mechanisms are induced as a response to environmental change (i.e., the induction of stringent response by ppGpp, which halts RNA synthesis in the absence of sufficient aminoacids, Condon, Squires, & Squires, 1995). Traits such as salt or pH tolerance or preference and the ability to form heat-resistant endospores are phylogenetically conserved (Martiny, Jones, Lennon, & Martiny, 2015; Van Overbeek, Van Elsas, Trevors, & Wellington, 1997; Schimel, Balser, & Wallenstein, 2007). Within a community, members can be classified into functional response groups (FRGs, Lavorel & Garnier, 2002) according to their tolerance to environmental stress. Such a classification may enable a better understanding of the immediate effects of a disturbance on the community, or community resistance. However, the classification of microorganisms into functional response groups has only been done once, to our knowledge (Lennon et al., 2012). In the experiment performed by Lennon and colleagues, 45 bacterial and fungal strains were grouped according to their respiration rate across a gradient of soil moisture (Lennon et al., 2012). Their results showed how the wide range of responses resulted in different communities at varying soil moisture. Thus, a priori knowledge of the FRGs may allow for an estimation of the community composition immediately after an environmental change—in this case, a change in soil moisture.
Changes within microbial communities may occur in the aftermath (>1 day) of a disturbance as well (Figure 1B). Immediately after a microbial community experiences a disturbance, the affected biota may alter its energy allocation pattern, go dormant, or die. Subsequently, survivors may grow quickly as nutrients from the dead cells become available. Both the increase in the prevalence of such opportunists and the absence or reduction of function of sensitive populations may, in turn, affect populations with which these interact. This thus propagates the effects of the disturbance, similar to secondary succession. We here define groups of organisms with similar temporal response patterns as functional effect groups (FEGs, Lavorel & Garnier, 2002), with the underlying assumption that their contribution to patterns of community assembly is somewhat related. Classifying community members in this way may yield valuable insight into microbial community assembly (Martin et al., 2015; Shade et al., 2013). For example, during 72 hours after rewetting of soils, Placella and colleagues observed three groups of taxa, which exhibited three distinct temporal response patterns (rapid, intermediate and delayed responders). The members within the three groups were phylogenetically conserved at the subphylum level, suggesting that the temporal patterns reflect distinct ecological, physiological or metabolic roles (Placella et al., 2012).

FEGs may be used to study the recovery component of resilience, which describes the successional dynamics that follow the disturbance. This may include sequential changes in community structure and function which occur through the elimination of sensitive species. Thus, replacement by tolerant organisms may ensue due to relief of competition, shifts in interspecies interactions due to reduced fitness of sensitive species or the absence of predators, or physiological or genetic adaptation (Medina et al. 2007). Microbial succession in soil has been generally used to indicate shifts in microbial community composition along a successional gradient, such as forests (Hu et al., 2013) or abandoned agricultural fields (Cline and Zak, 2015). Accordingly, the time scales used have often been too large to accurately capture the highly dynamic microbial communities (Gilbert et al., 2010).

The community properties which drive succession have been obscured by the large spatiotemporal scales over which communities are monitored (years to centuries) relative to microbial life histories. Thus, most changes in community structure and function have been attributed to physicochemical parameters (Dini-Andreeto, Stegen, van Elsas, & Salles, 2015; Fierer & Jackson, 2006; Hansel, Fendorf, Jardine, & Francis, 2008). However, novel research has shed light on some of the patterns of community assembly following disturbance (Moroenyane et al., 2016; Placella et al., 2012; Song et al., 2015; X. Zhang et al., 2016a). In one recent study, soil bacteria were plated onto a range of media and plates were incubated for 2-84 days, producing communities whose composition depended on nutrient availability and incubation time. Very low between-replicate variability was found. This showed that community assembly was largely dependent on the individual niches occupied by members of the community, at least for the culturable fraction of the soil microbes (Song et al., 2015). These deterministic patterns are in accordance with other disturbance experiments, both in the field and in laboratory (Moroenyane, Chimphango, Wang, Kim, & Adams, 2016; Placella et al., 2012; X. Zhang et al., 2016).

The sequential nature of succession implies that both the time since the previous disturbance (frequency) and the type of disturbance (legacy) play a crucial role in determining the community’s response to further perturbation. In soil, the effect of disturbance legacy on resilience has been mostly studied from an applied perspective, for instance exploring the effect of previous land use or contamination on resilience (Tobor-Kaplon et al., 2005). Such studies overwhelmingly find that resilience is negatively affected by perturbation, and that intensively managed or polluted soils are less resilient to disturbance than sustainably managed or pristine ones (Chaer et al., 2009; Kuan et al., 2006; Philippot et al., 2008; Tobor-Kaplon et al., 2006; Zhang et al., 2010a). For example, Müller and colleagues found that mercury-contaminated, heat-shocked soils responded much more slowly to substrate additions than transiently tylosin-contaminated or control soils (Müller et al., 2002). The authors observed a significant decrease in the microbial diversity of the mercury-contaminated soils, which may explain the reduced response following additional disturbances. While mercury contamination is a persistent disturbance, studies have also found that even when the soils are allowed to recover from transient perturbations, their resilience (here, measured as the response to further disturbances) is slower than that of the control soils. Kuan and colleagues found that grassland soils which had experienced various forms of perturbation (reseeding, application of sewage-sludge, biocide/nitrogen and lime additions) recovered their abilities to decompose local plant residues.

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more slowly following both copper and transient heat stresses than the un-
perturbed controls (Kuan et al., 2006). Different responses are found when,
in case of dual stressors, both disturbances exert similar selective pressures.
Bérard and colleagues found that pre-exposing soils to drought increased
their resilience to heat, as measured by their ability to decompose 8 carbon
substrates (Bérard et al., 2012). How legacy affects microbial recovery dynam-
ics, and how the identity of the prior disturbance affects the responses of the
communities to future perturbations are, however, two poorly understood
phenomena.

AIM OF THIS THESIS

The general aim of this thesis is to improve our understanding of how soil
microbiomes respond to stress and whether stress may result in altered com-
community responses to further perturbation, or whether it may alter functional
relationships. Finally, this thesis evaluates the applicability of these findings
to climate change scenarios, in particular the effect of altered precipitation
patterns on the microbiomes of soils under different management regimes.

HYPOTHESES

Given the current state of knowledge regarding microbial community re-
responses to short-term perturbation, I posed the following hypotheses for fur-
ther exploration in this thesis:
• By assessing microbial community resistance across a gradient of increas-
ing disturbance intensities, it is possible to resolve FRGs. These FRGs will
show some degree of phylogenetic conservation.
• Soil microbial community recovery from disturbance is deterministic and
proceeds in stages, which—in the absence of abiotic change—are driven
by the soil biota.
• Soil microbial communities undergoing recovery from disturbance exhibit
different recovery trajectories from further perturbation than those with-
out a disturbance legacy.
• Soil perturbation affects microbial function by disrupting the functional
dependencies between bacteria
• Soil microbial communities under intensive agricultural management ex-
hibit different resilience patterns in response to intensified precipitation
regimes than those in sustainably managed soils.

THESIS OUTLINE

The aforementioned hypotheses are explored throughout chapters 2-8 of this
thesis.

In chapter 2, I review current data from the literature that connect micro-
bial diversity and ecosystem functioning, focusing on resilience as a long-term
function of soil. A key point of this review is an examination of the intricacies
of the experimental methods that are currently used for manipulating diver-
sity. Throughout the rest of this thesis, I employ soil micro- and mesocosm
experiments to study the temporal dynamics underlying microbial resilience,
and the relationship between resilience and community structure. Contrary
to most experiments reported in the literature, the experiments detailed in
this thesis employ controlled disturbances (a heat shock or intensive land
management) as a means to reduce microbial diversity, and test the effects
of these reductions on further perturbation. I thereby avoid greatly altering
the spatial distribution and connectivity of the soil microbiota that is naturally
present in the system.

In chapter 3, I subjected soil microbial communities to heat shocks of in-
creasing duration in a microcosm setting. By measuring community compo-
sition in terms of the bacterial 16S ribosomal RNA (rRNA) types, community
members were thus classified according to their tolerance ranges. A positive
phylogenetic signal was found in this classification, indicating ecological co-
herence within this grouping. From this experiment, I selected a heat shock
duration which causes 50% mortality of the total microbiomes.

In chapter 4, I explored secondary succession in the soil microbial com-
unity by disturbing soil microcosms with the previously selected heat shock.
I then monitored the community composition in the recovering microbiomes
in terms of the 16S rRNA types for 49 days. During this time, the microbiomes
revealed a temporal clustering of samples, which I interpreted as the emergence of successional patterns. I group the microbial populations into FEGs, and compare them to macro-ecological successional groups. By connecting the pattern of community turnover to the phylogeny of each community member over time (as in Stegen et al., 2013), I detected strong deterministic selection, which in the absence of environmental variation I attributed to direct or indirect biotic interactions.

In chapter 5, I explored the effect of disturbance legacy on soil microbial community resilience. I exposed the same microbial communities to the aforementioned heat shock in order to create a disturbance legacy, and later (25 d) exposed them to either an identical second heat shock or a cold shock. I monitored the community for 25 additional days through the amplification of reverse-transcribed 16S rRNA molecules. My results show that microbial communities in soils with a disturbance legacy become more resilient to the same specific disturbance, but disproportionately less resilient to novel disturbances.

In chapter 6, I focus on the nitrifying microbial communities in soil, which have been extensively studied in the past (Bouskill et al., 2012; Wertz et al., 2006, 2007), and serve as a model for a ‘disturbance-sensitive’ organismal group in soil. Nitrification is a two-step process: ammonia is converted to nitrite via hydroxyl amine, and then nitrite is converted to nitrate. Each step involves two groups of ecologically distinct Bacteria and Archaea (Attard et al., 2010), with different tolerance ranges. Furthermore, the dependence of nitrite oxidation on ammonia oxidation allows us to examine the effect of a decrease in one population on a dependent one. I used real-time PCR in order to quantify marker genes (16S rRNA, amoA, and nxrA) for each functional group in the disturbance legacy experiment performed in Chapter 5. By monitoring the abundance of the four groups of nitrifiers along a recovery gradient, I tested whether disturbances affect resistant taxa by reducing the populations on which these taxa depend. The results show that the response of each functional group is dependent both on disturbance type as well as the soil’s legacy. However, due to the low temporal resolution of sampling, it was not possible to identify decoupling between ammonia and nitrite oxidizers.

Chapter 7 of this thesis focuses on the applicability of the previous findings to real-world disturbances. Here, I performed a mesocosm experiment using soils from adjacent, sustainably versus intensively managed plots, and subjected them to month-long extreme precipitation events (flood and drought), taking the last two decades of precipitation data from the region into account. I examined how the microbiomes in the mesocosms recover from the flood and drought scenarios for one month after the treatment. I found that the communities from the intensively-managed soils are vulnerable to both drought and flood, while those from the sustainably managed soils are only vulnerable to flooding. I also found faster recovery dynamics in intensively-managed soils, and attributed these to the higher percentage of fast-growing taxa.

Finally, in chapter 8, I present a synthesis and discussion of the results obtained throughout this thesis. In particular, I discuss soil microbial community resilience within the context of secondary succession. Integrating my findings with contemporary literature, I present a unified conceptual framework of secondary succession in soil microbial systems (“microsuccession”), and discuss a more complex concept of soil microbial resilience might better inform long-term soil management.