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CONTENTS

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A review of diversity-stability relationship of soil microbial community: What do we not know?

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Abstract

The impact of decreased biodiversity on ecosystem stability, or the diversity-stability (D-S) relationship, is one of the major concerns of modern ecological studies. Studies on the D-S relationship for soil microbial communities began in 2000 when the fumigation method was developed to generate different levels of soil microbial biodiversity. The studies used various measures and levels of biodiversity, and covered several functional parameters. Due to the lack of general concepts and reliable approaches to define microbial species, studies on the D-S relationship of soil microbial communities concentrate on genetic diversity and functional diversity more than species diversity. Contradictory results were observed in various studies on D-S relationship with possible factors affecting or even changing the directions of the D-S relationship including: (1) the methods of stability measurement, (2) the techniques in microbial diversity measurement, (3) the measures and levels of diversity, (4) the type and strength of disturbance, (5) the traits of functions, and (6) the hidden treatments stemming from diversity manipulation. We argue that future studies should take diversity, species composition and interaction, and soil environmental conditions holistically into account in D-S studies to develop modeling to predict soil functional stability. We also suggest that studies should be carried out on a wider range of disturbance types and functional parameters, and efforts be shifted towards long-term field studies.

Key words: resistance; resilience; disturbance; diversity manipulation
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Introduction

Increasing environmental pollution, over-exploitation of natural resources and global climate changes exert enormous stresses on biodiversity (Dobson et al., 1997; Collins, 2009). A large number of experimental studies have shown that biodiversity is crucial in maintaining ecological processes (Loreau et al., 2001) and the accelerated decline of biodiversity in recent decades (Global Biodiversity Outlook) has stimulated serious concerns about the impact of biodiversity loss on ecosystem functions (Hooper et al., 2005). Studies on soil microbial diversity and soil ecosystem functions have been promoted in the last two decades through a series of research programs, e.g., the Diversitas program.

Ecosystem functional stability refers to the ecosystem's ability to minimize dynamic fluctuation and the ability to defy changes after disturbances (McCann, 2000). The role of biodiversity in functional stability or the diversity-stability relationship (D-S relationship) has fascinated ecologists for several decades (Loreau et al., 2001). Early observations from Elton (1958) reported that agricultural monocultures were more prone to pest outbreaks than mixed communities, and species-poor ecosystems are more prone to invasion by new species than species-rich ecosystems.

Classical theories such as the averaging effect, insurance effect and negative covariance effect provide conceptual supports for a positive D-S relationship (Table 1) (Lehman and Tilman, 2000). However, none or even a negative D-S relationship, as well as positive D-S relationships, were observed in various experimental studies on soil microbial communities, plant communities (Pfisterer and Schmid, 2002; Bai et al., 2004; Tilman et al., 2006) and algal communities (Steiner et al., 2005; Zhang and Zhang, 2006).

The soil microbial community has a special model of D-S relationship and factors influencing the D-S relationship may be different from that of the plant community such as: (1) microbes are sensitive to disturbances but also fast to acquire resistance, (2) soil can provide shelter for microorganisms and buffer disturbances, (3) soil micro-organisms constitute a food web rather than a single-trophic-level community, (4) soil micro-organisms carry out a wide range of functions and dynamics of various functional groups after disturbances may differ from each other, (5) most micro-organisms are un-culturable and thus diversity manipulation is difficult, (6) "microbial community diversity" refers to genetic/functional diversity more than "species diversity". Since Griffiths et al. (2000)

Table 1 Theories concerning the effect of biodiversity on ecosystem stability

Theories	Statements
Insurance effect	Increasing diversity increases the possibility of the presence of functionally redundant species, which provides an "insurance" against perturbation or environmental fluctuations and thus plays an important role in stabilizing ecosystem function.
Averaging effect	Species have different responses to changes in the ecosystem over time, thus the averaging of these responses will cause a more temporally stable ecosystem if more species are in the ecosystem.
Negative covariance effect	Some species deteriorate while competitors thrive, thus the losses in one species caused by disturbances are offset by the gains of another.

extended research from the plant community to the soil microbial community, studies of the D-S relationship in soil microbial communities have been expanded to address various measures (e.g., richness and evenness) and levels (e.g., genetic and functional diversity) of biodiversity, and have covered a range of functional attributes. Nevertheless, our knowledge in this field is still limited. Results varied between studies as well, including (1) positive D-S relationship (Girvan et al., 2005) and (2) no correlation between diversity and stability (Wertz et al., 2007).

In this article, we review studies on the D-S relationship for soil microbial communities, identify areas of research to potentially advance our understanding of the D-S relationship, discuss factors influencing stability and weakening the D-S relationship, and make recommendations for future studies.

1 Key elements in D-S study

1.1 Stability

Ecosystem stability is defined as the system's ability to minimize dynamic fluctuation and the ability to defy change (Pimm, 1984; McCann, 2000). Ecosystem stability mainly focuses on three aspects: (1) the ability to resist exotic species (Elton, 1958; Levine, 1999), (2) temporal stability (Naeem and Li, 1997; Isbell et al., 2009), and (3) resistance and resilience (Pfisterer and Schmid, 2002; Kuan et al., 2006). In soil ecosystems, resistance refers to the ability of soil functions to withstand a disturbance and resilience the ability to recover to its non-disturbed level (Seybold et al., 1999). Both resistance and resilience are generally described as the ratio of functional parameters in the perturbed treatment to those in the unperturbed control. Temporal stability is described as functional variation over time (Table 2) while the ability to resist exotic species is measured as the chance that invaders can survive or the influence of invaders on the native community (Dukes, 2001; Arenas et al., 2006).

Table 2 Different indices of resistance, resilience and temporal stability

Equation	References
Resistance and resilience	
$(\frac{C_x-P_x}{C_x})\times 100$	Griffiths et al., 2000, 2001
$\frac{P_x}{C_x}$	Kaufman, 1982; Herbert et al., 1999
$\frac{P_x}{C_x}\times 100$	Sousa, 1980; Kuan et al., 2007
$1-\frac{2\lvert D_0\rvert}{(C_0+\lvert D_0\rvert)}$ *, $\frac{2\lvert D_0\rvert}{(\lvert D_0\rvert+\lvert D_x\rvert)}-1$ **	Orwin and Wardle, 2005
Temporal stability	
$\frac{\sigma}{\mu}\times 100$	van Ruijven and Berendse, 2007

C_x and P_x is the value of functional parameter for unperturbed control and perturbed treatment, respectively, at time x. For resistance, x can be a time shortly after a disturbance while for resilience usually the end of incubation. For temporal stability, μ is the mean value of the observed functional parameter during a term; σ is standard deviation of observation to mean value.

* A formula for resistance calculation, where $D_0 = C_0 - P_0$; C_0 and P_0 refer to the values of the functional parameter for control and perturbed treatment, respectively, at the end of the application of the disturbance.

** A formula for resilience calculation, where $D_x = C_x - P_x$.

1.2 Microbial diversity

Manipulation of community diversity is a common way to examine the D-S relationship. Methods of manipulation can be grouped into artificial and natural methods. The former refers to artificial construction of a community with the explicit aim of altering diversity while the latter uses a community with different levels of naturally formed diversity (de Ferrari and Naiman, 1994; Lacombe et al., 2009). Artificial methods include species selection methods and treatment-induced methods. Species selection methods construct a community by randomly grouping species (Bell et al., 2005; Isbell et al., 2009; Wittebolle et al., 2009). The treatment-induced methods alter biodiversity by exerting a treatment effect (Tilman and Downing, 1994) such as the application of a pollutant, dilution (Griffiths et al., 2001) and fumigation (Griffiths et al., 2000) to decrease biodiversity, or the application of organic matter to increase biodiversity (Wada and Toyota, 2007).

Fingerprinting methods have been commonly used to assess soil microbial diversity on the basis of operational taxonomic units (OTUs) rather than species. This is due to the difficulty of defining microbial species. For example, although bacteria with 16S rRNA genes that are ⩽ 98.7% identical are treated as different species in some studies, distinct species have been occasionally described with 16S rRNA genes that are > 98.7% identical or even completely identical (Achtman and Wagner, 2008). Whole-genome sequencing with higher genetic resolution than 16S rRNA genes was proposed to determine genomic parameters (Achtman and Wagner, 2008). However, prokaryotic genomes undergo homologous recombination between micro-organisms that are more than 25% divergent in the sequences of homologous genes, and prokaryotes can accept and express new genes on plasmids from extremely divergent sources (Cohan, 1996). This high frequency genetic exchange between microorganisms in the environment makes it difficult to identify microbial species (Rosselló-Mora and Amann, 2001).

1.3 Disturbance

Disturbance is defined as events that generate modifications to the habitats (Cruz-Palacios and van Tussenbroek, 2005). Some other terms like perturbation, stress and stressor are often used instead of disturbance, although there are slight differences in that perturbation and stress refer to the physiological and genetic response of organisms to a disturbance or a stressor (Rykiel, 1985).

Disturbances to the soil ecosystem can be heavy metal, heat (Griffiths et al., 2001; Kuan et al., 2006; Banning and Murphy, 2008), oil (Franco et al., 2004), antibiotics (Westergåård et al., 2001), stimulated rainfall (Steenwerth et al., 2005), pesticides, freeze-thaw cycling and wet-dry cycling (Mertens et al., 2007). Disturbances can be classified into transient and long-term types. Transient disturbances, such as heat, can be withdrawn after short-term application, while long-term disturbances, such as heavy metal pollutants or PAHs (Deng et al., 2009, 2011; Guo et al., 2011), cannot be removed from soil or degraded easily, exerting relatively long-term stress on soil ecosystems.

1.4 Ecosystem functions

The purpose of studies on the D-S relationship is to provide insights into community diversity and its links to ecosystem functions, which is a broad term covering ecosystem properties and ecosystem goods and services (Christensen et al., 1996; Kremen, 2005). Ecosystem services comprise microbial and biochemical processes in an ecosystem. Soil microbial activity (Velasco et al., 2009; Chaer et al., 2009), organic matter decomposition (Griffiths et al., 2000; Griffiths et al., 2001), denitrification and nitrite-oxidation (Wertz et al., 2007), as well as suppression of pathogens have been used as indicators for ecosystem services in studies on D-S relationship of the soil microbial community (Balvanera et al., 2006). Gardi et al. (2009) further classified ecosystem services derived from soil microbial communities into eight aspects, including (1) the regulation of the nutrient cycling, (2) promotion of nutrient availability for plants, (3) degradation of pollutants, (4) changes in species and mobility of heavy metals, (5) stabilization of soil aggregates, (6) improvements in soil porosity and water retention, (7) food webs and trophic levels ultimately supporting higher organisms, (8) resistance to exotic species and pathogens. From this point of view, only items 1 and 8 have been studied with respect to the D-S relationship.

2 Factors affecting D-S relationship

2.1 Methods of stability measurement

A reliable sampling time and calculation method are crucial in measuring resistance and resilience. Resistance has been measured several hours (Banning and Murphy, 2008), one day (Griffiths et al., 2001) or three days (Chaer et al., 2009) after disturbances. Although resilience is always measured at the end of incubation, the incubation time varies from case to case (Griffiths et al., 2001; Girvan et al., 2005; Banning and Murphy, 2008; Deng et al., 2009). As shown in Fig. 1, if resistance was determined at time point "b" and resilience at time point "c", then community A would be more resistant and resilient than B. However, if resistance was determined at time point "a" and resilience at time point "d", we will have a contrasting result. Moreover, since ecosystem function is usually randomly fluctuating over time, the function value at a single time point cannot be used to determine resistance and resilience. A study conducted by Zhang et al. (2010) should be highlighted since resilience was calculated from several time points rather than once at the end of incubation. We further propose to measure resistance and resilience from a continuous dynamic curve of function against time so that the influence of random fluctuation of any single point can be avoided. The formulas are modified from Zhang et al. (2010):

$$f(t) = \frac{P}{C} \times 100\% \tag{1}$$

$$R_{\mathrm{st}} = \int_0^i f(t)\mathrm{d}t/i \tag{2}$$

$$R_{\mathrm{sl}} = \int_i^m f(t)\mathrm{d}t/(m-i) \tag{3}$$

where, P refers to the function after a disturbance and C refers the function in control treatment; R_{st} and R_{sl} refer to resistance and resilience, respectively; t refers to the incubation time; i refers to time for a function to reach the lowest value; m refers to time for a function from the lowest value to the end of incubation. According to the formula, resistance and resilience are described not only by the value of functional parameters but also by the time to reach the lowest point and the speed of recovery.

2.2 Techniques in microbial diversity measurement

Fingerprint approaches are adopted in D-S studies to determine soil microbial diversity, including community-

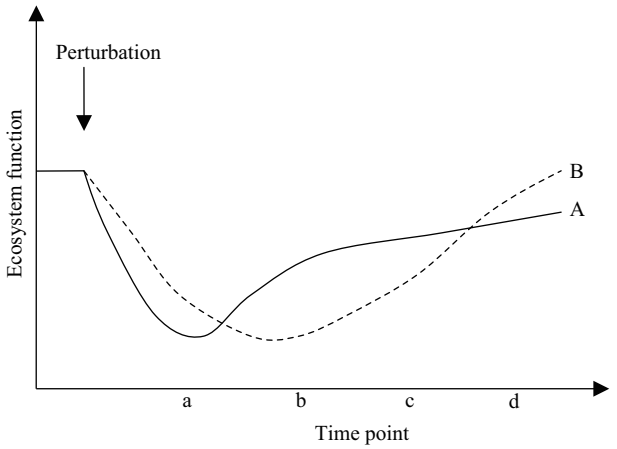

Fig. 1 Dynamic of ecosystem function between community A and B following perturbation. This figure suggests that our judgment of stability between communities may be strongly influenced by the time point. If resistance were determined at time "a/b", then community A would be less/more resistant than B; if resilience were determined at time "c/d", community A would be more/less resilient than B.

level physiological profiles (CLPP) (Degens et al., 2001), phospholipid fatty acid analysis (PLFA) (Lacombe et al., 2009), denaturing gradient gel electrophoresis (DGGE) and terminal restriction fragment length polymorphism (T-RFLP) of the 16S rRNA gene (Griffiths et al., 2000, 2001; Girvan et al., 2005; Matos et al., 2005). Nitrite-oxidizing community diversity was analyzed by DGGE for the *norA* gene (Wertz et al., 2007). In general, the number of OTUs tested by fingerprint approaches can reflect species diversity. However, shortcomings of these approaches may have potential influences on the D-S relationship (Table 3). For example, by T-RFLP, single species can generate several restriction fragments because the restriction enzyme cutting sites may not be unique and their numbers vary with species (Matos et al., 2005). Additionally, DNA from different species may converge into one DGGE band and different species or groups may have a common PLFA in their signatures (Dey and Guha, 2007). As for the CLPP approach, changes in the composition of a microbial community can occur during incubation since this approach favors the fast-growing micro-organisms (Nannipieri et al., 2003; Kirk et al., 2004). Consequently, the richness of OTUs, tested by fingerprint methods, is likely to vary with species composition rather than species number.

2.3 Levels and measures of microbial diversity

"Diversity" is a general term covering various levels (Table 4) and measures (e.g., richness, evenness), which should be determined in the D-S relationship. For example, genetic diversity is closely related to the stability of a specific function since more redundant species means a higher opportunity for a community to be resistant to perturbation. Functional diversity could be closely related to the invasiveness of exotic species since assemblages with more functional groups can make use of resources more efficiently and thus exotic species can be competitively excluded through low resource availability (Dukes, 2001; Britton-Simmons, 2006). Studies also showed that the D-S relationship depends on what measures are used. In addition to richness, evenness is another measure of biodiversity and was shown to affect community functional stability (Bell et al., 2005). Isbell et al. (2009) found that the temporal stability of plant community productivity did not vary between treatments of low and high species evenness, but positively correlated with species richness. This finding could be explained by the convergence of evenness between treatments during the experiment and the fact that the low evenness treatment exhibited species asynchrony, which resulted in compensatory dynamics. Weigelt et al. (2008) calculated plant community diversity by applying Rao's quadratic diversity Q, which took species traits into consideration. Results showed that community dynamic stability was positively correlated with Q rather than species richness.

Table 3 Currently used methods for detecting microbial diversity in D-S studies and their main drawbacks that may lead to distorted diversity

Method	Main drawbacks in deciding microbial diversity
CLPP	Favors culturable and fast-growing micro-organisms.
PLFA	Low taxonomic resolution (Ramsey et al., 2006). Different species share common PLFA.
T-RFLP	PCR biased T-RF richness varies with restriction enzymes. Several/single species may generate single/several T-RF(s).
DGGE	PCR biased Different species may generate a single band.

CLPP: community-level physiological profiles; PLFA: phospholipid fatty acid analysis; T-RFLP: terminal restriction fragment length polymorphism; DGGE: denaturing gradient gel electrophoresis.

Table 4 Definitions of different levels of microbial diversity used in this review (Jones and Bradford, 2001; Allison and Martiny, 2008)

Term	Definition
Species diversity*	The number of different species in a given habitat or biome.
Genetic diversity	The variability within the genetic pool of one species.
Functional redundancy	The ability of one microbial taxon to carry out a process at the same rate as another under the same environmental conditions.
Functional diversity	The variety of biological processes, functions or characteristics of a particular ecosystem.
Trophic diversity	The number of trophic levels present in an ecosystem. Trophic diversity is an indicator of the complexity of the food web.
Structural diversity	The number of parts or elements within a system, indicated by such measures as the number of species, genes, communities or ecosystems.
Habitat diversity	The variability among habitats in a landscape or a region.

* Achtman and Wagner (2008) thought the concept "Species are (segments of) meta-population lineages" applies well to microbes.

2.4 Type and strength of disturbances

D-S relationships in empirical studies can be affected by disturbance type and strength. It is possible that functionally redundant species are major contributors to resistance and resilience following long-term disturbance, while after transient disturbance, redundant species mostly contribute to resistance, and both redundant species and the recovery of inhibited species contribute to resilience. If so, various D-S relationships can be obtained depending on different disturbance types and strengths.

Four scenarios for the impact of long-term disturbance with different strengths on D-S relationships include: (1) the disturbance is weak and poses little stress on the soil microbial community in either a species-rich or -poor community, thus no correlation between diversity and stability is evident; (2) the disturbance is strong and some species are inhibited or eliminated, but there are still resistant species in the community and the D-S relationship is dependent on to what extent the resistant species can functionally replace sensitive species; (3) the disturbance is stronger compared to the second scenario, thus some species in a more diverse community and all species in a less diverse community are inhibited or eliminated. In this scenario the redundant species in a more diverse community will contribute to resistance and resilience, and therefore a positive D-S relationship is expected; (4) the disturbance is strong enough to inhibit or eliminate

all species in either a species-rich or -poor community, therefore it is likely that no correlation between diversity and stability is evident.

The impact of transient disturbance is different from that of long-term disturbance in scenarios 2, 3 and 4 above since inhibited species will recover after transient disturbance and contribute to resilience. An empirical evidence for this scenario is that even though all species in an algal community were inhibited during heat disturbance, the community recovered after heat was removed (Allison, 2004). In addition, we reviewed studies that used both heat and copper disturbances and found that in most cases soils after heat disturbance exhibited higher resilience than after copper disturbance (Griffiths et al., 2001; Kuan et al., 2006, 2007; Gregory et al., 2009; Zhang et al., 2010). Scenarios 1 and 4 should be avoided for D-S relationship studies. In a study conducted by Wertz et al. (2007), heat disturbance was applied using criteria that temperature impacted on but did not eliminate functions.

2.5 Traits of functions

There has been a consensus that general functions are more stable than specific functions after disturbances. General functions, such as organic matter decomposition, are maintained by a wide range of micro-organisms, while specific functions, such as nitrification, are maintained by a specific group of micro-organisms (Griffiths et al., 2001). Therefore, general functions are influenced by more species than specific functions (Chaer et al., 2009). General functions are more stable than specific functions, which can be considered as indirect evidence of a positive D-S relationship. Nonetheless, different functions may respond differently to perturbation and thus stability may not be attributed solely to diversity. One example is that the expression and activity of ammonia monooxygenase and methane monooxygenase genes can be activated by Cu (Nielsen et al., 1997; Hakemian and Rosenzweig, 2007), thus perturbation by adding Cu shows a hormetic effect on the potential ammonia oxidation rate (PAO), in comparison to an inhibitory effect on microbial biomass carbon (C_{mic}) and substrate induced respiration (SIR) (Deng et al., 2009), even though PAO belongs to the category of specific functions while C_{mic} and SIR are general functions.

2.6 Hidden treatments

Since soil heterogeneity is one driver of microbial diversity, biodiversity manipulations are inevitably linked to variations in environmental conditions and biological properties, such as species composition biomass (Ives and Carpenter, 2007). Therefore the D-S relationship is greatly influenced by many other factors. Huston (1997) named them as hidden treatments and proposed that three hidden treatments can be generated along with the manipulation of biodiversity: (1) abiotic or biotic conditions, which are altered to create differences in species diversity, (2) non-random selection of species with special attributes that produce treatment differences that can not be explained by "diversity" alone, and (3) the increased probability of including a species with a dominant negative or positive effect in groups with more randomly selected species. The first two hidden treatments may result from natural and treatment-induced methods while the third hidden treatment results from the species selection method.

As for natural methods, soils that exhibit a variation in biodiversity probably differ in chemical and physical properties. These properties could affect the stability of the soil microbial community, reducing the effect of biodiversity by itself. For instance, soil with higher organic matter or clay content can buffer pollutant disturbances more effectively (Luthy et al., 1997; Sandaa et al., 1999) and offer better shelter for micro-organisms (Kuan et al., 2007; Gregory et al., 2009). To minimize the interference of soil physical and chemical properties on stability, Girvan et al. (2005) applied EC_{50} concentrations as disturbances of equivalent toxicity in a resistance and resilience experiment on soils with different physical and chemical properties. As for treatment-induced methods, initial pollutant load and the pollutant addition as a disturbance can form a non-interactive or interactive mixture of contaminants in soil, depending on the traits of both pollutant and disturbance. For non-interactive mixtures the toxicity can be additive (Mumtaz et al., 1994) while for interactive mixtures the toxicity can be stronger or weaker than expected on the basis of additivity (Feron and Groten, 2002).

Diversity manipulation methods also exert alteration in microbial biomass, activity and species composition (Chander and Brookes, 1991; Dickens and Anderson, 1999), except that microbial biomass and activity can recover to their original state following dilution and fumigation (Griffiths et al., 2000, 2001; Wertz et al., 2007). Nonetheless, co-variance between species composition and diversity is hard to avoid (Worm and Duffy, 2003). Griffiths et al. (2004) found that soil microbial communities with the same genetic diversity but different community structures showed different functional stabilities following heat and copper disturbances. In the case that diversity was manipulated with pollutants, tolerant species can multiply and promote community tolerance and co-tolerance (Demoling and Bååth, 2008), increasing resistance and resilience to a series of pollutants (Deng et al., 2009).

Treatment-induced methods including pollutant addition, dilution and fumigation can exert high pressures on minor groups of micro-organisms or even eliminate them. This can destroy the food web of soil organisms and lead to the loss of keystone species, which have a disproportionately large effect on ecosystem functions relative to their abundance (Suzuki et al., 2005; Crowley, 2008). Atrazine degradation efficiency, for example, was not linearly related to the species richness of degraders but relied on keystone species (Monard et al., 2011). Therefore eliminating keystone species may profoundly impair functional stability. Predators such as nematodes, amoebae and mites are generally absent from experimentally constructed communities but they are indispensable in stabilizing soil food webs (Berlow, 1999; O'Gorman and Emmerson, 2009). An empirical study conducted by

Hunt and Wall (2002) showed that eliminating one kind of fauna in soil changed the abundance of other faunal types and bacteria and fungi, as well as ecosystem functions. Eliminating soil fauna could increase bacterial and fungal abundance and possibly improve the resilience of bacterial and fungal communities (Griffiths et al., 2001).

3 Recommendations for future research

3.1 Beyond diversity

From current studies, we can infer that biodiversity is not a decisive factor that affects soil ecosystem stability. Other factors include soil chemical and physical properties, land use history, disturbance type and strength, key species for resistance and resilience, and so on. Future studies are needed to investigate the contribution of these factors to soil ecosystem stability, as well as to develop models to build the linkage between them to predict soil resistance and resilience.

3.2 More disturbances and functions

The earth is undergoing more extreme climate events and natural disasters than ever before. The distribution of many species has recently extended towards polar regions as a response to climate warming (Perry et al., 2005). The way that microbial diversity and functional stability respond to these stresses is an area that requires study.

Soil ecosystems carry out functions within and beyond soil. Studies found that mycorrhizal fungi diversity affects nutrient uptake by plants and plant productivity (van der Heijden et al., 1998; Munkvold et al., 2004). These studies shed light on future studies of linkage between soil microbial diversity and terrestrial ecosystem function and food productivity. We also suggest investigation of the relationship between soil trophic diversity and aboveground ecosystem functions as the soil food web plays a crucial role in energy flow from soil to other ecosystems.

3.3 Long-term experiment and field study

Following severe or long-term disturbances, soil function is difficult to recover within a short-term period because degradation and aging of pollutants, as well as development of resistant microorganisms, takes a long time. In addition, many disturbing events occur with periodicity such as climate fluctuations or application of pesticide. Therefore long-term studies and studies on temporal stability are needed to better understand D-S relationships. Periodic application of a disturbance can also reveal the tipping level of the disturbance that results in ecosystem degradation (Veraart et al., 2011). To carry out a long-term experiment for D-S relationships, we suggest avoiding the dilution method as diversity manipulation since this method does not change soil habitat, thus diversity is likely to recover during long-term incubation.

In traditional laboratory experiments, soils from different habitats are incubated in homogenous laboratory environments. Therefore field studies are needed to provide realistic assessments of stability. Sometimes disturbances (e.g., drought, oil pollution) happen across large spatial scales and the functional resilience may need to be monitored with the combination of remote sensing technology and *in situ* measurement.

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