MODELLING SPATIOTEMPORAL DYNAMICS OF BIODEGRADATION UNDER DISTURBANCES

Insights into functional stability of microbial ecosystems

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"I don’t pretend to see the path, but I know it’s there all the same.
One day, we’ll look back and wonder how we ever missed it."
- Peter V. Brett

Sara König: *Modelling spatiotemporal dynamics of biodegradation under disturbances* ,

ABSTRACT

Terrestrial environments are highly complex and dynamic. It consists of various types of soils which are constantly exposed to fluctuating conditions affecting their physical and biological properties. Moreover, soils are delivering several ecosystem services with high relevance for the human well-being such as water purification, nutrient cycling, or biodegradation. For many of those ecosystem services, microorganisms are the main drivers. In consequence, it is important to understand the functional response of microbial ecosystems to disturbances. Thus, identifying key factors for the functional stability of microbial ecosystems in terrestrial environments is of high interest.

A powerful tool for analysing dynamics and underlying mechanisms of ecosystems are computational simulation models. Within this doctoral thesis, a spatiotemporally explicit bacterial simulation model was developed for assessing dynamics of biodegradation as a typical microbial ecosystem function under the influence of disturbances. Disturbances were introduced as lethal events for the bacteria within a certain, randomly picked disturbance area. The disturbance characteristics vary in the spatial configuration and frequency of the disturbance events. Functional stability was analysed in terms of the ability to recover the function after a single disturbance event, i.e. functional resilience, and the ability to maintain the function during recurrent disturbance events, i.e. functional resistance. Key factors for functional stability were assessed by systematically varying properties and processes of the microbial ecosystem and characteristics of the disturbance regime.

Simulation results show a high influence of the disturbance characteristics, especially its spatial distribution pattern, on the stability of biodegradation. Functional resistance and resilience increase with fragmentation of the spatial pattern of the disturbances. The frequency of recurrent disturbance events proved also essential for the functional resistance: if the disturbances occur too often, the emergence of a functional collapse may not be preventable. However, if the fragmentation of the applied disturbance patterns increases, the function is also maintained under more frequent disturbances without a functional collapse. Ecological processes such as bacterial dispersal and growth are shown to enhance the biodegradation performance, but only under specific disturbance regimes, again depending on frequency and fragmentation of the disturbances. Dispersal networks are shown to increase the functional stability in many scenarios and, thus, may serve as a buffer mechanism against disturbances.

Therefore, strategies facilitating these ecological processes, for instance stimulating fungi that act as dispersal networks for bacteria, or modulating the physical soil structure to alter the spatial configuration of disturbances are proposed to increase the functional stability of microbial ecosystems.

CONTENTS

1

INTRODUCTION

1.1 BIODEGRADATION IN SOIL

1.1.1 *Pollution of soil*

The ecosystem soil is essential for life as it provides a medium for plant growth, habitats for many different organisms such as insects and microorganisms, and delivers several ecosystem services including food production, filtration of sediment water, nutrient cycling, and waste disposal [Wall, 2004; Crawford et al., 2005]. Thus, it is important to assess the vulnerability of the soil system and its processes to altering conditions and disturbances.

Since the beginning of the industrialisation over 200 years ago, soil pollution got a world-wide environmental issue and will likely get worse in several regions in the future as production and use of chemicals will further increase. Major types of pollutants include salts, heavy metals, mineral oil and organic pollutants such as polycyclic aromatic hydrocarbons (PAHs), biphenyls or pesticides [Science Communication Unit, 2013]. Pollutants are reaching the soil system on many different ways. However, basically all sources are human-made - intentional such as landfills but also accidental inputs. Major contributors to pollution include agrochemicals, for instance, the emission of pesticides (Fig. 1.1a), urban waste disposal (Fig. 1.1b), industrial (Fig. 1.1c), atmospheric and incidental [Mirsal, 2004; Science Communication Unit, 2013]. The consequences of these contaminations are drastic. Beyond the direct effect to the soil system and its organisms the pollutions could also enter the human body due to skin contact, inhalation of released contaminants, uptake by contaminated ground water or even by children eating soil. In 2013 approximately three million sites may have been affected by activities which can cause soil pollution. About 250,000 of these sites are estimated to likely need immediate remediation [Science Communication Unit, 2013]. For managing contaminated sites different approaches can be employed. They can basically be classified by the type of treatment process such as chemical/physical, thermal and biological but also whether the activity is in situ or ex situ and on site or off site. Examples for treating sites chemically are immobilisation to solid matrices, oxidation or hydrolysis. Physical treatments include all approaches in which the contaminants are separated from the soil matrix by exploitation of differences in physical properties such as removal by electrokinetic processes or soil washing. The thermal approach is the destruction or immobilisation by increasing the temperature [Vik, E. A. and Bardos, P., 2002]. However, those remediation strategies are often costly both economically and environmentally. Therefore, biological treatments have gained more focus.

(a) Use of pesticides in agriculture

(b) Leachate at waste dump in Puerto Williams, Navarino, Chile

(c) Industrial area Bitterfeld, Germany

Figure 1.1: Examples for sources of soil pollution. (sources: André Künzelmann, Helmholtz Centre for Environmental Research - UFZ (a,b); Dr. Reinart Feldmann, Helmholtz Centre for Environmental Research - UFZ (c))

1.1.2 *Bacterial degradation as ecosystem service*

A promising remediation strategy for removing organic pollutants is bacterial degradation. Bacteria are able to use some organic contaminants as carbon and/or energy source and, thus, for their catabolism [Madigan et al., 2008; Alvarez and Illmann, 2006]. With this clean-up ability microorganisms in soil are delivering an important regulating ecosystem service which is subdivided into natural and enhanced bioremediation. The main difference between the two treatments is the level of anthropogenic activity. Natural bioremediation means that naturally occurring microorgansims degrade organic pollutants without further human intervention. For enhanced bioremediation, the conditions for microorganisms are actively improved for increasing biodegradation performance. Here, biostimulation and bioaugmentation can be distinguished. Which approach is suitable depends on the microbial ecosystem present in the contaminated soil. If already enough active microorganisms are available, oxygen, nutrients and moisture are added for stimulating and enhancing the natural activity of the bacteria. If the microbial composition of the contaminated site is not sufficient, specific accumulated cultures of communities of microorganisms are added to supply the intended biological activity [Vik, E. A. and Bardos, P., 2002]. Nevertheless, contaminants are accumulating in soil because the release rate is often much higher than the degradation rate [Harms and Bosma, 1997]. Therefore, for successful bioremediation it is necessary to

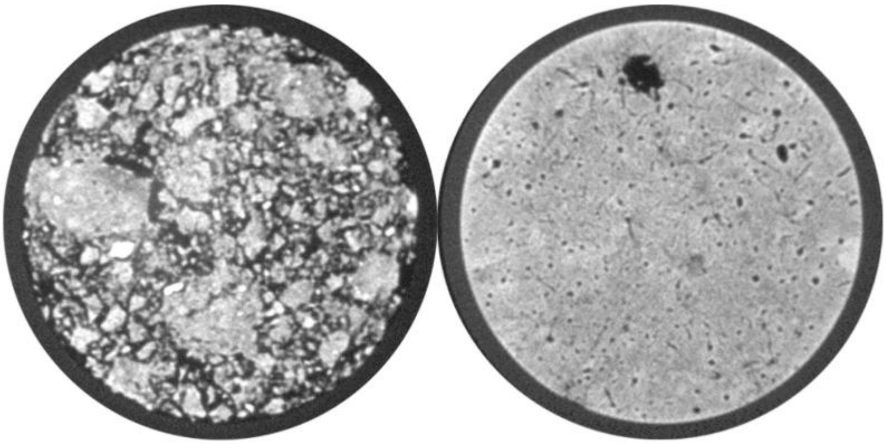


Figure 1.2: Cross-section of computed tomography images of two natural soil samples with a high amount of clay (left) and silt (right). White areas are soil particles and dark areas are the soil pores. (source: Gerke [2012])

understand what is inhibiting effective microbial degradation and how the activity can be increased. Beyond properties of the contaminants and the microorganisms itself the surrounding environment is also an influencing factor.

1.1.3 *Soil as heterogeneous environment*

Finding a common definition for soil is a complex task. It depends on the different concepts of soil as many different disciplines are working with soil such as geology, chemistry, agricultural science, engineering or ecology [Jenny, 1994; Tan, 2009]. The following definition from Kellogg [1941] seems close to the understanding of soil from an environmental scientist's point of view:

> "Soils are considered natural bodies, covering parts of the earth surface that support plant growth, and that have properties due to the integrated effect of climate and organisms acting upon the parent material, as conditioned by relief, over a period of time." [Kellogg, 1941; Tan, 2009]

This definition includes the close relationship of soil and the environment and the highly dynamic properties of soil in time. Parent material means the rock out of which the soil is originally formed, this may be, for example, sand, limestone, loess, shale, or peat. The developed soil can basically be classified by its composition of sand, clay and silt portion, which determines with the different particle sizes the pore size distribution of the soil system [Jenny, 1994]. Natural soil is usually a heterogeneous distribution of the named soil components and soil organic matter (Fig. 1.2). Therefore, the pore size distribution is also heterogeneous and dynamically changing over time due to environmental influences such as erosion by wind and water or bulking due to dispersing organisms [Horn and Baumgartl, 1999].

A big problem for bacteria in soil is the availability of nutrients. Especially the concentration of bioavailable carbon in natural soils is very low. However, even if enough carbon is present - for example due to a contamination with degradable organic pollutants - the heterogeneity of the soil system can make it difficult for the bacteria to reach the carbon source. A low water content and air-filled pores may prevent the contact of bacteria and carbon source, the bioavailability of the contaminant is thus low [Angle, 1999; Young and Crawford, 2004; Boswell et al., 2007]. The contact probability may further decrease due to a dynamic change in the spatial distribution of the soil or other factors stressing the system such as drought. In turn, other factors in soil can help increasing the contact probability of bacteria and nutrients, for instance, fungal networks.

1.1.4 *Fungal networks*

Fungi are the most dominant organisms in soil with regard to their biomass, but also addressing their various functions. Besides their ability to decompose and mineralize complex compounds of plant and animal origins, fungi are also living in symbiosis with other soil organisms such as plant roots or bacteria. Furthermore, fungi are less sensitive against fluctuating conditions and heterogeneities than other soil microorganisms [Thorn, 1999; Boswell et al., 2007]. For instance, they are able to grow in air-filled pores and therefore overcome water gaps in the soil pore network [Thorn, 1999; Wösten et al., 1999]. The surfaces of the hyphae of this hydrophilic fungi have been found to be surrounded by a continuous liquid film. Experimental studies have revealed that bacteria could use this water film as pathway for enhanced dispersal and, in consequence, for an increased distribution in soil systems [Kohlmeier et al., 2005; Wick et al., 2007]. Model simulations also showed that the use of this fungal highways facilitate bacterial degradation in heterogeneously distributed pore networks [Banitz et al., 2011a]. Therefore, fungal networks may be a stabilizing factor for the ecosystem service biodegradation as they increase the spatial performance of the bacteria and, thus, the contact probability of bacteria and pollutant. Further studies also indicate other functions of the fungi such as the transport of pollutants [Furuno et al., 2010; Wick et al., 2010; Banitz et al., 2013] and water [Guhr et al., 2015], with the potential for enhancing the stability of biodegradation against disturbances.

1.2 ENVIRONMENTAL DISTURBANCES

1.2.1 *Disturbance in ecology*

An environmental disturbance is defined by Pickett and White [1985] as

> "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." [Pickett and White, 1985]

According to this definition a disturbance is almost everything changing the present situation of the ecosystem. This may be a physical event such as a hurricane or a flood, a wildfire, excessive climatic changes of temperature or moisture, biological influences due to competition or predation, or pollution with contaminants. The effect of the specific disturbance may be a reduction of biomass of some organisms, a limitation of substrate occurrence or availability, a restriction of dispersal ability due to

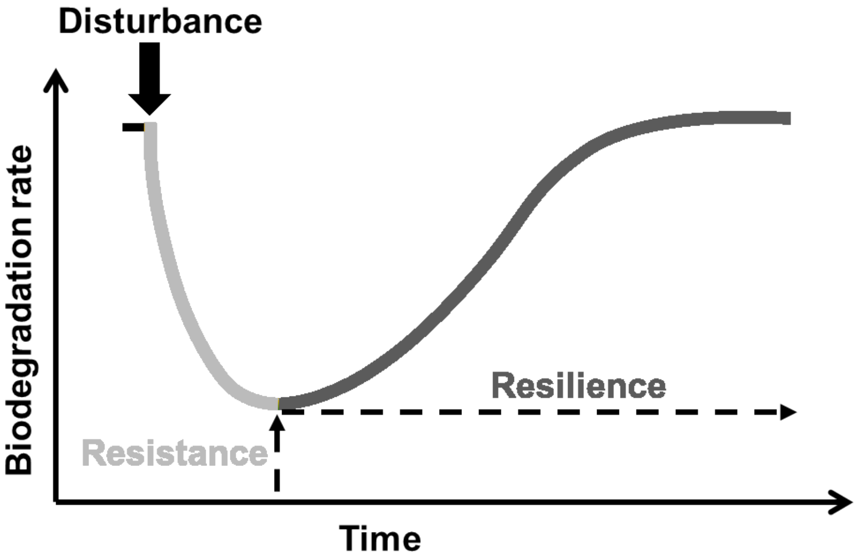


Figure 1.3: Stability properties in ecological theory: Ability of a system to i) withstand a disturbance - resistance (light grey)- ii) return to a reference state after a disturbance - resilience (dark grey)

changed conditions or newly arose physical barriers, or a shift in community composition [Pickett and White, 1985; Freedman, 1995]. Disturbances are also characterized by their temporal and spatial occurrence, their disturbance regime. For instance, the type of disturbance can be classified as pulse and press. A pulse disturbance is an extreme but short event which quickly decreases in strength. In contrast, a press disturbance is a continuous event which may arise sharply but lasts over a longer period of time on a constant level of intensity [Lake, 2000; Shade et al., 2012]. However, in any case it is of main interest how the ecosystem responses to the disturbance and how stable the system is, regarding its structure but also regarding its ecosystem functioning. The stability of a system is described by two concepts: the ability of a system to withstand a disturbance, which is called resistance, and the ability to recover the damage and return to a reference state or dynamic after a disturbance, which is referred to as resilience (Fig. 1.3) [Harrison, 1979; Grimm and Wissel, 1997; Lake, 2000; Biggs et al., 2012]. For understanding the response of an ecosystem service to disturbances both named stability properties are of interest. If the key factors for resisting a disturbance or recovering afterwards are determined, specific management strategies may be developed to strengthen these factors.

1.2.2 *Microbial response to disturbances*

Basically all ecosystems are undergoing disturbances from time to time in different intensities and frequencies. Thus, microorganisms living in such disturbed ecosystems have to deal with disturbance events. Many species are adapted to natural fluctuating conditions allowing them to occupy also extreme environments. However, if microbial ecosystems are exposed to new types of disturbances the effects may be as drastically as for every other organism. Some disturbances in soil such as a contamination with toxic chemicals or the immigration of predators may reduce the biomass of the bacteria. Others like drought may decrease their motility or metabolism. Bioturbation may further reduce the bioavailability of substrate due to a change of the connectivity between pores in the soil system [de Ruiter et al., 2002; Botton et al., 2006; Shade et al., 2012]. Different studies have investigated the change in community composition in response to disturbances such as drought, chemical contamination, increased salinity or unspecific mortality events [e.g. Bressan et al., 2008; Berga et al., 2012; Manzoni et al., 2012; Kim et al., 2013; Amend et al., 2016]. For instance, Kim et al. [2013] investigated the influence of a physical disturbance with a lethal effect to parts of a soil bacterial community. Results showed a high sensitivity of the community biodiversity but also a change in species composition [Kim et al., 2013].

Most studies have concentrated on the structural stability in terms of bacterial biomass or community composition of the considered microbial ecosystem. However, in matters of ecosystem service research the response of the function of the microbial ecosystem is of major interest and the structure must not necessarily correlate with the function. Therefore, studies should include direct investigations of the functional response to disturbances. Berga et al. [2012] examined the influence of salinity disturbances with different intensities and frequencies to the composition of a natural bacterial community, but to their function as well. They found changes in both community structure and functioning depending on the disturbance strength, but for the recovery rate also a dependence on the type of function [Berga et al., 2012].

For increasing the stability of a microbial ecosystem and its functions it is most of all important to determine the key factors driving the resistance and resilience processes in response to a disturbance. Those key factors may be biotic such as specific properties of the affected organisms or abiotic such as spatiotemporal characteristics of the disturbance itself or the structure of the environment. For example, Altermatt et al. [2011] showed that increased connectivity between disturbed and undisturbed patches in bacterial metacommunities increased the recovery rate after a disturbance with a lethal effect to some of the populated patches. With this observation, they identified dispersal as a major factor for community stability [Altermatt et al., 2011]. However, the driving processes and factors for functional stability of microbial ecosystems are poorly studied although they may be the key for developing management strategies for enhancing their stability. A mechanistic analysis of the response to disturbances is needed for understanding the systems reaction and finding solutions for enhancing the functional stability.

1.3 MICROBIAL SIMULATION MODELS

For examining the structural and functional dynamics of a microbial ecosystem, simulation models have proven to be a powerful tool. Computational models allowing for analysing spatially resolved dynamics at different scales including heterogeneities of the environment. With individual-based models (IBMs) the behaviour of single bacterial cells as a response to different environmental conditions can be observed in time and space [Kreft et al., 2013]. Cellular properties regarding growth kinetics, dispersal and functional activity can arbitrarily assigned and even be varied over time, mimicking evolution. However, the stochastic nature of IBMs make large numbers of simulation runs necessary for each parameter combination [Grimm et al., 2005]. Moreover, the amount of individual cells which can be simulated are limited in IBMs. This is a problem as the relevant volumes in microbial populations are comparably high. In population-based models all individuals of one population are assumed to be equal in behaviour and properties. Typically, those models are described with differential equations and are deterministically in nature, hence not requiring repeated simulation runs. The influence of stochasticity in environmental conditions is thus easier to determine also on larger scales [Esser et al., 2015]. But also the variation of the simulated spatial area colonized by microbes is a solvable challenge for modelling. Upscaling is an important issue, especially in soil research where processes are taking place on the micrometer scale as well as on the meter scale [O'Donnell et al., 2007]. Here, a highly important issue are also heterogeneities regarding the different compositions of soil particles and pore sizes. In spatially explicit models, heterogeneities of both the environment and the distribution of organisms may be simulated. Another big advantage of modelling is an easier mechanistic understanding of processes underlying the simulated system such as growth or dispersal. The parameters describing those processes are arbitrarily modifiyable, and processes can even be completely switched of to assesss their relevance for overall systems behaviour. [Esser et al., 2015].

Microbial simulation models are successfully used for understanding systems behaviour in various application areas such as genomics, food safety, epidemic or medical research [e.g. Brady and Salzberg, 2011; Ferrier et al., 2013; Mallet et al., 2013; Gatto et al., 2013; Silva et al., 2014]. In environmental microbiology, modelling approaches are also used in different fields. For instance, in environmental biotechnology microbial biofilms are modelled to understand the ability of bacteria to transfer electrons for developing microbial fuel cells [Picioreanu et al., 2007; Korth et al., 2015]. For analysing microbial processes in porous media reactive transport models are used in different studies dealing with the simulation of biogeochemical processes [Murphy and Ginn, 2000; Centler et al., 2010; Gharasoo et al., 2012], or the problem of bioclogging [Thullner and Baveye, 2008; Brovelli et al., 2009].

However, in microbial ecology modelling tools are not yet fully utilised in their full potential although they are already recognized as being applicable to tackle questions relevant in the field of microbial ecology [Wade et al., 2016]. Some approaches were developed for assessing the kinetics of degrading bacteria [Banitz et al., 2012; Stolpovsky et al., 2012; Wehrer et al., 2012], the community composition during litter decay [Kaiser et al., 2014], or denitrification processes in unsaturated soil aggregates [Ebrahimi and Or, 2015].

1.4 AIM OF RESEARCH

This doctoral thesis aims at understanding the functional stability of the ecosystem service 'biodegradation'. As discussed in Section 1.1, many biotic and abiotic factors may influence the ecosystem service biodegradation and may be included in a study examining the functional resilience and resistance. In this thesis we focus on the following aspects: the heterogeneity of the soil environment, the influence of fungal networks, properties of the microbial ecosystem itself, and disturbance regimes with different spatial characteristics and temporal occurences (Fig. 1.4).

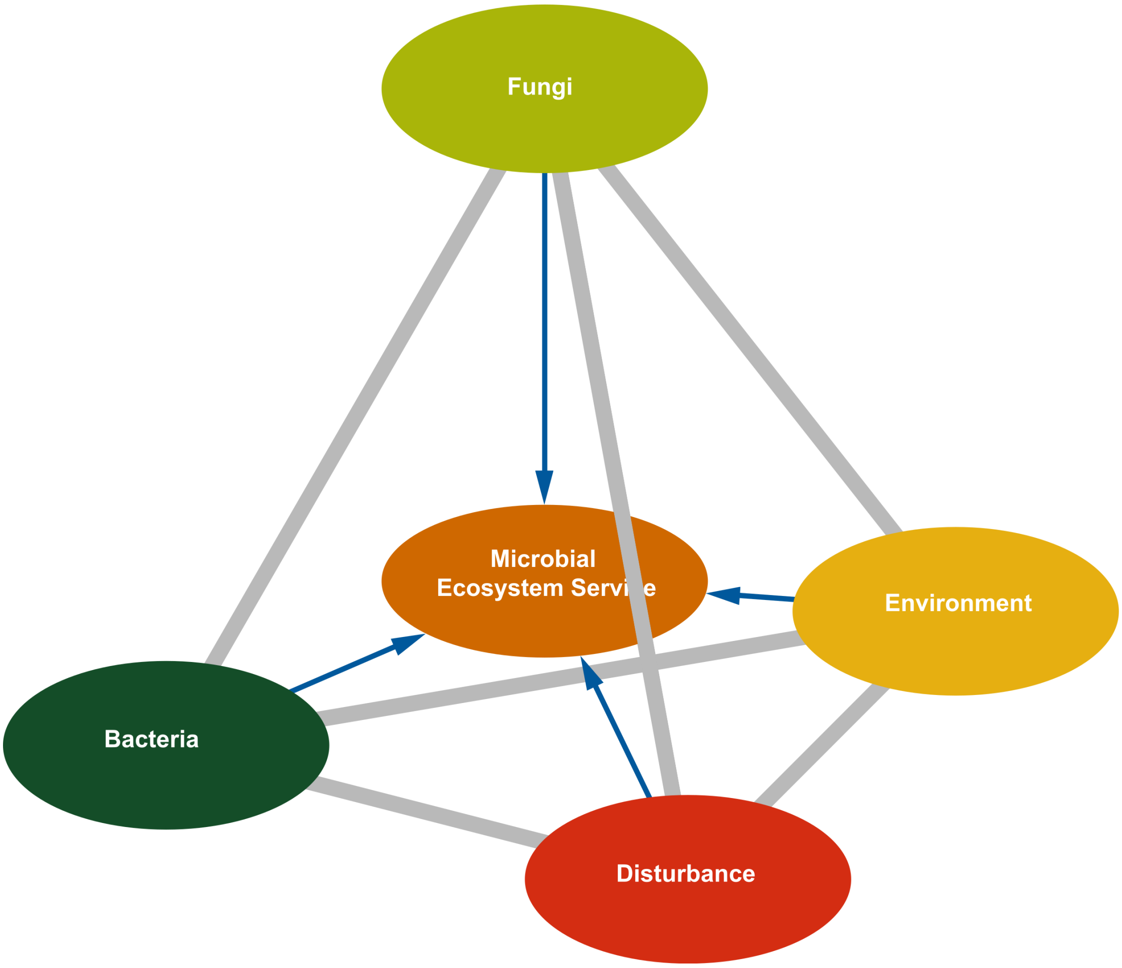


Figure 1.4: Conceptual relationships and aspects which are examined within this thesis

1.4.1 *Research objectives*

The main research objectives are:

- Identifying **key factors** for **functional resilience** of biodegradation after disturbances
- Examining the **functional resistance** to recurrent disturbances
- Determining the benefit of **dispersal networks** for functional stability of microbial ecosystems

1.5 CHAPTERS OVERVIEW

Within this thesis, different aspects of the functional stability of microbial ecosystems are analysed and discussed. An overview of the main determinants regarding the analysed factors, type of stability and disturbance characteristics are shown in Figure 1.5.

1.5.1 *Chapter 2: The modelling framework eColony*

In Chapter 2 the simulation model *eColony* is presented. The base model describing microbial consumer-resource systems for simulating bacterial degradation dynamics is introduced in detail. Extensions of this model are developed allowing for the analysis of the stability of bacterial degradation in response to disturbance events.

1.5.2 *Chapter 3: Functional resilience to single disturbance events*

In Chapter 3 the response of the model system to a single pulse disturbance is examined for understanding the basic mechanisms underlying the functional resilience. The recovery behaviour is systematically analysed, first in a temporal aggregated manner for comparison of the effect of different disturbance intensities and the recovery time is determined. Afterwards the spatial dynamics of the system are highlighted: differences in the recovery trend at different positions in the system and also the influence of the disturbance pattern i.e. the degree of fragmentation of the disturbed area. Finally, a mechanistic view - in which the main processes (bacterial growth, bacterial mobility, substrate diffusion) are consecutively switched-off during the simulations - revealed the relevance of the spatial and non-spatial processes at different recovery phases. The results provided important implications for application of disturbance regimes such as the time scale for relevant frequencies which have to be applied.

1.5.3 *Chapter 4: Functional resistance to recurrent disturbance events*

Chapter 4 addresses the functional resistance under disturbance regimes with recurrent disturbance events. The system is periodically disturbed with different disturbance return intervals and the degree of fragmentation of the disturbance area is varied. Spatiotemporal dynamics of biodegradation are observed for analysing the key factors for functional resistance to recurrent disturbances. Furthermore, in this chapter dispersal networks are introduced to the model system. The simulations were continued with the presence of dispersal networks on which the bacteria are able to move faster for analysing the influence of an enhanced dispersal to the functional resistance.

1.5.4 *Chapter 5: Emergence of functional collapse and its prevention*

In Chapter 5 recurrent disturbances varying in their spatial occurrence are applied for assessing conditions and processes preventing a functional collapse. The disturbance return interval is systematically varied and the resistance in terms of total biodegradation performance and complete collapse of the system observed. For analysing ecological key processes for preventing the functional collapse, the growth rate and the diffusion coefficient of the bacteria are varied. Again, the scenarios were simulated with additional dispersal networks for analysing whether increased dispersal may prevent the functional collapse.

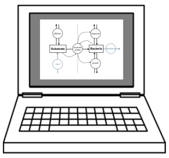
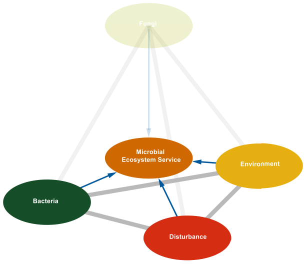
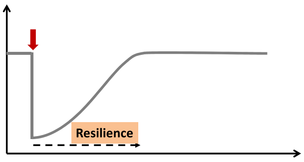
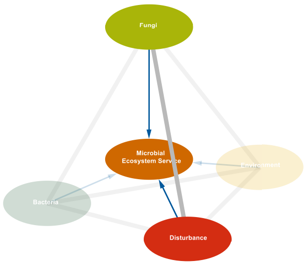
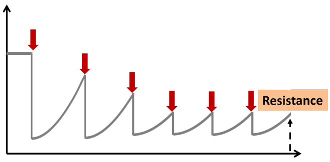
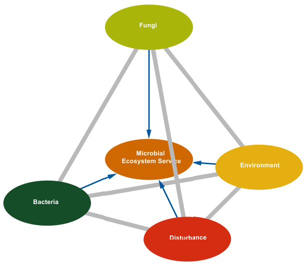
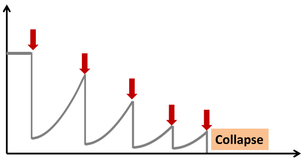
	Main focus	Disturbance	Stability concept
		Implementation	-
Chapter 3		single varying fragmentation	
Chapter 4		recurrent varying fragmentation varying return interval	
Chapter 5		recurrent varying fragmentation varying return interval varying spatial configuration	

Figure 1.5: Overview of chapters of this thesis regarding the main focus, applied disturbance event and stability concept.

1.5.5 *Chapter 6: Synthesis and Outlook*

Within Chapter 6 , the main results are summarized and discussed regarding the objectives of this thesis and implications for natural systems. The developed model is critically assessed considering both strengths and limitations. The chapter finishes with open questions and ideas for further studies. Several potentially key factors for the functional stability are discussed.

2

THE MODELLING FRAMEWORK *eColony*

For addressing the specific research questions of this thesis, we develop the bacterial simulation model *eColony*. The model describes a bacterial consumer-resource system for simulating bacterial growth, bacterial dispersal and degradation of organic pollutants for analysing spatiotemporal dynamics of microbial activity under different heterogeneous conditions and disturbances of varying spatial configurations. Following a 'virtual lab' approach using *eColony*, we aim to give insights into general phenomena and provide principle understanding of determinants of functional stability rather than investigating a specific case study. Accordingly, virtual microbial ecosystems are exposed to systematically varied disturbances for analysing the key factors of the functional stability in terms of resistance and resilience at the global and the local scale. In the following, the underlying base model and its processes are described and afterwards the developed extensions are presented in detail.

2.1 BASE MODEL

The population-based, deterministic model *eColony* describes the dynamics of bacterial biomass and substrate spatiotemporally explicitly on a circular area representing an agar-plate with a diameter of 88 mm consisting of habitats with a size of 1 mm^2. Boundaries of the system are reflective.

The spatiotemporal dynamics of both bacterial and substrate concentrations are approximated with a finite difference method [Banitz et al., 2011a] according to the following set of reaction-diffusion equations:

$$\frac{\partial C_x}{\partial t} = \nabla(D_x(C_x, C_s)\nabla C_x) + (q(C_s)Y_G - a - d(C_x, C_s))C_x, \tag{2.1}$$

$$\frac{\partial C_s}{\partial t} = D_s \nabla^2 C_s - q(C_s)C_x, \tag{2.2}$$

where C_x is the concentration of bacteria ($g_x l^{-1}$) and C_s the concentration of substrate ($g_s l^{-1}$). D_x and D_s are the diffusion coefficients of bacteria and substrate ($cm^2 s^{-1}$), q is the specific substrate uptake rate of bacteria ($g_s g_x^{-1} h^{-1}$), Y_G the growth yield coefficient ($g_x g_s^{-1}$), a the specific maintenance rate (h^{-1}), and d the specific dispersal cost, expressed as a biomass decrease rate (h^{-1}).

One simulation time step of one minute includes the following processes: substrate uptake by bacteria, uptake allocation to energy-demanding tasks, bacterial dispersal, bacterial growth and reproduction, and substrate diffusion.

The specific substrate uptake rate of bacteria q is calculated using Monod kinetics according to

$$q = q_{max} \frac{C_s}{C_s + K_s}, \tag{2.3}$$

with q_{max} as maximum specific uptake rate ($g_s g_x^{-1} h^{-1}$) and K_s as half-saturation constant ($g_s l^{-1}$). The maximum specific uptake rate q_{max} depends on the maximum specific growth rate μ_{max}, the specific maintenance rate a and the growth yield coefficient Y_G of the bacteria

$$q_{max} = \frac{\mu_{max} + a}{Y_G}. \tag{2.4}$$

The bacterial diffusion coefficient D_x and the specific dispersal cost d are variables that depend on the bacterial concentration C_x and the substrate concentration C_s. D_x is related to the bacterial concentration and the substrate uptake rate q according to

$$D_x(C_x, q) = \alpha(C_x) \cdot D_x(q). \tag{2.5}$$

The term $\alpha(C_x)$ describes the dependence on the bacterial concentration

$$\alpha(C_x) = \begin{cases} \varphi_{min} + (1 - \varphi_{min}) \frac{C_x}{C_{x,\varphi}}, & C_x \leqslant C_{x,\varphi} \\ 1 & C_x > C_{x,\varphi}, \end{cases} \tag{2.6}$$

with φ_{min} being the minimum dispersal fraction and $C_{x,\varphi}$ the dispersal reduction limit ($g_x l^{-1}$). Thus, dispersal is reduced if the bacterial concentration C_x falls below the dispersal reduction limit $C_{x,\varphi}$. The bacterial diffusion coefficient D_x in dependence of the substrate uptake rate q is calculated using

$$D_x(q) = D_{x,max} \cdot \begin{cases} 0 & q < \widetilde{a}. \\ \frac{q - \widetilde{a}}{(\widetilde{a} + \widetilde{d}_{max}) - \widetilde{a}} & \widetilde{a} \leqslant q < (\widetilde{a} + \widetilde{d}_{max}). \\ 1 & (\widetilde{a} + \widetilde{d}_{max}) \leqslant q. \end{cases} \tag{2.7}$$

Thus, the value of D_x is set to the maximum bacterial diffusion coefficient $D_{x,max}$ if the substrate uptake is above the energy costs for maintenance $\widetilde{a}$ ($g_s g_x^{-1} h^{-1}$) and for maximum dispersal $\widetilde{d}_{max}$ ($g_s g_x^{-1} h^{-1}$), and the bacteria disperse as fast as they can. Dispersal is reduced if substrate uptake is lower than these energy costs and set to 0 if the uptake falls below the maintenance cost.

The specific dispersal cost d (h^{-1}) is then determined by the bacterial diffusion coefficient D_x

$$d = d_{max} \frac{D_x}{D_{x,max}}. \tag{2.8}$$

For simulating dispersal networks acting as highways for the bacteria (Sec. 1.1.4), corridors with a higher diffusivity are implemented. Is this additional module activated, the bacteria disperse faster in the corresponding habitats through which the network is going. Here, the maximum bacterial diffusion coefficient $D_{x,max}$ is higher. However, the efficient bacterial diffusion coefficient D_x depends on the substrate concentration according to Equation 2.7, but not on the bacterial concentration C_x.

2.1.1 *Model validation*

The model was validated with selected laboratory experiments with *Pseudomonas putida* PpG7 as a model organism and glucose as model substrate [Banitz et al., 2012]. Bacterial colonies were grown in Petri dishes of diameter 88 mm on minimal medium agar with homogeneously distributed substrate at 30°C. According to the results obtained from this experiments, the maximum bacterial diffusion coefficient $D_{x,max}$ was fitted by direct search optimization. Diffusion coefficients on dispersal networks were fitted according to laboratory experiments using disposable polymer coated glass fibres for simulating the properties of fungal hyphae to build a continuous water film [Banitz et al., 2011a].

The maximum growth rate μ_{max} was approximated from growth on liquid minimal medium containing 2 gl^{-1} glucose as sole energy source as decribed by Wick et al. [2001].

2.2 EXTENDED MODEL

For analysing the biodegradation dynamics under disturbances the model *eColony* was extended within this thesis by implementing disturbance events and a permanent substrate input. In Figure 2.1 processes and relationships of the extended model *eColony* are summarized.

2.2.1 *Disturbance events*

Disturbance events were introduced as an instantaneous drastic reduction of bacterial biomass C_x within a defined disturbance area DA at specific time points t_{dist} according to

$$C_x(t_{dist+1}, i, j) = \widehat{\varepsilon}(i, j) \cdot C_x(t_{dist}, i, j), \tag{2.9}$$

where i and j are Cartesian coordinates of habitats, t_{dist} refers to the time point of the disturbance event, t_{dist+1} to the directly following timepoint, and $\widehat{\varepsilon}(r)$ indicates the fraction of surviving bacterial biomass

$$\widehat{\varepsilon}(i, j) = \begin{cases} \varepsilon & i, j \in DA, \\ 1 & \text{otherwise}, \end{cases} \tag{2.10}$$

where $0 < \varepsilon < 1$ is the fraction of bacterial biomass surviving a disturbance area DA.

2.2.2 *Substrate input*

A permanent substrate input was implemented representing a subsequent dissolution [cf. Keymer et al., 2006; Centler et al., 2011]. In each simulation step the substrate is refilled depending on the difference between a given maximum ($C_{s,max}$) and the current (C_s) substrate concentration within a habitat

$$\frac{dC_s}{dt} = \lambda \cdot (C_{s,max} - C_s), \tag{2.11}$$

with λ as the substrate input rate parameter (h^{-1}).

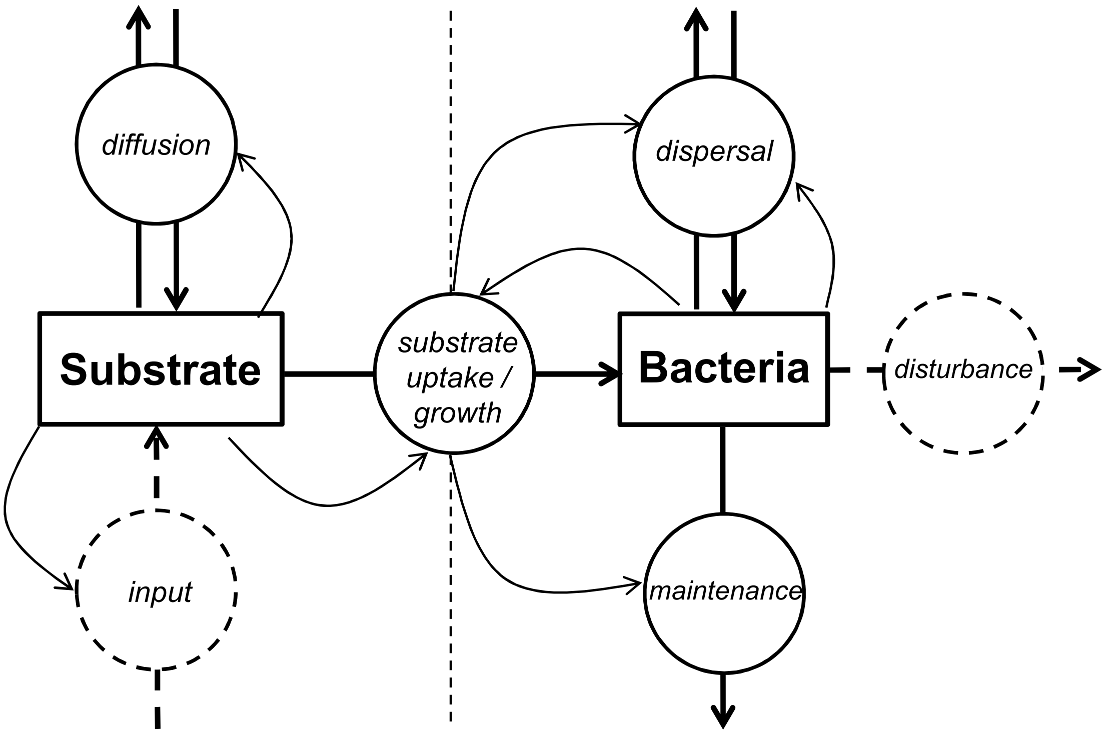


Figure 2.1: Simplified diagram of the model entities 'bacteria' and'substrate' and the processes described (cf. Eqs. 2.1, 2.12). The amount of substrate in each habitat is increased due to the substrate input (Eq. 2.11) and incoming substrate from surrounding habitats by diffusion. In turn, substrate is reduced by diffusion to surrounding habitats. Bacteria are directly reducing the substrate by the process substrate uptake, the amount consumed depends both on the present concentrations of substrate and bacteria (Eqs. 2.3, 2.12). Bacteria are dispersing within the system in dependence of their concentrations and the substrate uptake (Eqs. 2.5, 2.7). Bacterial biomass is increased due to growth, which is determined by the substrate uptake (Eq. 2.1). Bacterial biomass is decreased due to negative growth if the substrate uptake is below the maintenance cost (Eq. 2.1). Bacterial biomass is also decreased in case of a disturbance event at time point t_{dist} (Eq. 2.9). Processes developed for the extended model are marked with dashed lines.

Considering the depicted extension, the reaction-diffusion Equation 2.2 was extended to

$$\frac{\partial C_s}{\partial t} = D_s \nabla^2 C_s + \lambda \cdot (C_{s,max} - C_s) - q(C_s) C_x. \tag{2.12}$$

2.3 SCENARIOS

2.3.1 *Initial conditions*

Based on the substrate input (Eq. 2.11), a steady state of the undisturbed system is defined at which the substrate input matches exactly the uptake of the bacteria in the system and this uptake matches exactly their maintenance

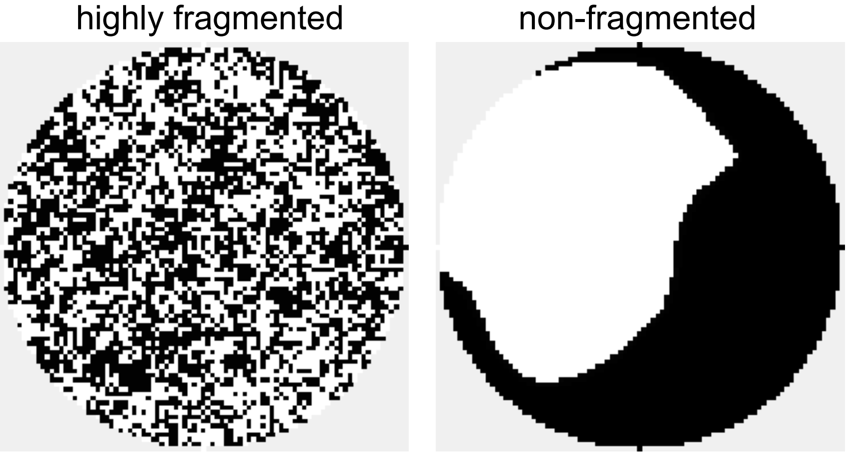


Figure 2.2: Examples of disturbance patterns with highest (H=-1) and lowest (H=2) fragmentation (black: disturbed area, white: undisturbed area).

$$\lambda \cdot (C_{s,max} - C_s) = q \cdot C_x = \frac{a}{Y_G} \cdot C_x. \tag{2.13}$$

Thus, the steady state bacterial population remains constant as it continuously receives sufficient energy for maintenance but not for growth and dispersal. Initial bacterial biomass concentration C_x^* and initial substrate concentration C_s^* were set to the steady state values. These steady state conditions and the associated substrate uptake rate were used as reference for the performance of the disturbed systems.

2.3.2 *Disturbance regimes*

Disturbance events were applied at a variable time point t_{dist} on a randomly picked disturbance area and assumed to be lethal, i.e. reducing the bacterial biomass within the disturbance area. Bacteria in the undisturbed area were not directly affected by the disturbance.

For analysing the influence of the spatial distribution of the disturbance, patterns with different spatial configurations were applied following an ensemble approach [Brown et al., 2010; Gal et al., 2014]. Disturbance patterns were created using the midpoint displacement algorithm to create random fractal landscapes [e.g. Saupe, 1988]. The disturbed area was defined by its relative size p and the fragmentation parameter H [cf. Banitz et al., 2011b]. The relative size p was set to 50 % of the simulation area for all studies. The fragmentation parameter H was varied for generating disturbance patterns with different fragmentation levels. Examples for generated disturbance patterns are given in Figure 2.2. The fragmentation ranged from highly fragmented disturbance pattern with H=-1 to completely non-fragmented disturbance patterns with H=2. See single chapters for exact variations within the specific studies.

Each randomly generated disturbance pattern can be fixed over different simulations such that the same disturbance pattern is used for several simulations in which other parameters were varied, for instance, the fraction of surviving biomass ε or certain parameters determining ecological processes such as bacterial growth or dispersal.

This allowed for excluding potential effects created by particularities of different exact spatial configurations and enhanced the comparability among several simulations.

2.3.3 *Parameterization*

An overview of the used parameters and initial conditions is given in Table 2.1. Values are valid for all modelling studies except for Chapter 5, where the maximum specific growth rate μ_{max} and the maximum bacterial diffusion coefficient $D_{x,max}$ were varied (cf. Tab. 5.1).

Parameter/State variable	**Symbol**	**Value**	**Unit**^{a}	**Source**
Maximum specific growth rate	μ_{max}	0.347	h^{-1}	[Banitz et al., 2016]
Specific maintenance rate	a	0.0003	h^{-1}	[Banitz et al., 2011a]
Growth yield	Y_G	0.6	$g_x g_s^{-1}$	[Banitz et al., 2011a]
Maximum substrate uptake rate	q_{max}	0.578	$g_s g_x^{-1} h^{-1}$	Eq. 2.4
Half-saturation constant	K_S	0.09	$g_s l^{-1}$	[Banitz et al., 2011a]
Maximum bacterial diffusion coefficent	$D_{x,max}$	5.9E-07	$cm^2 s^{-1}$	[Banitz et al., 2012]
Maximum bacterial diffusion coefficent along dispersal networks	$D^{dn}_{x,max}$	0.0004	$cm^2 s^{-1}$	[Banitz et al., 2011a]
Substrate diffusion coefficent	D_s	6.46E-06	$cm^2 s^{-1}$	[Zhang and Fang, 2005]
Substrate input rate	λ	0.24	h^{-1}	[Keymer et al., 2006]
Maximum substrate concentration	$C_{s,max}$	0.1	$g_s l^{-1}$	-
Initial bacterial concentration	C^*_x	47.98	$g_x l^{-1}$	steady state of undisturbed system
Initial substrate concentration	C^*_s	0.78E-05	$g_s l^{-1}$	steady state of undisturbed system

^{a} g_x - grams of dry biomass, g_s - grams of substrate

Table 2.1: Model parameters and initial conditions.

2.3.4 *Analyses*

The functional stability can be assessed at the global and the local scale by analysing the biodegradation performance in the entire system as well as in single habitats.

Spatial analyses can be performed for understanding the influence of the spatial configuration of the disturbance pattern, for instance by varying the degree of fragmentation. Moreover, ensembles of disturbance patterns with the same degree of fragmentation but different explicit spatial configuration can be generated. These ensembles can be analysed using statistical measures such as the mean, standard deviation and range between minimum and maximum values of biodegradation performance over all runs with the same disturbance characteristics. The latter two measures indicate whether the different explicit spatial configurations are decisive. All three measures can be analysed and compared for different degrees of fragmentation. Furthermore, the influence of the spatial configuration of the disturbance pattern on the functional stability can also be analysed by implicitly characterizing the disturbance patterns in terms of the distances between disturbed and undisturbed area within the system. Therefore, as a typical implicit spatial metric, the mean distance Δ between habitats in the disturbed and the nearest habitat in the undisturbed area was calculated according to

$$\Delta = \frac{1}{|DA|} \sum_{(i,j)\in DA} min_{(k,l)\in UA} \sqrt{(k-i)^2 + (l-j)^2}, \qquad (2.14)$$

where $|DA|$ is the number of disturbed habitats, DA is the set of disturbed habitats, UA the set of undisturbed habitats, and i, j, k and l are Cartesian coordinates of habitats. The suitability of this aggregated spatial metric as an indicator for the functional stability was tested.

3

FUNCTIONAL RESILIENCE TO SINGLE DISTURBANCE EVENTS*

3.1 INTRODUCTION

As discussed in Section 1.2, environmental disturbances may have an important impact on microbial ecosystems and should be considered when analysing their dynamics, functions and stability properties. As microbial ecosystem services such as biodegradation are known to be determinants for various aspects of human well-being, their supply ought to be sufficiently secure, even in face of change and disruption in the environmental conditions affecting the underlying microbial ecosystem [Millennium Ecosystem Assessment, 2005]. This underpins the importance of 'functional resilience' of microbial ecosystem services, measured in terms of the recovery of their performance in responses to a certain disturbance (Fig. 3.1), and the urgency to understand its determinants [Biggs et al., 2012]. To understand the key factors enhancing functional resilience, however, is a challenge. It requires insights into the functioning of the underlying microbial ecosystem, its dynamic response to the disturbance, and the mechanisms determining its ability to recover. An approved approach for analysing dynamics and mechanisms in ecosystems is the use of modelling. Computational simulation models give us the opportunity to observe spatiotemporal dynamics and also to examine the underlying mechanisms in detail. By simulating different scenarios with varying parameters, the sensitivity of certain processes and mechanisms is detectable. This allows for identifying the main key factors of the system controlling the state variable or function of interest.

In environmental microbiology, modelling approaches are successfully used for understanding and predicting systems behaviour, as was already depicted in Section 1.3 [Murphy and Ginn, 2000; O'Donnell et al., 2007; Esser et al., 2015]. However, no attempts have yet been made to model the dynamic responses of the ecosystem service 'biodegradation' to a certain disturbance and to analyse its recovery.

In this chapter, we present a methodology for systematically assessing the functional resilience of biodegradation to disturbance events of different intensities and spatial patterns of occurrence. The methodology is based on ecological modelling in combination with scenario analysis. The modelling framework *eColony* presented in Chapter 2 is used to systematically simulate versatile disturbance scenarios with the aim to reveal insights into (i) key factors of the functional resilience of biodegradation, (ii) the temporal dynamics of the functional recovery after disturbances of varying intensities, (iii) the relative importance of involved processes such as bacterial growth and bacterial dispersal, and (iv) possible indicators for the recovery behaviour derived from the spatial pattern of occurrence of the disturbance itself.

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* A research paper with analogous content to this chapter has been submitted (title: 'Modelling functional resilience of microbial ecosystems: analysis of governing processes')

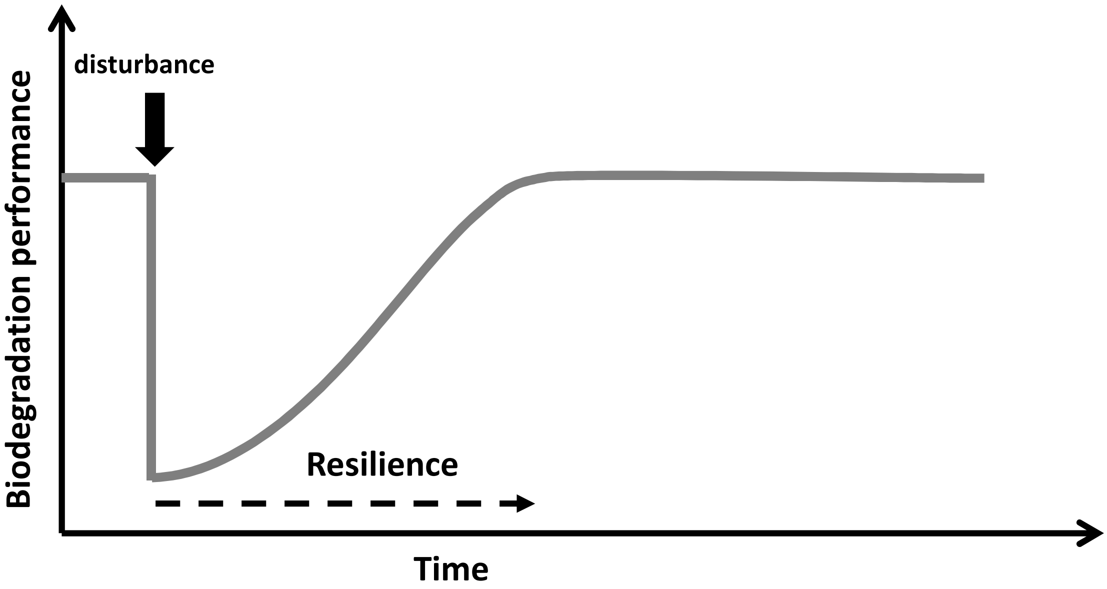


Figure 3.1: Scheme of functional resilience: The function biodegradation is recovered after a pulse disturbance

Figure 3.2: Examples of disturbance patterns with (a) high (H=0), (b) moderate (H=0.5), and (c) low (H=1) fragmentation (black: disturbed area, white: undisturbed area).

3.2 METHODS

3.2.1 *Scenarios*

Initial conditions of bacterial biomass and substrate concentration were set according to the reference state (Tab. 2.1). Single disturbance events were introduced according to Equation 2.9, occurring once for each simulation after 20 hours. The survivorship ε was varied between 10^{-9} (highest disturbance intensity) and 10^{-2} (lowest disturbance intensity) in logarithmic steps.

Disturbance patterns were generated as described in Section 2.3.2 and the fragmentation parameter H varied with 0 for high fragmentation, 0.5 for moderate fragmentation and 2 for no fragmentation (Fig. 3.2).

3.2.2 *Analysis*

For any given scenario and any point in simulation time, the biodegradation performance is defined as the current substrate consumption rate ($g_s h^{-1}$) in relation to the consumption rate in steady state. Accordingly, the recovery time is defined as the time required after a disturbance event to reach 95% biodegradation performance (i.e. to recover 95% of the steady state performance).

Additionally, the spatiotemporal dynamics of recovery were observed. For that purpose, the biodegradation performance was measured aggregated in the whole system as well as for each single habitat, and the dynamics of recovery analysed with respect to the habitats' position relative to the disturbance area.

A mechanistic analysis was performed by calculating the difference in the trend of the biodegradation performance of the same scenarios with switched-off processes. Selected scenarios with the highest disturbance intensity and a moderately fragmented disturbance pattern were simulated with each of the following main processes completely switched-off separately: bacterial growth, bacterial dispersal and both spatial processes (bacterial dispersal and substrate diffusion). Therefore, in these cases, either the bacterial growth rate or the bacterial diffusion coefficient or both the bacterial and the substrate diffusion coefficient were set to 0.

Following an ensemble approach, sets of disturbance patterns with the same degree of fragmentation were applied for testing the influence of the spatial configuration of the disturbance pattern. For analysing the relevance of the explicit spatial configuration of the disturbance pattern for the recovery of the biodegradation performance and the predictive power of aggregated spatial metrices, the mean distance between habitats in the disturbed and the nearest habitat in the undisturbed area Δ was calculated according to Equation 2.14.

3.3 RESULTS AND DISCUSSION

3.3.1 *Spatiotemporal dynamics of recovery*

The recovery of the biodegradation performance after a moderately fragmented disturbance event affecting half of the system's area (e.g. see Fig. 3.2b) varies with the disturbance intensity (Fig. 3.3). Obviously, an increasing percentage of biomass surviving the disturbance event enhances recovery and reduces the recovery time. Recovery times range from 32 hours for the lowest applied disturbance intensity ($\varepsilon = 10^{-2}$) to 249 hours for the highest applied disturbance intensity ($\varepsilon = 10^{-9}$). Strikingly, in addition to varying recovery times, the shapes of the biodegradation curves vary for different disturbance intensities as well. For less intensely disturbed scenarios, the recovery curves show the typical exponential shape often reported in ecological theory: a quick increase of the biodegradation rate followed by a saturation up to full recovery. The biomass that survived in the disturbed area is able to recover the biodegradation activity quickly and thus the effect of the disturbance on the function is low. When the disturbance is more intense (i.e. fewer bacteria survive in the disturbed habitats), the biodegradation curves increasingly deviate from the exponential shape and become sigmoidal instead. After a comparable quick increase during the first hours, the biodegra-

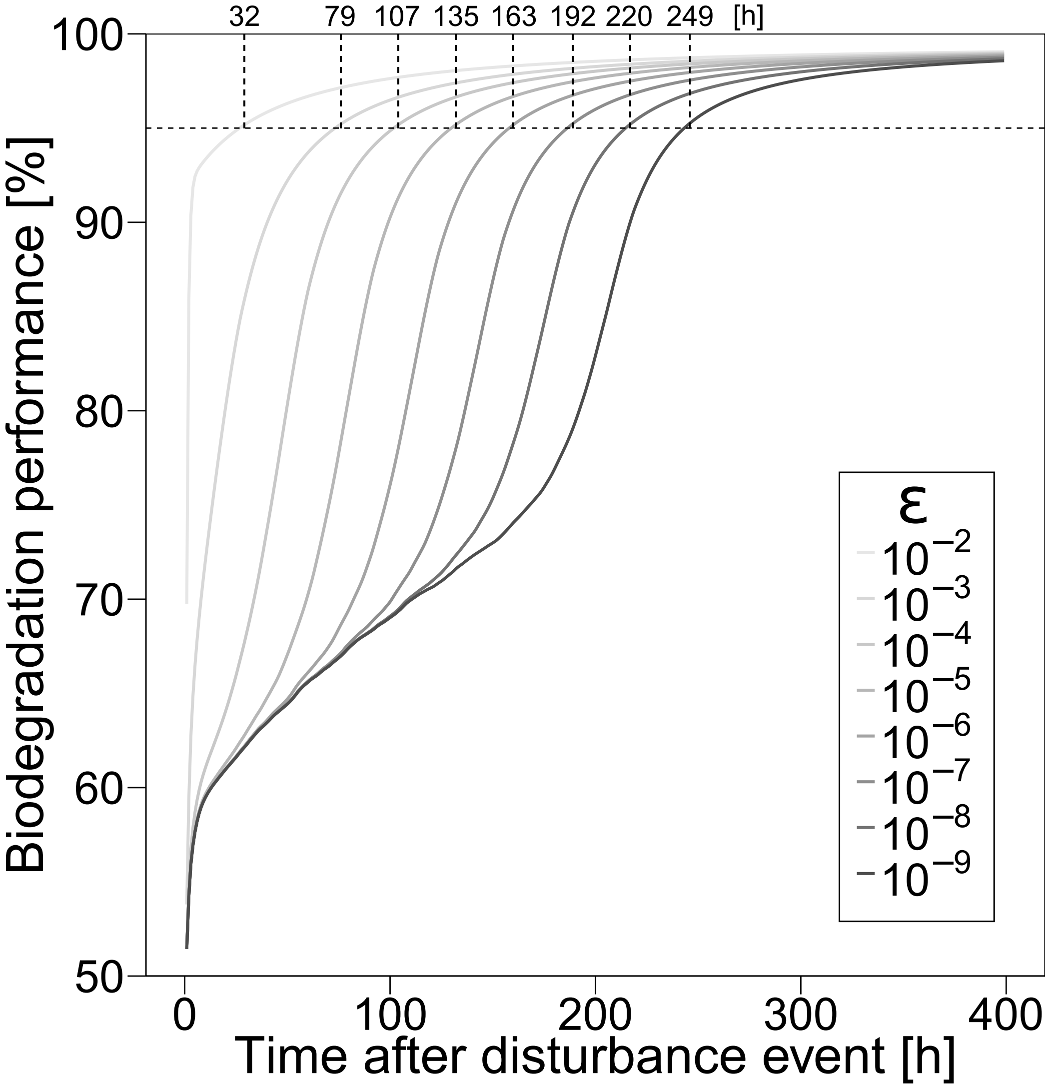


Figure 3.3: Biodegradation performance over time after a moderately fragmented disturbance event with different fractions of biomass surviving the disturbance event (ε) decreasing from light grey to dark grey. Dashed lines on the top of the graph indicate recovery times (with respect to 95% of steady state performance).

dation performance slows down until it enters a second phase of quick increase and approaches the saturation towards maximum recovery. With increasing disturbance intensity, the initiation of this second phase of quick increase is obviously delayed and shifted to later points in time (cf. spread of different curves in Fig. 3.3). However, recovery trends between the various scenarios do not differ during the increase in the first hours. This indicates that, in the first phase, the quick recovery is insensitive to the disturbance intensity and thus other factors than the surviving bacterial biomass in disturbed areas seem to be responsible for the recovery. Consequently, different processes may determine the overall recovery of biodegradation during different phases, and additionally spatial processes can play a role in performance recovery.

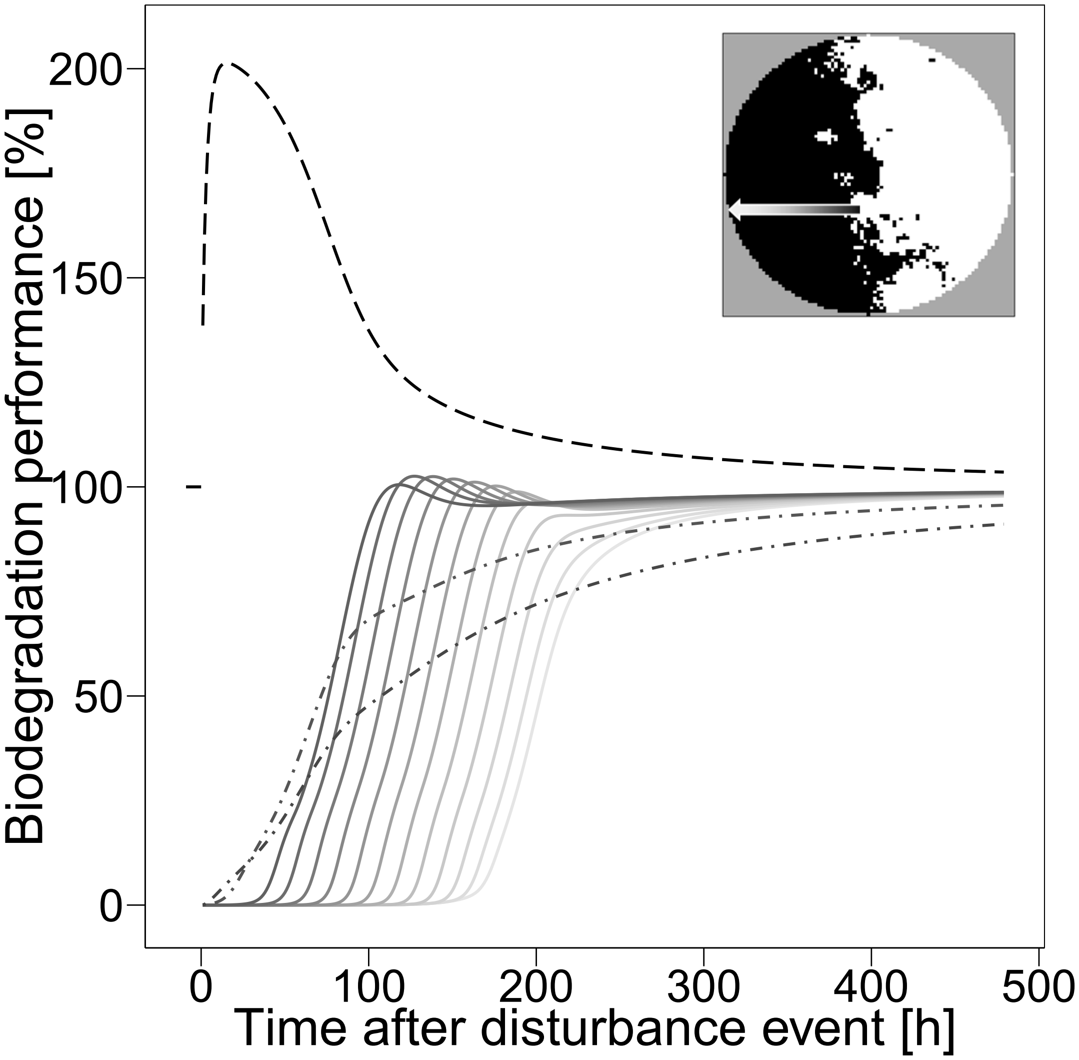


Figure 3.4: Local biodegradation performance over time after a moderately fragmented disturbance event in different habitat types. Habitats along a transect are shown (see arrow in the inset), including one undisturbed habitat at the direct interface to the disturbed area (black, dashed line) and disturbed habitats with increasing distance to the undisturbed area (lines from dark grey to light grey, dot-dashed lines show closest habitats to the undisturbed area). ε is set to 10^{-9}.

To further analyse these spatiotemporal recovery dynamics, we assessed the local biodegradation performance over time in different habitats. This analysis of different locations shows that the initiation of recovery is more and more delayed with increasing distance to the undisturbed area (Fig. 3.4). An exception are the border habitats in the vicinity of the undisturbed area. In these habitats, initial recovery after the disturbance event is faster than in the more distant habitats (dark grey dot-dashed lines in Fig. 3.4). However, after a few hours, the biodegradation rate increases much more slowly compared to the other disturbed habitats. The relative position of the habitats to the undisturbed area, thus, is a key factor determining the functional recovery. In the undisturbed border habitat, a very high increase of up to twice the steady state biodegradation performance is observed in the first hours after the disturbance event. Shortly afterwards, the biodegradation performance declines until it approaches the steady state level. The strong increase in the first hours is due to incoming substrate from the nearby disturbed area. Due to the reduced biomass in the disturbed area, most of the inflowing substrate is not consumed and diffuses to surrounding habitats with lower substrate concentrations (i.e. the undisturbed habitat where bacterial consumption leads to low substrate concentrations). In consequence, bacteria in the undisturbed border habitats receive more substrate, can grow from this additional substrate and, thus, increase the biodegradation performance compared to steady state conditions. This, in turn, also explains the biodegradation dynamics in the disturbed border habitats: The higher bacterial biomass and substrate consumption in the undisturbed border area fosters diffusion of substrate away from the disturbed border area and, thus, slows down the biodegradation performance recovery in these disturbed border habitats. However, when the bacterial biomass in the disturbed area increases again, this phenomenon gets less pronounced and, in consequence, the biodegradation performance in the undisturbed border habitat decreases again (cf. black dashed line in Fig. 3.4).

3.3.2 *Relevance of processes*

For further disentangling the mechanisms governing the observed spatiotemporal recovery dynamics, the simulations were repeated and either bacterial growth, bacterial dispersal or both spatial processes (bacterial dispersal and substrate diffusion) were switched off separately. The obtained results were compared to the reference scenario where all processes were activated (Fig. 3.5). This analysis allows for the identification of limiting processes based on how and when their deactivation alters functional recovery.

In the undisturbed habitat (Fig. 3.5a), the biodegradation rate remains at steady state level when all spatial processes are switched off, thus this habitat type plays no role in the system's recovery. In contrary, when only bacterial dispersal is switched off, the biodegradation performance is even higher compared to the reference scenario. This observation is explainable due to the fact that bacteria could not emigrate to surrounding habitats and, thus, they strengthen the local biodegradation performance. Without growth, biodegradation is also higher in this undisturbed border habitat as the competition with the neighbouring disturbed habitats is lower due to the absence of regrowing bacterial biomass in these habitats. In consequence, incoming substrate allows for the high increase of the biodegradation performance in this habitat type.

In the disturbed border habitat (Fig. 3.5b), the recovery of biodegradation is slower when the bacteria are immobile because the recolonization by bacteria from the neighbouring undisturbed habitats is prohibited. A similar effect can be seen when the process growth is switched off because then bacteria can immigrate into the disturbed border habitats but can not further strengthen the performance by growth. When both spatial processes are switched off, the surviving organisms in the disturbed border habitats benefit from the substrate accumulation, since substrate does not diffuse to the surrounding habitats.

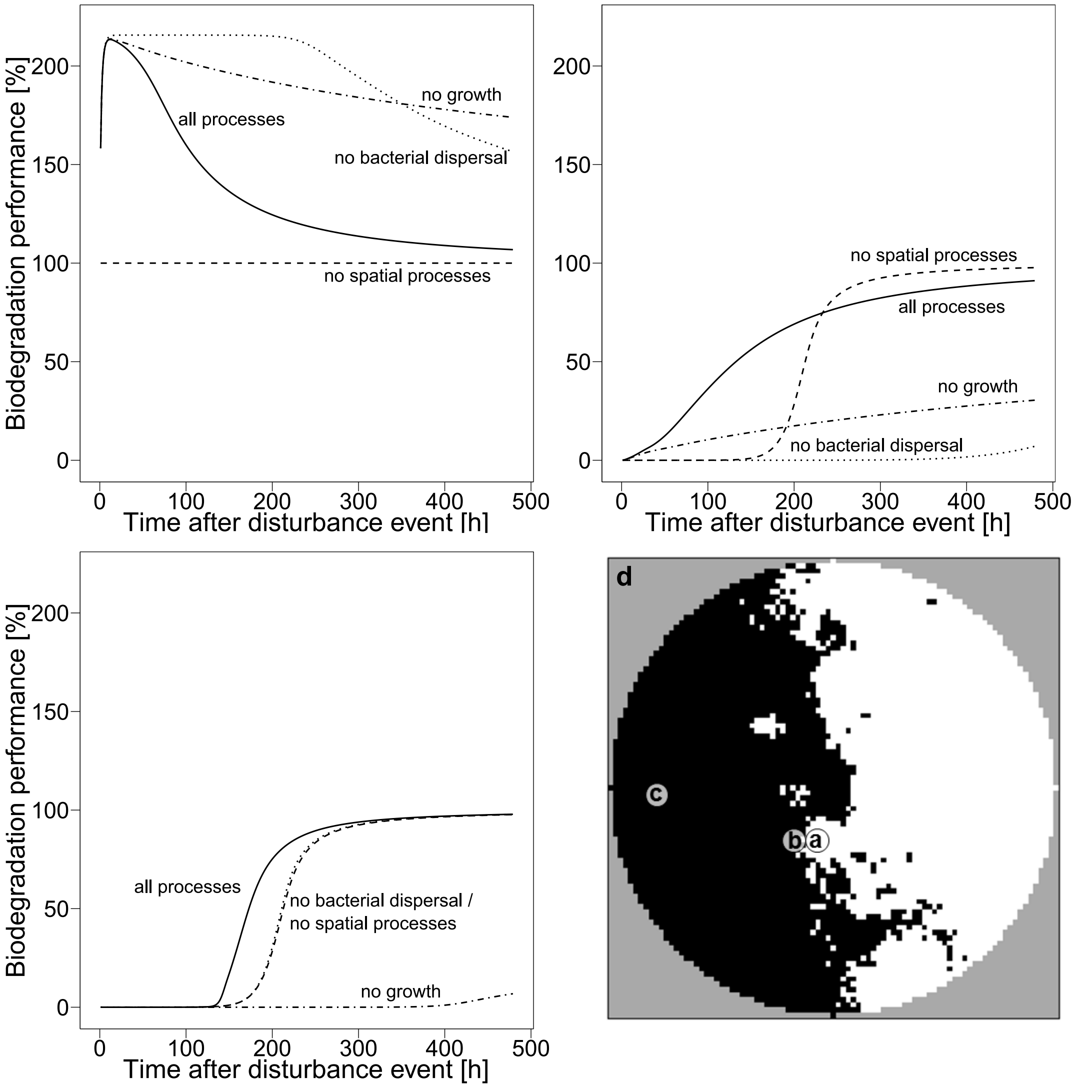


Figure 3.5: Local biodegradation performance over time in three different habitat types: an undisturbed border habitat (a), a disturbed border habitat (b), and a disturbed habitat farther away from the undisturbed area (c), locations are indicated on simulated disturbance pattern (d). The simulations were performed with the bacteria being not able to grow (dot-dashed line), not mobile (dotted line), the substrate not diffusing and the bacteria not mobile (dashed line) and with all processes switched on (solid line).

In the habitat with a longer distance to the undisturbed area (Fig. 3.5c), the functional recovery is dominated by regrowth of the surviving bacteria, as can be seen from the very long time until biodegradation performance increases when growth is switched off. Switching off spatial processes makes only a small difference compared to the standard scenario.

In summary, the limiting processes for local recovery change substantially depending on the relative position of the habitat. Spatial processes are the limiting factor at the border of disturbed and undisturbed area. With increasing distance to the undis-

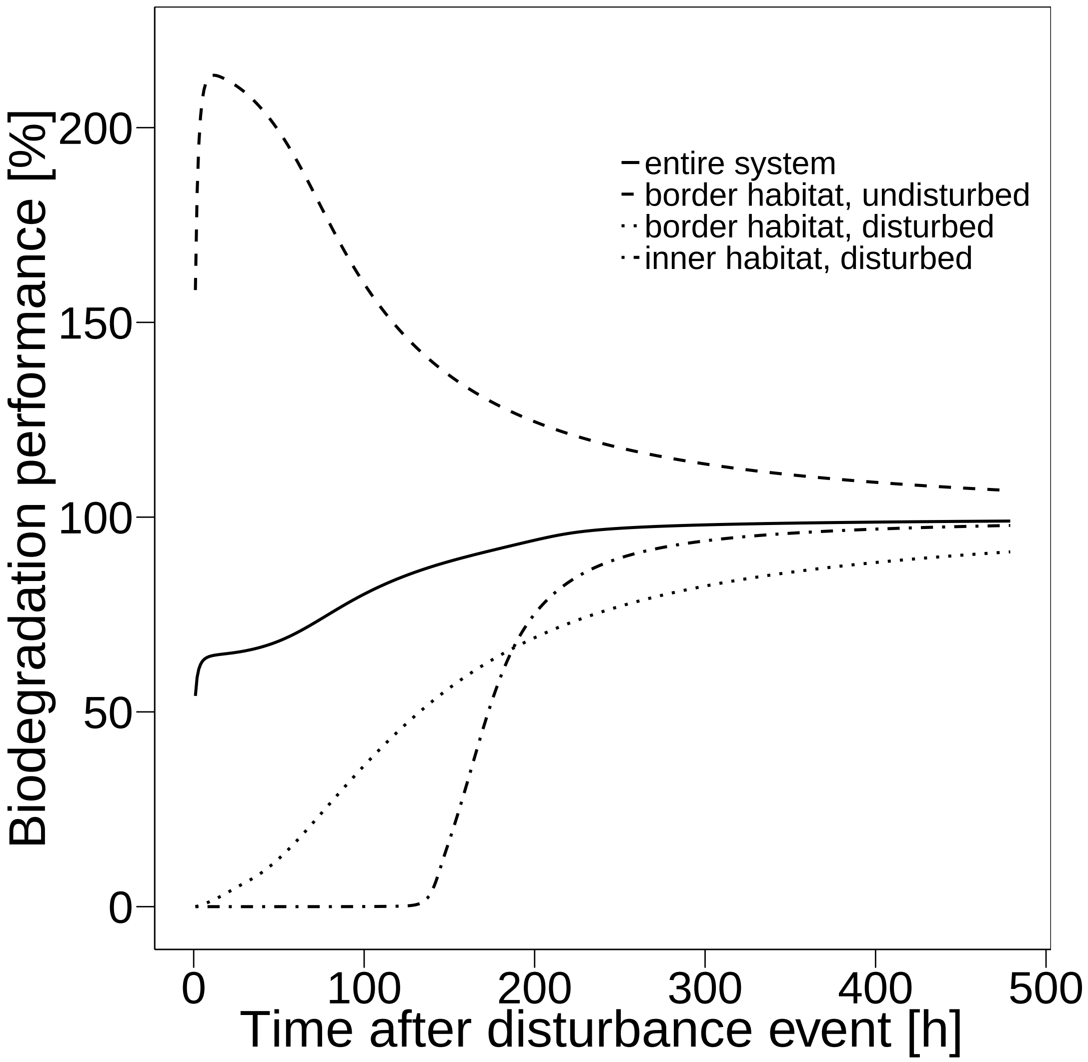


Figure 3.6: Overall biodegradation performance of the system (solid line) compared to local biodegradation performances in three habitats of different location: undisturbed area at the border (dashed line), disturbed area at the border (dotted line) and farther away from the undisturbed area (dot-dashed line).

turbed area the process growth gets more and more important for the recovery of biodegradation.

3.3.3 *Relevance of spatial disturbance pattern*

The whole system's biodegradation performance over time shows that different habitats are mainly responsible for different phases of the functional recovery (Fig. 3.6). The initial increase of biodegradation performance after the disturbance event is predominantly caused by undisturbed habitats at the interface to the disturbed area (dashed line, Fig. 3.6), where performance increases rapidly beyond the steady state level, before falling back to steady state level. The recovery in the initial phase is therefore driven by the spatial process of substrate diffusion which is the limiting factor in the undisturbed border habitats. In the phase afterwards, predominantly the habitats near the undisturbed areas are increasing the whole system's biodegradation performance as bacteria that have arrived here from undisturbed habitats consume the accumulated substrate (dotted line, Fig. 3.6). In this phase, bacterial dispersal is the main process for functional recovery and the limiting factor in the disturbed border habitats. In the last phase, regrowth of bacteria in the whole disturbed area brings the system back to its full biodegradation performance (dot-dashed line, Fig. 3.6). Thus, the limiting mechanisms for functional recovery depend on the habitats' locations with respect to the disturbed area, and consequently, this recovery is influenced by the spatial occurrence of the disturbance pattern.

Therefore, we simulated scenarios with different degrees of fragmentation of the disturbance pattern as depicted in Section 3.2.1. As shown in Figure 3.7, the sensitivity of the biodegradation performance to these spatial variations in the disturbance patterns substantially changes with the disturbance intensity (measured in terms of the bacterial survivorship in the disturbed area ε, cf. Sec. 3.2.1). For a lower disturbance intensity, the biodegradation performance shows little variation among the different disturbance patterns (Fig. 3.7a). For a high intensity, in contrast, the situation is more complex. The shape of the biodegradation performance markedly differs for disturbance scenarios of different degrees of fragmentation. Among disturbance patterns of the same fragmentation degree, however, the variation in the biodegradation performance is low for high and low fragmentation, but high for moderate fragmentation (Fig. 3.7b). As depicted in Figure 3.7c,d, there is a clear correlation between the mean distance of disturbed to undisturbed habitats Δ and the recovery time: the less fragmented the disturbance pattern and thus the higher the mean distance, the slower is the functional recovery in the system. However, there is a threshold of the mean distance Δ above which its influence on the recovery time decreases down to no effects on the recovery time at all (Fig. 3.7c, d; threshold around $\Delta = 5$ mm). This is due to the shift in the driving process for the recovery in these scenarios: After less fragmented disturbances, functional recovery is not reached within the first phases dominated by spatial processes (Fig. 3.7a, b). Hence, bacterial growth, which dominates the last phase of functional recovery, becomes the key factor for further increasing the biodegradation performance. As growth is not influenced by the spatial configuration of the disturbance pattern, the recovery time is not further changing with an increased mean distance between disturbed and undisturbed habitats. In disturbance scenarios with a higher survivorship, the recovery times are much shorter than with lower survivorship (cf. Fig. 3.3), but in both cases, the correlation between recovery time and mean distance, and also the threshold mean distance for less fragmented disturbances, are visible (Fig. 3.7c, d). These results indicate that, when knowing the disturbance intensity, an estimation of the recovery time is possible solely based on the spatial configuration of the disturbance. Below a specific threshold of the mean distance Δ between disturbed and undisturbed habitats, the recovery time is increasing with this mean distance. These are the scenarios in which spatial processes were identified as most important for the functional recovery. However, above this threshold mean distance, the recovery time is unaffected by the spatial configuration of the disturbance pattern. Therefore, the mean

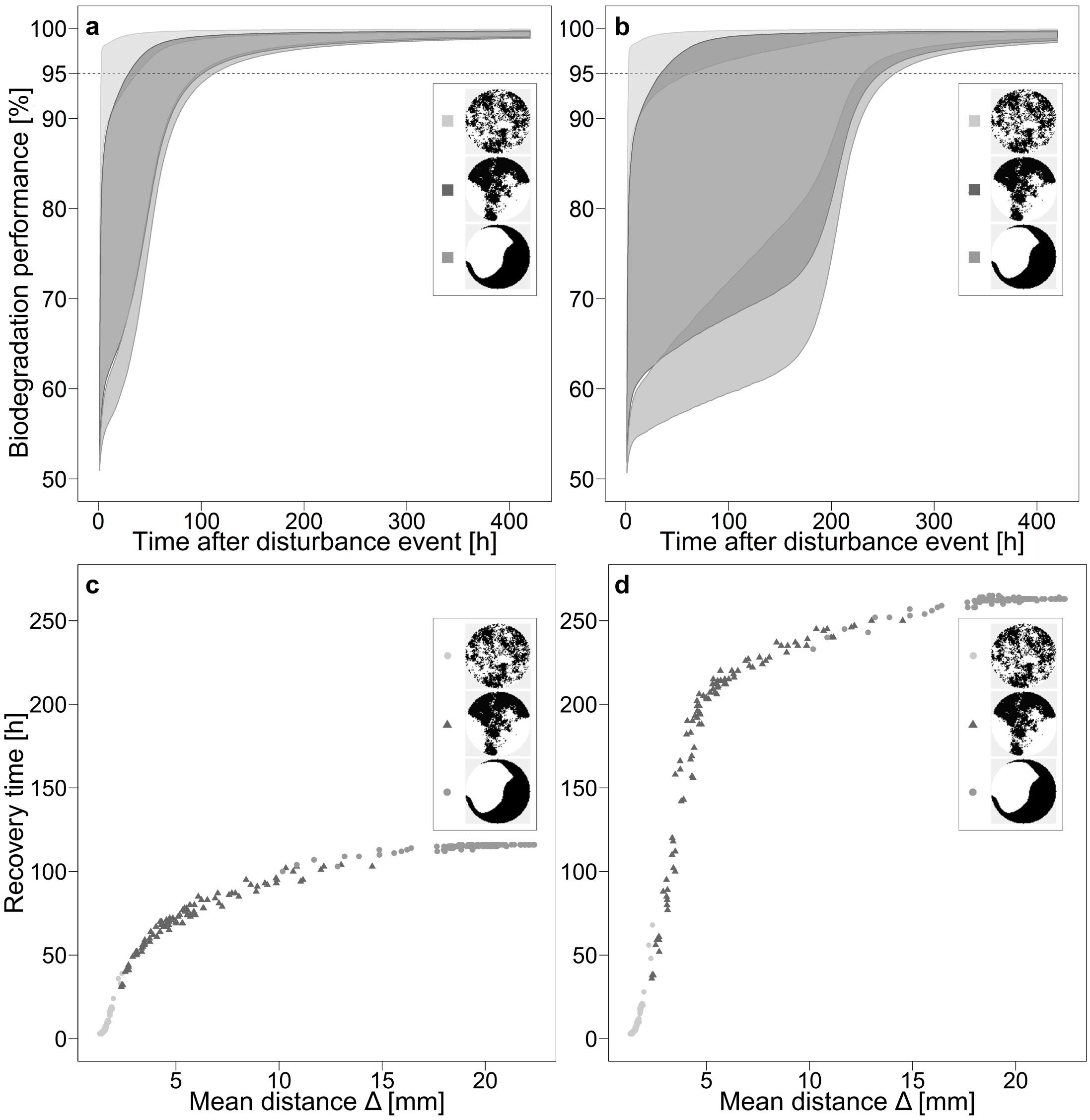


Figure 3.7: Ranges of biodegradation performance over time after a disturbance event (a and b) and recovery times over mean distance between disturbed and undisturbed habitats Δ (c and d) of 100 simulation runs for three different degrees of disturbance fragmentation and two different survivorships (a,c: $\varepsilon = 10^{-4}$; b,d: $\varepsilon = 10^{-9}$).

distance of disturbed to undisturbed area may be an indicator for determining the rate of recovery of biodegradation performance after a disturbance.

An increased structural and functional recovery of microbial ecosystems due to a higher connectivity between disturbed and undisturbed areas was shown in previous studies [Altermatt et al., 2011; Baho et al., 2012; Shade et al., 2012]. For instance, Altermatt et al. [2011] found a higher resilience of population density when a disturbed habitat was connected with an undisturbed habitat. Baho et al. [2012] observed a faster functional recovery after salt stress due to immigrating microorganisms from undisturbed areas. The importance of the spatial structure of the disturbance area and dispersal was also shown in previous modelling studies [Johst and Drechsler, 2003; Banitz et al., 2008].

3.3.4 *Implications for general ecological theory*

Despite its focus on resilience aspects of microbial ecosystems and biodegradation, the findings of this study can also enrich the debate on several concepts from general ecology. In textbooks on "ecological resilience", for instance, one often finds recovery functions with an exponential shape indicating a constant recovery rate and the chance to predict the respective recovery time on the basis of short-term information. Our study provides a case where the recovery function has a more complex shape as it is subdivided into phases with distinct recovery rates and governing processes mediated by spatiotemporal heterogeneity [Moloney and Levin, 1996; Hiebeler and Michaud, 2012; Seifan et al., 2012]. A phenomenon of particular relevance for the recovery of biodegradation was the "emergence of delays" the driving forces and impacts of which are of general interest in ecology. Among other processes, the study clarifies the role of dispersal for functional recovery and reveals that this role is context-dependent, as it can change in the course of the recovery and depend on the spatial pattern of the disturbance. This adds to the debates on "dispersal and evolution" [e.g. Lewis et al., 2013] and more specifically on "dispersal and survival in fragmented landscapes" [e.g. Settele et al., 1998; Heinz et al., 2006; Pe'er et al., 2011]. There is a certain analogy to findings that dispersal can only markedly enhance species survival if the dispersal range exceeds both the correlation length of local extinction and the distance between habitat fragments [Frank and Wissel, 1998; Palmqvist and Lundberg, 1998]. Last but not least, the study adds to the debate on "ecological implications of fragmentation" [for a synthesis review, see Lindenmayer and Fischer, 2013]. While the focus of this debate is primarily on habitat loss and fragmentation as regional threats to biodiversity and selected ecosystem services, this study adds a complementary perspective by addressing microbial ecosystems and their functional resilience and considering fragmentation as a characteristic of the spatial pattern of disturbances. These examples show that microbial ecosystems can serve as object for testing or advancing theories on general ecology, in particular if they are combined with appropriate modelling approaches.

3.3.5 *Implications for natural systems and applications*

Some of the presented results can lead towards model-based tools for decision-support in environmental management for enhancing the recovery of biodegradation after a single disturbance event. First, this concerns the functional recovery time which represents a characteristic time scale that can be used as yardstick for assessing the risk of degradation when the microbial ecosystem is exposed to recurrent disturbances. As was shown, the recovery time can be estimated from the disturbance intensity and an aggregated spatial metric of the disturbance pattern - the mean distance between disturbed and undisturbed habitats. Accordingly, the correlative relationship in Figure 3.7 (c, d) can be seen as a tool for assessing the recovery time. Second, the recognition that overall recovery is subdivided into phases of slowed and accelerated recovery sensitizes to a challenge: short-term information is not sufficient for extrapolating the long-term recovery dynamics, as this can lead to over- or underestimation of the total recovery time. Third, the study identifies the conditions under which dispersal is limiting for the recovery such that dispersal-enhancement is supposed to be an effective management strategy. This is the case if the disturbance is highly intense and at most moderately or less fragmented. Dispersal-enhancement can be achieved, for example, by fungal networks in soil that may act as transport vectors for bacteria [e.g. Kohlmeier et al., 2005; Wick et al., 2007].

Using spatial patterns as knowledge base for management support is well-known in the context of biological conservation [Drechsler et al., 2003; Frank, 2004]. The relevance of the disturbance characteristics shows the importance of the soil type. Depending on pore size distribution and spatial arrangement, the area affected by disturbance events may be highly clumped or rather evenly distributed in space. This may lead to different processes governing the functional resilience of microbial ecosystems in different soil types. Therefore, further studies investigating the functional resilience in soil systems should involve the influence of different pore network structures.

3.3.6 *Potentials and restrictions of the presented modelling approach*

The presented model results improve the mechanistic understanding of the functional resilience of microbial ecosystems to single disturbance events. The results provide clarity about general phenomena such as: (i) recovery dynamics at different spatiotemporal scales and the characteristic recovery times, (ii) governing processes, (iii) the role of characteristics of the disturbance itself (i.e. intensity, spatial pattern), and (iv) the question whether the explicit spatial configuration or an aggregated spatial metric of the disturbance pattern is sufficient for assessing the functional recovery. As shown above, these results have serious implications for both theory building and management practice.

These insights, however, could only be revealed as a spatially explicit model (here: *eColony*) was used at a small scale and a range of specific model analyses was conducted. Particularly important in this study was the ability to switch processes on or off, the comparison of scenarios (here: different assumptions on disturbance characteristics), and the work with an ensemble approach [Brown et al., 2010; Gal et al., 2014]. Core of the latter was the use of a landscape generator [Frieden et al., 2014; Hesse et al., 2014], for creating random disturbance patterns which differ in the explicit spatial configuration but coincide in coverage and degree of fragmentation. Polygon plots over the recovery functions from the ensemble and correlative analyses between simulated recovery time and certain spatial metrics of the disturbance pattern finally enabled revealing the relevance of the explicit spatial configuration. To seek for aggregated spatial metrics which approximate or correlate with the outcome of a fully spatial model is common in landscape ecology and relates to the concept of "ecologically scaled landscape indices" [Zaragozí et al., 2012; Uuemaa et al., 2013]. Examples are landscape indices to estimate landscape connectivity and dispersal success [Schumaker, 1996; Estreguil et al., 2014], metapopulation capacity [Hanski and Ovaskainen, 2000], or the mean lifetime of a metapopulation [Frank and Wissel, 2002; Frank, 2005], or to assess the effect of dispersal networks on biodegradation performance [Banitz et al., 2016].

Certainly, our assumptions on the disturbances and their effects are simplifying. Using a population-based approach with an aggregated variable for the entire bacterial population, we may underestimate the relevance of community composition which was found to be crucial for functional stability in previous studies [e.g. Griffiths et al., 2001;

Botton et al., 2006]. However, those simplifications allowed for a mechanistic understanding of microbial dynamics. The occurrence of the phenomena investigated in our study within a more complex setting is certainly of interest for future studies. For the interpretation of the results obtained for such more complex systems the mechanistic understanding provided by our study is a necessary prerequisite.

3.4 CONCLUSION

The presented simulation approach highlights the benefit of simplified model systems focusing on the interaction of specific processes and aiming at providing mechanistic system understanding and testable hypotheses for future studies. With the applied ecological modelling methodology, we were able to gain the following insights into the phenomenon of functional recovery of microbial ecosystems and their biodegradation performance after disturbances: (i) the recovery dynamics subdivide into phases with slowed and accelerated recovery and specific governing processes, (ii) both the shape of the recovery function and the relative importance of processes such as bacterial growth and dispersal depend on intensity and spatial pattern of the disturbance itself, (iii) despite the complex spatiotemporal system dynamics, the recovery time correlates with an aggregated spatial metric of the disturbance pattern – the mean distance between disturbed and undisturbed habitats – that subsumes all relevant spatial effects. The present study of the dynamics after single disturbances provides a starting point for predicting key factors for maintaining a microbial ecosystem function under the influence of recurrent disturbances with different temporal and spatial characteristics. Thus, further work should involve more complex disturbance regimes and investigate their effect on the dynamics of the functional performance.

4

FUNCTIONAL RESISTANCE TO RECURRENT DISTURBANCE EVENTS

4.1 INTRODUCTION

Disturbance events may occur repeatedly on various frequencies and, thus, adversely affect the microbial ecosystems and their functions (see also Sec. 1.2.2), for instance, by inhibiting bacterial growth, reducing substrate availability, or increasing bacterial mortality [de Ruiter et al., 2002; Botton et al., 2006; Shade et al., 2012]. In response to such disturbances, bacterial biomass distributions and biodegradation activity may change considerably and overall biodegradation performance decline accordingly. Especially when disturbance events recur in short intervals, the ecosystem may not be able to recover quickly enough causing a cumulative effect of the recurrent disturbances on the ecosystem function [Ho et al., 2015]. In consequence, the resistance of the functional performance of biodegradation to recurrent disturbance events has to be examined (Fig. 4.1).

Terrestrial environments are characterized by spatial and temporal heterogeneities in the distribution of abiotic factors such as water, oxygen, toxicants, of organic compounds serving as substrates, and of metabolically active bacteria. Such heterogeneities can lead to mismatching distributions of bacteria and substrate, reduce bioavailability and thereby limit the biodegradation performance [Harms and Wick, 2006; Semple et al., 2007]. Dispersal networks such as fungal hyphae, however, may help overcoming the limitations, increase bioavailability by accelerating the contact frequency of degrader cells and contaminants, and enhance biodegradation performance [Kohlmeier et al., 2005; Wick et al., 2007; Furuno et al., 2010; Banitz et al., 2011b; Knudsen et al., 2013; Ellegaard-Jensen et al., 2014; Simon et al., 2015].

One particularly important aspect is the dependence of functional resistance and resilience on the characteristics of the disturbance regime itself, especially the spatial pattern and frequency of the recurrent disturbance events. This has not been systematically analysed so far. Spatial aspects are generally important for the stability of microbial ecosystems under disturbances [Altermatt et al., 2011; Baho et al., 2012; Shade et al., 2012]. For instance, high cell density may increase the resistance of bacteria to disturbances [Miyamoto and Eguchi, 1997; Butler et al., 2010]. This shows the importance of pattern formation in microbial ecosystems, a phenomenon that is known to cause locally increased cell densities [Grundmann et al., 2001; Keymer et al., 2006; Centler et al., 2011; Gharasoo et al., 2014]. However, whether such pattern formation also enhances the functional resistance of a microbial community to disturbances depends on the spatial occurrence of the disturbance. Thus, both the temporal and spatial characteristics of disturbance regimes should be considered when analysing dynamics, functions and stability properties of microbial ecosystems [Moloney and Levin, 1996; Frank and Wissel, 1998; Johst and Drechsler, 2003; Frank, 2005; Banitz et al., 2008; Meli et al., 2014].

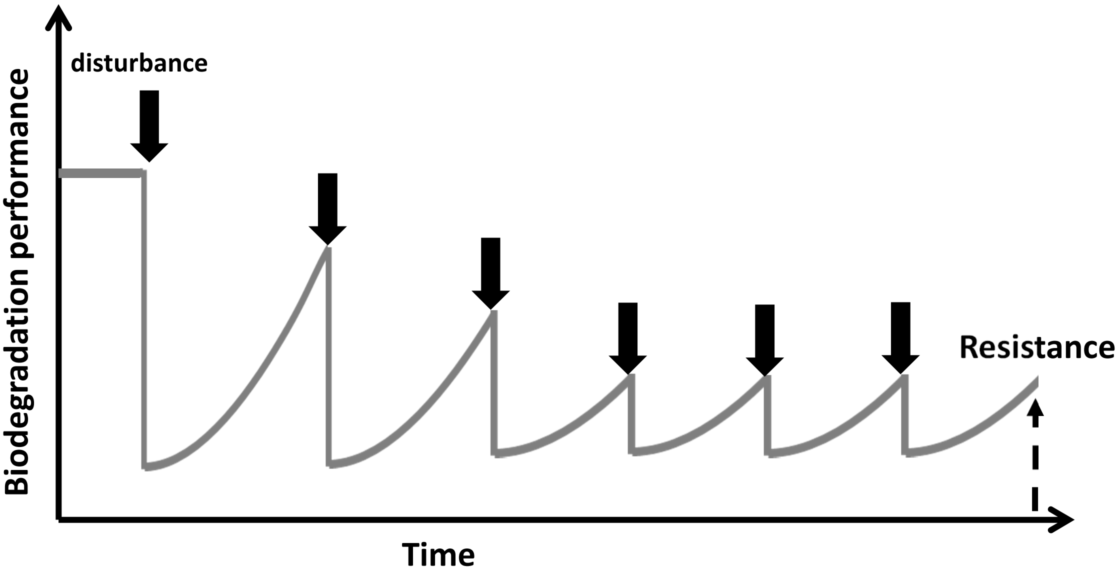


Figure 4.1: Scheme of functional resistance: The function biodegradation is maintained during periodic disturbances

In the present chapter, we investigate the functional resistance of biodegradation to recurrent disturbances and provide mechanistic explanations of its determinants. In a first step, we applied disturbance events occurring at the same area at each new disturbance event, assuming that the applied disturbance area depends on the spatial arrangement of a pore network system in soil. We tackle this task using *eColony*, the microbial simulation model developed in Chapter 2.

The model gives us the opportunity to inspect dynamics at arbitrary locations at the local scale and to take into account environmental heterogeneities. Our particular aim is to reveal factors determining the functional resistance measured in terms of the maintenance of the biodegradation performance under recurrent disturbances. In a first step, we systematically assess the relative importance of the disturbance regime characteristics, especially spatial pattern and frequency of the disturbance events, for the long-term biodegradation performance. With respect to spatial aspects, we particularly explore whether the explicit spatial configuration or certain summarizing spatial characteristics such as the degree of fragmentation of the disturbance pattern are decisive for the effect on the functional resistance. In a second step, we assess the influence of dispersal networks on the long-term responses of bacterial populations and their biodegradation performance to selected disturbances.

4.2 METHODS

4.2.1 *Scenarios*

The initial conditions for bacterial biomass and substrate concentration were again set to the calculated steady state (Tab. 2.1). According to Equation 2.9 the surviving fraction Δ was set to 10^{-9} for the present study. Disturbance events were continuously recurring at a constant frequency, that is after the (constant) disturbance return interval.

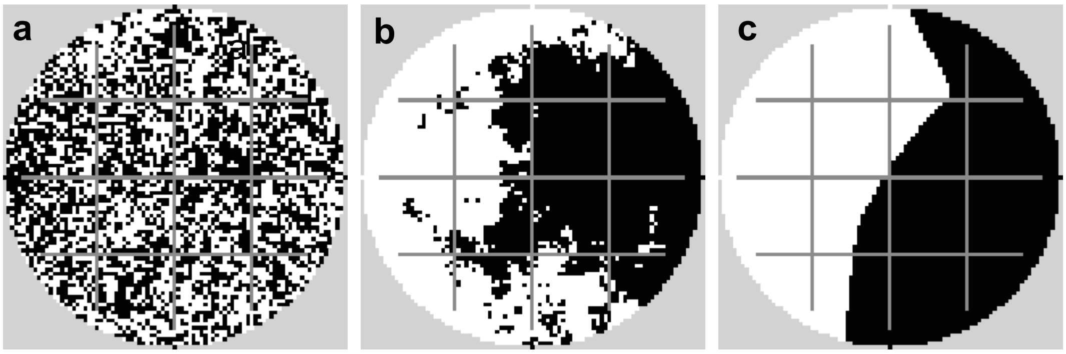


Figure 4.2: Examples of disturbance patterns with high fragmentation (a, H = -1), moderate fragmentation (b, H = 0.5) and no fragmentation (c, H = 2). Each scenario was simulated with and without dispersal networks (black: disturbed area, white: undisturbed area, grey: dispersal networks).

The disturbance return interval length in the different simulations varied from 10 to 250 hours.

The fragmentation parameter H of the disturbance was varied from -1 to 2 in steps of 0.2 for representing a span between the extreme situations of completely random (H=-1) and highly clustered (H=2) disturbance patterns. The disturbance events occurred always with the same spatial disturbance pattern, that is always the same set of habitats was affected by the disturbances during a given simulation run, assuming that the applied disturbance area depends on the spatial arrangement of a pore network system in soil.

All scenarios were simulated with and without dispersal networks with the shown structure (Fig. 4.2), thus, each disturbance pattern was applied once with and once without the additional module of dispersal networks.

4.2.2 *Analysis*

We simulated each scenario until average performance levels between two disturbance events exhibited no further changes. The height of this new mean performance level describing a quasi-steady state is taken as a measure for functional resistance and depends on the disturbance return interval and on the degree of fragmentation of the disturbance pattern (Fig. 4.3). This characteristic of the shifted quasi-steady state was the basis for subsequent analyses of the mean biodegradation performance, calculated for each habitat and for the whole system. For analysing the influence of the spatial configuration of the disturbance patterns to the resistance of the biodegradation performance, the mean distance between habitats in the disturbed and the respective nearest habitat in the undisturbed area Δ was calculated according to Equation 2.14. Additionally, as an indicator for the influence of dispersal networks, the difference of the degradation performance in scenarios without and with dispersal networks was calculated.

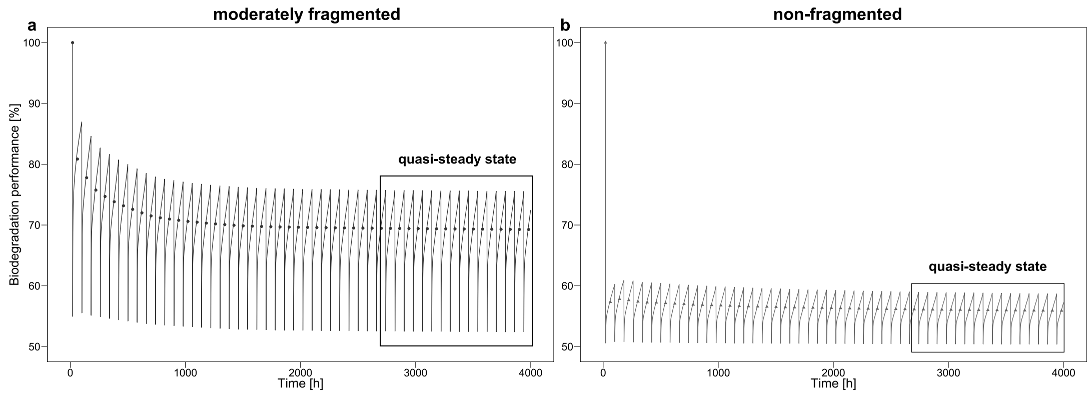


Figure 4.3: Biodegradation dynamics under disturbance regime with moderately (a, H = 0.5) and non-fragmented (b, H = 2) disturbance pattern and a disturbance return interval of 80 hours. Points indicate mean performance of corresponding disturbance return interval, indicating functional resistance.

4.2.3 *Classification of habitat types*

The spatiotemporal dynamics were examined by classifying each habitat's mean biodegradation performance over a time span equivalent to the disturbance return interval in relation to the undisturbed steady state performance (denoted as 100 %). Choosing a deviation of 5 % as a relevant change, the defined habitat types are: : (i) 'enhanced' habitats, if the biodegradation performance is higher than 105 %, (ii) 'unchanged' habitats, if the performance is between 95 % and 105 %, (iii) 'reduced' habitats, if the performance is between 5 % and 95 %, and (iv) 'inhibited' habitats, if the performance is below 5 %. (Tab. 4.1).

Relative biodegradation performance	**Habitat type**	**Color**
$< 5\%$	inhibited	🟦
$> 5\%$ and $< 95\%$	reduced	🟦
$> 95\%$ and $< 105\%$	unchanged	⬜
$> 105\%$	enhanced	🟥

Table 4.1: Classification of habitat types according to mean biodegradation performance in quasi-steady state in relation to biodegradation performance of undisturbed system.

4.3 RESULTS

4.3.1 *Relevance of spatial disturbance pattern*

For all scenarios, the biodegradation performance of the disturbed systems is markedly higher than 50 % of the performance of the undisturbed system, which is the expected minimum as 50 % of the simulation area remains undisturbed. This indicates that the

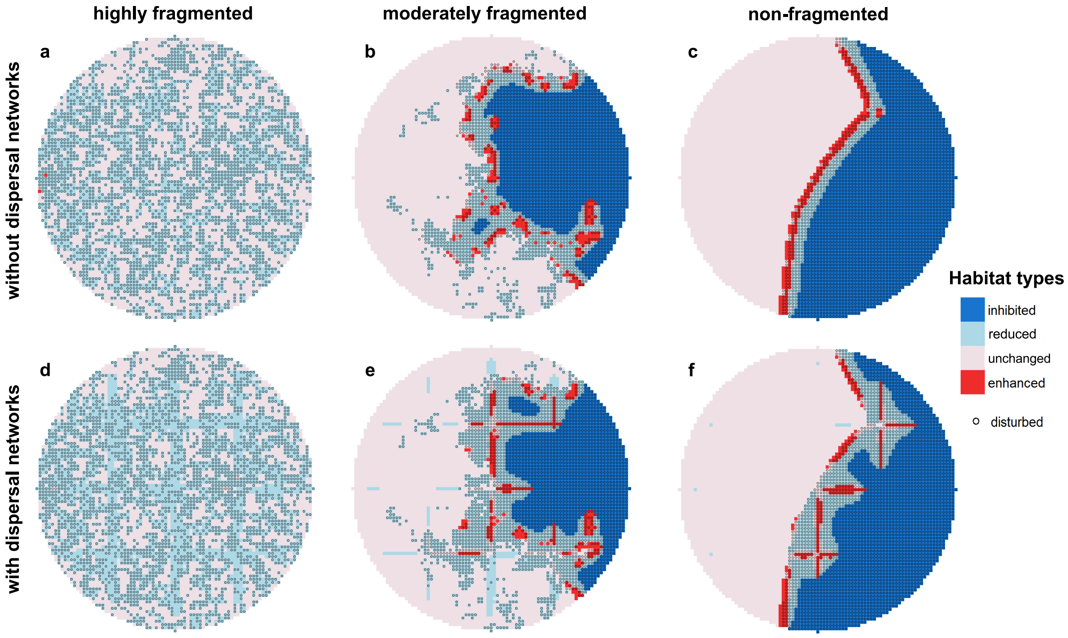


Figure 4.4: Mean biodegradation performance in quasi-steady state without (a-c) and with dispersal networks (d-f) under recurrent disturbances with a disturbance return interval of 80 hours. Three different degrees of fragmentation of the disturbance pattern are shown: highly (a, d; H = -1), moderately (b, e; H = 0.5), and non-fragmented (c, f; H = 2). Habitats within the disturbance area (50 % of total area) are marked with grey circles.

disturbed areas still contribute to the overall biodegradation performance and/or the undisturbed areas exhibit a higher performance than without disturbances.

Analysing exemplary results for a disturbance return interval of 80 hours, the spatial distribution of the biodegradation performance in quasi-steady state reveals a heterogeneous distribution of biodegradation activity in response to the spatial disturbance pattern (Fig. 4.4). Some of the disturbed habitats still show biodegradation activity above 5 %, and more habitats are active under highly fragmented than under less fragmented disturbances.

Under the influence of highly fragmented disturbances biodegradation takes place in all habitats, undisturbed as well as disturbed (Fig. 4.4a). Basically, only two habitat types are present: in the undisturbed area most habitats are 'unchanged' and a few 'reduced', whereas all disturbed habitats are 'reduced'. There are almost no habitats where biodegradation is 'enhanced' due to the disturbance regime, and also no habitats where it is 'inhibited'. In presence of dispersal networks the composition of active habitat types in the undisturbed area is slightly changed (Fig. 4.4d). Here, more undisturbed habitats show a 'reduced' biodegradation performance.

In scenarios where the disturbance is moderately fragmented clusters of 'enhanced' habitats occur at the interface between disturbed and undisturbed areas (Fig. 4.4b). Those clusters are surrounded by 'unchanged' habitats in the undisturbed area and 'reduced' habitats in the disturbed area. However, most disturbed habitats show 'inhibited' biodegradation performance. Dispersal networks increase the amount of active habitat types in the disturbed area due to the enhanced bacterial dispersal which allows for bacteria from undisturbed areas to quickly colonize also more distant disturbed habitats resulting in an increased biodegradation performance in those habitats (Fig. 4.4e).

For non-fragmented disturbance patterns almost the entire disturbed area consists of 'inhibited' habitats except for the areas at the direct interface to the undisturbed area, where 'reduced' and 'enhanced' habitats are present (Fig. 4.4c). However, due to the low fragmentation of the disturbance pattern the number of these habitats is low and, consequently, the biodegradation performance is mainly provided by the undisturbed area. Similar to the scenario with moderately fragmented disturbance patterns, the presence of dispersal networks causes an increase of active habitats in the disturbed area (Fig. 4.4f).

The total biodegradation performance decreases with decreasing degree of fragmentation of the disturbance pattern. In scenarios with dispersal networks the total biodegradation performance under moderately and non-fragmented disturbances increases compared to the scenario without dispersal networks (Fig. 4.5).

Under highly fragmented disturbances the total biodegradation performance is around 90 %, and thus higher than under less fragmented disturbances. The contribution of all habitats keeps the total biodegradation performance on this high level. Dispersal networks are causing a reduction of 'unchanged' habitats in the undisturbed area which is, however, compensated by higher biodegradation performance in other 'reduced' habitats (Fig. 4.5a, d). Hence, the total biodegradation performance is almost unaffected. Under moderately fragmented disturbances the biodegradation performance is mainly provided by 'unchanged' habitat types, but also the 'enhanced' and 'reduced' habitats are contributing to the biodegradation performance. In presence of dispersal networks the total biodegradation performance is enhanced due to the contribution of the increased amount of active habitats in the disturbed area (Fig. 4.5b, e). For non-fragmented disturbance patterns the total biodegradation is even lower due to the increase in 'inhibited' habitat types. Again, biodegradation performance is enhanced due to dispersal networks as they decrease the number of 'inhibited' (i.e. inactive) habitats (Fig. 4.5c, f). Thus, the degree of fragmentation of the disturbances influences both the occurrence and spatial composition of habitat types and the overall biodegradation performance of the entire microbial population.

Systematic variation of the degree of fragmentation (increasing value of parameter H from -1 to 2 in steps of 0.2, cf. Sec. 4.2.1) indicates a negative correlation between the level of biodegradation performance in quasi-steady state and the mean distance Δ from disturbed to undisturbed habitats (Fig. 4.6). For short mean distances, where disturbed habitats are close to the undisturbed area, the mean biodegradation performance is high. With decreasing degree of fragmentation, which leads to increasing mean distances, the biodegradation performance declines exponentially. With dispersal networks, the biodegradation performance follows a similar decline, but the total biodegradation performance is enhanced compared to the scenarios without dispersal networks, except for very low mean distances where biodegradation performance is rather high even without networks. Here, the dispersal networks do not provide an additional benefit for biodegradation. With increasing mean distance the difference in

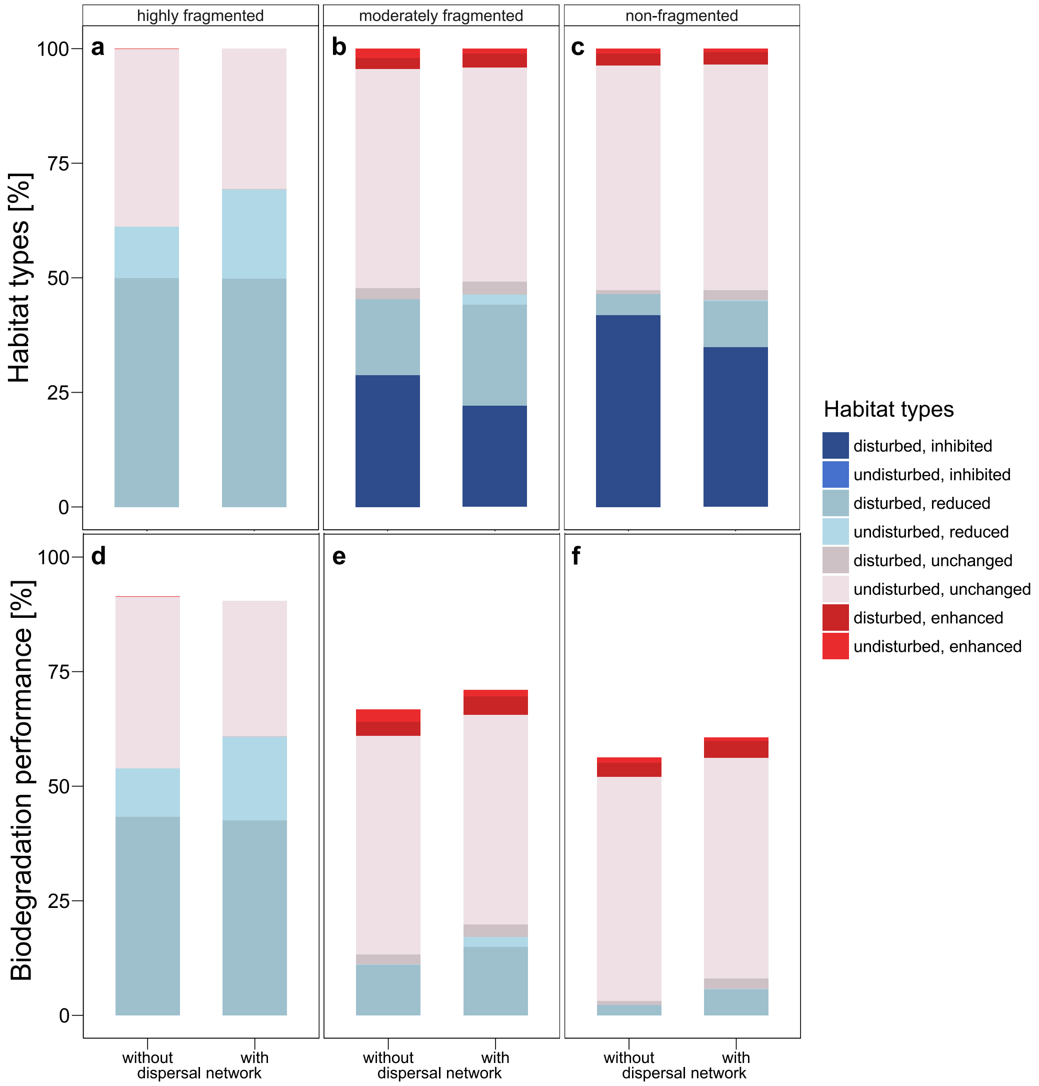


Figure 4.5: Distribution of habitat types (a- c) and corresponding mean biodegradation performance (d-f) in quasi-steady state as an indicator for functional resistance without and with dispersal networks (see x-axis) under recurrent disturbances with a disturbance return interval of 80 hours. Three different degree of fragmentation of the disturbance pattern are shown: highly (a, d; H = -1), moderately (b, e; H = 0.5), and non-fragmented (c, f; H = 2). Habitats are classified according to four different types (cf. Sec. 4.2.3 for details). In subplots (d-f), bar heights show total biodegradation performance and colored segments show the respective habitat types' contribution.

the performance with and without dispersal networks also increases until reaching a level of approximately 5 % at a mean distance of 12 mm. For longer mean distances, the benefit in the biodegradation performance remains almost constant. This shows that, although the spatial distributions of bacterial biomass and biodegradation activity constantly change over time, the resulting mean biodegradation performance strongly

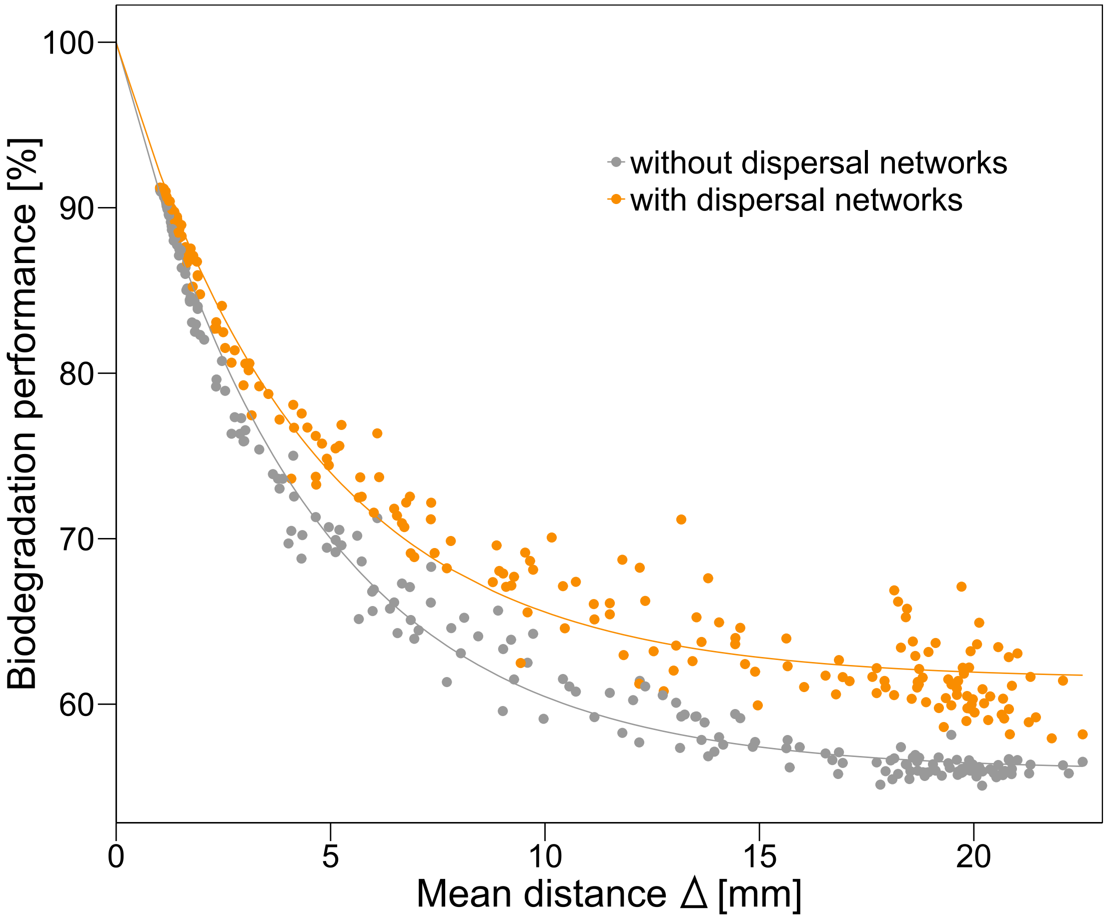
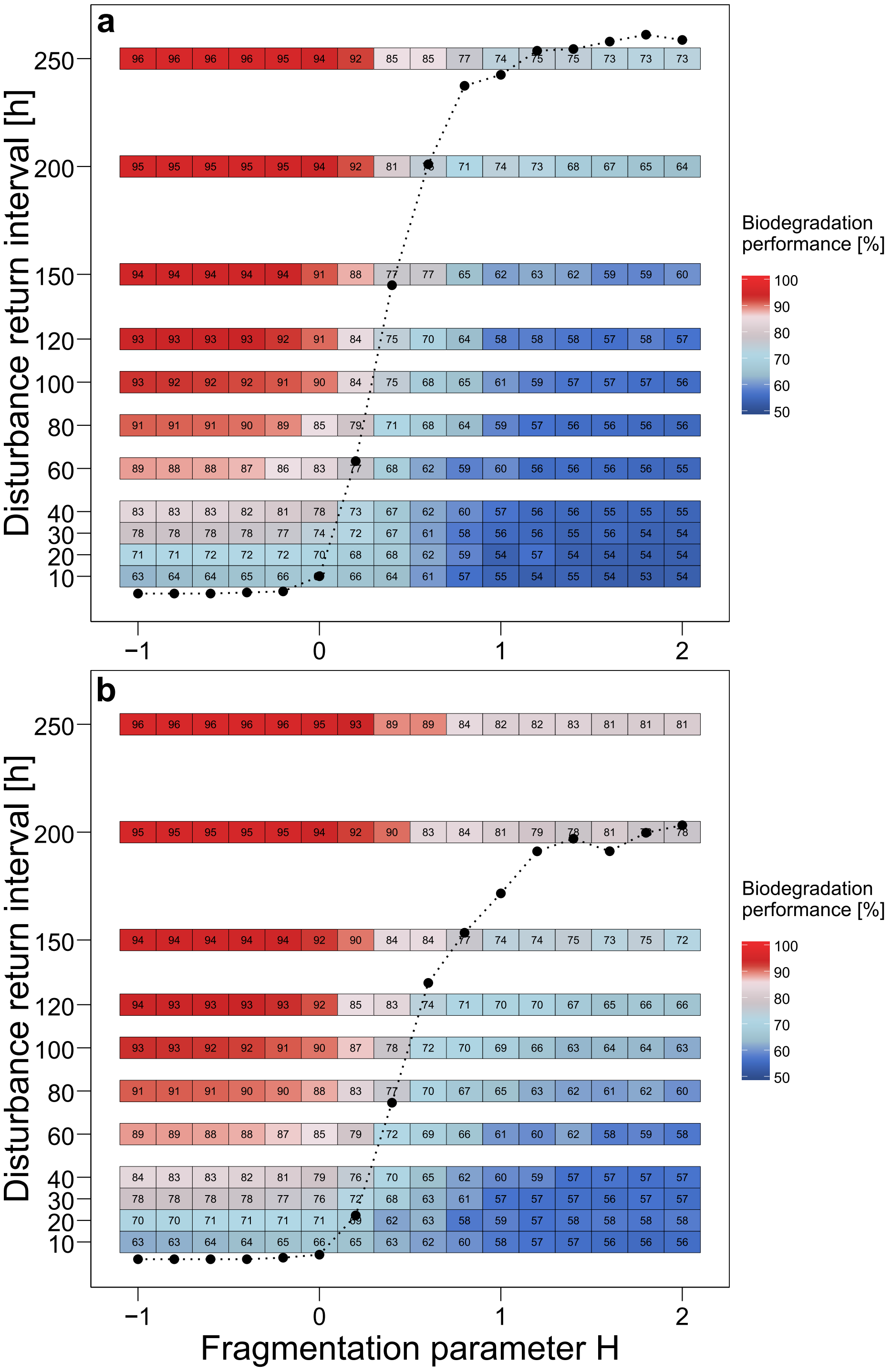


Figure 4.6: Biodegradation performance in quasi-steady state as an indicator for functional resistance over mean distance Δ between disturbed and nearest undisturbed habitats in without (grey) and with (orange) of dispersal networks under recurrent disturbances with a disturbance return interval of 80 hours. Disturbance fragmentation was varied between H=-1 and H=2 in steps of 0.2, with 20 simulation runs with different disturbance patterns per step. Solid line indicates exponential fit (R=0.933 without dispersal networks, R=0.984 with dispersal networks).

correlates with a single spatial measure of the recurrent disturbance pattern: the mean distance between disturbed and undisturbed habitats. This summarizing metric is obviously subsuming all spatial effects of the disturbance pattern relevant for functional resistance under the given conditions.

4.3.2 *Relevance of disturbance return interval*

Varying the length of the disturbance return interval indicates that the revealed relationship between mean biodegradation performance in quasi-steady state and the disturbance pattern's degree of fragmentation is qualitatively independent of the disturbance return interval length (Fig. 4.7). Generally, for all disturbance return intervals the biodegradation performance decreases with decreasing degree of fragmentation of the disturbance pattern. However, also decreasing the return interval length (i.e., more



a

250	96	96	96	96	95	94	92	85	85	77	74	75	75	73	73	73
200	95	95	95	95	95	94	92	81	78	71	74	73	68	67	65	64
150	94	94	94	94	94	91	88	77	77	65	62	63	62	59	59	60
120	93	93	93	93	92	91	84	75	70	64	58	58	58	57	58	57
100	93	92	92	92	91	90	84	75	68	65	61	59	57	57	57	56
80	91	91	91	90	89	85	79	71	68	64	59	57	56	56	56	56
60	89	88	88	87	86	83	77	68	62	59	60	56	56	56	56	55
40	83	83	83	82	81	78	73	67	62	60	57	56	56	55	55	55
30	78	78	78	78	77	74	72	67	61	58	56	56	55	56	54	54
20	71	71	72	72	72	70	68	68	62	59	54	57	54	54	54	54
10	63	64	64	65	66	[illegible]	66	64	61	57	55	54	55	54	53	54

b

250	96	96	96	96	96	95	93	89	89	84	82	82	83	81	81	81
200	95	95	95	95	95	94	92	90	83	84	81	79	78	81	78	78
150	94	94	94	94	94	92	90	84	84	77	74	74	75	73	75	72
120	94	93	93	93	93	92	85	83	74	71	70	70	67	65	66	66
100	93	93	92	92	91	90	87	78	72	70	69	66	63	64	64	63
80	91	91	91	90	90	88	83	77	70	67	65	63	62	61	62	60
60	89	89	88	88	87	85	79	72	69	66	61	60	62	58	59	58
40	84	83	83	82	81	79	76	70	65	62	60	59	57	57	57	57
30	78	78	78	78	77	76	72	68	63	61	57	57	57	56	57	57
20	70	70	71	71	71	71	69	62	63	58	59	57	58	58	58	58
10	63	63	64	64	65	66	65	63	62	60	58	57	57	56	56	56

Figure 4.7: Mean biodegradation performance in quasi-steady state as an indicator for functional resistance for different disturbance return intervals and degrees of fragmentation. Boxes show mean values of 10 independent simulation runs. (a) Without dispersal networks. (b) With dispersal networks. Dots indicate the mean time needed to recover 95 % biodegradation performance after one single disturbance with the specific degree of fragmentation.

frequent disturbance events) decreases the biodegradation performance in both cases, without (Fig. 4.7a) and with dispersal networks (Fig. 4.7b). Is the disturbance return interval longer than the time needed for recovering 95 % of the function after one single disturbance (cf. Ch. 3), the biodegradation performance is high under recurrent disturbances as well (Fig. 4.7, dots). Thus, the functional resilience after single disturbance events measured in terms of recovery is already a good indicator for the functional resistance under recurrent disturbance events.

Comparing the biodegradation performance in quasi-steady state with and without dispersal networks reveals improvements due to dispersal networks (Fig. 4.8a). However, these improvements only apply to a certain zone of disturbance regimes characterized by moderately or less fragmented disturbance pattern and a minimum return interval. Outside this zone, there is no such benefit from dispersal networks, and for some disturbance regimes the mean biodegradation performance was even slightly decreased in presence of dispersal networks. The latter was particularly observed for very short disturbance return intervals (10 and 20 hours). The influence of the specific spatial configuration of the disturbance pattern is highest under moderately fragmented disturbances (Fig. 4.8b), which confirms the outcomes described in Section 3.3.3 also for the response to disturbance regimes.

4.4 DISCUSSION

4.4.1 *Factors controlling functional resistance*

Our simulation results show that the functional resistance of biodegradation to recurrent disturbances relies on the bacterial ability to quickly recolonize the disturbed area by endemic re-growth or invasion from undisturbed habitats and varies with the spatial and temporal characteristics of the disturbance pattern. The results reveal that functional resistance negatively correlates with the mean distance between disturbed and undisturbed habitats which is closely related to the degree of fragmentation of the disturbance pattern. This indicates that a single summarizing spatial metric condenses all spatial effects of the disturbance pattern which are relevant for the functional resistance, while its particular explicit spatial configuration is of minor relevance. Under highly fragmented recurrent disturbances, almost the complete system remains active, in undisturbed as well as in disturbed areas resulting in a high functional resistance. This is due to a higher proximity of disturbed to undisturbed habitats allowing bacterial dispersal from undisturbed to almost all habitats within the disturbance return interval. With decreasing fragmentation of the disturbance pattern the biodegradation activity concentrates on highly active spots at the interface of undisturbed and disturbed habitats. The biodegradation performance in these habitats benefits from bacteria dispersing from undisturbed habitats and from unconsumed substrate diffusing from disturbed habitats with low or no activity.

However, the functional resistance declines with decreasing degree of fragmentation due to a complete inactivity in more distant parts of the disturbed area. In these disturbed habitats, the biodegradation performance cannot recover at all before the next disturbance event occurs. This is because the distance from undisturbed habitats is too long for bacteria to disperse to these disturbed habitats within the disturbance return

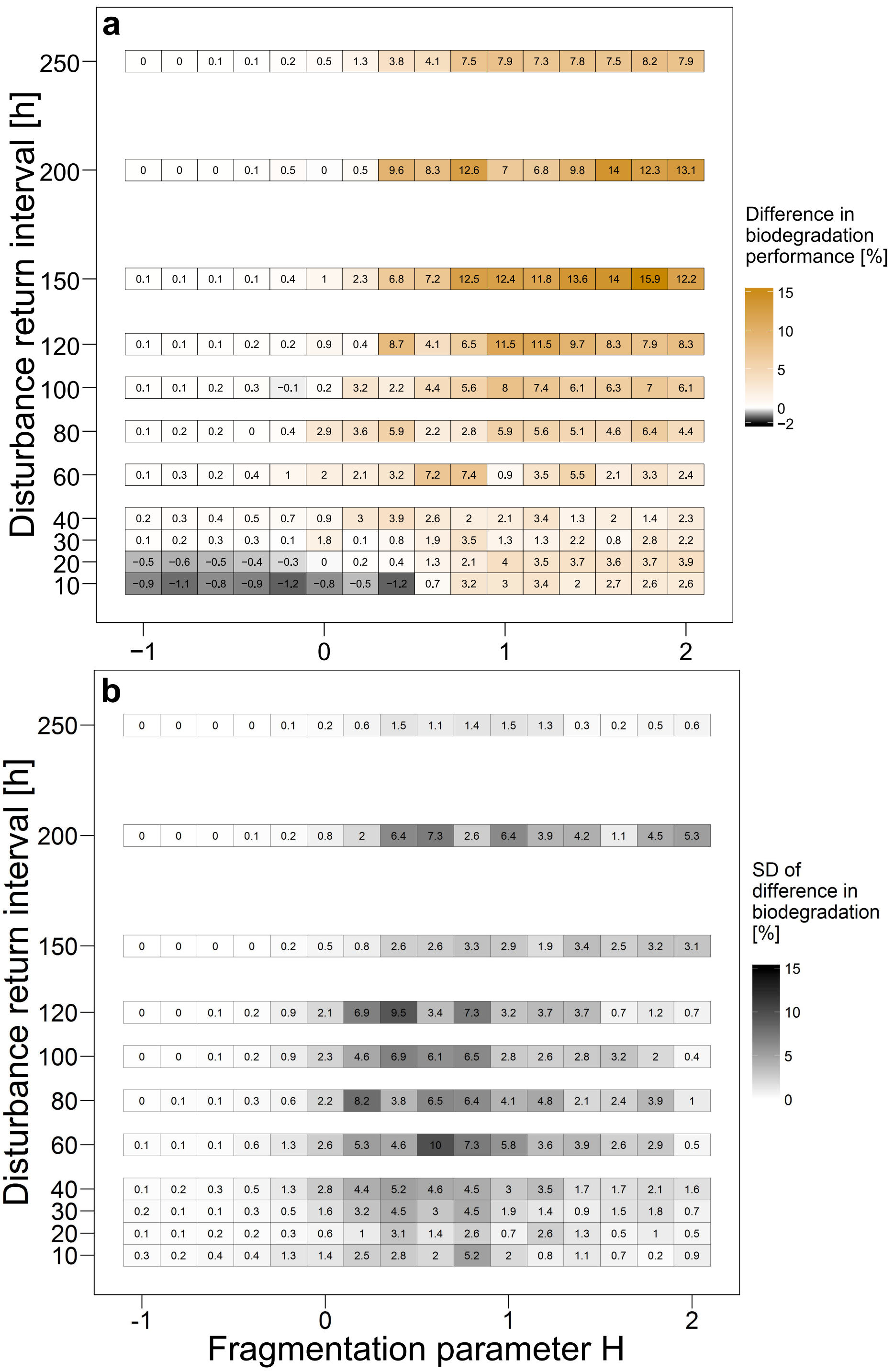


Figure 4.8: Difference in biodegradation performance between the scenarios with and without dispersal networks (a), positive differences indicate a better performance with dispersal networks, and corresponding standard deviation (b) (cf. Fig. 4.7)

interval. Disturbances with a non-fragmented spatial pattern lead to the highest number of inactive disturbed habitats as the mean distance from undisturbed habitats is maximized.

Thus, the shorter the distances for the bacteria to disperse from undisturbed to disturbed habitats, the higher is the resistance of the biodegradation function to recurrent disturbances. With increasing disturbance return interval length the biodegradation performance is enhanced as the bacteria have more time to colonize more distant disturbed areas. However, the degree of spatial fragmentation of the disturbances influences the functional resistance in any case, regardless of the disturbance return interval length.

The increased stability of microbial ecosystems under disturbances due to recolonization from undisturbed sources is in agreement with previous experimental and modelling studies analysing structural responses to disturbances [Altermatt et al., 2011; Baho et al., 2012; Galic et al., 2012; Shade et al., 2012]. For instance, Altermatt et al. [2011] showed that a higher connectivity between disturbed and undisturbed areas increases the ability of microorganisms to recover from a disturbance in terms of bacterial biomass density.

Furthermore, the importance of dispersal, or more generally of spatial processes, for functional resistance is in line with outcomes of previous studies

4.4.2 *Relevance of dispersal networks*

The 'favorable zone' revealed in Figure 4.8a, where dispersal networks lead to considerable biodegradation benefits, gives rise to the conclusion that such networks can substantially enhance the functional resistance and partly buffer the adverse impacts of a given disturbance regime, provided the disturbance is moderately or non-fragmented and the return interval exceeds a certain minimum. Under these conditions, bacteria can disperse much faster along the networks and enhance biodegradation activity in habitats farther inside the disturbed area. In consequence, the bacterial access to substrate in the disturbed area is enhanced by the dispersal networks. Outside the 'favorable zone', dispersal networks are not beneficial for functional resistance or might be even disadvantageous. This is because they are either not needed for ensuring high functional resistance (e.g. for highly fragmented disturbance patterns) or they are not able to overcome the negative impacts of the disturbance (e.g. for too short return intervals). These rules of thumb are independent of the explicit spatial configuration of the disturbance pattern, as is confirmed by Figure 4.8b showing low standard deviation in the benefit values of the different disturbance regimes for almost all parameter combinations.

Somewhat unexpectedly, our results also show that dispersal networks can lead to a slight decrease in biodegradation performance for some disturbance regimes. This may be explained as follows: due to enhanced bacterial dispersal on the networks, more bacteria disperse to the disturbance area in the interval between two disturbances. This causes on the one hand a higher access to accumulated substrate in the disturbance areas but on the other hand also an increase in total bacterial biomass prone to be removed during the next disturbance. In scenarios with a highly fragmented disturbance pattern this effect may be responsible for the decrease in biodegradation performance due to dispersal networks.

A negative effect of the dispersal networks on the local biodegradation performance in certain habitats is also visible in scenarios with a less fragmented disturbance pattern (cf. Fig. 4.4b, e, c and f). For the global biodegradation performance, however, these local negative effects are overcompensated by positive effects in other habitats. For instance, there are more habitats of type 'reduced' instead of 'inhibited' in the disturbed area. Therefore, it is important to differentiate between the different scales [cf. Peterson et al., 1998]: dispersal networks may have considerable negative effects on the biodegradation performance on a local but not on a global scale.

4.4.3 *Relevance for natural systems*

The high sensitivity of the biodegradation performance with respect to the spatial configuration of the disturbance patterns may be especially relevant with regard to different soil types with various pore networks, pore size distributions and connectivity. In soil, these spatial environmental characteristics may considerably influence the area affected by disturbances such as drought events, the release of chemicals toxic to the bacteria or increasing salt concentrations. This may lead to rather fragmented or highly clumped disturbance patterns. Thus, the degree of functional resistance to recurrent disturbances is likely also dependent on the soil texture. For instance, a soil system consisting of well-mixed particles may be highly fragmented and, thus, more resistant to recurrent disturbances. Contrarily, a soil system where different particles are aggregated in different areas may form a pore network in which disturbances occur in larger patches, leading to lower functional resistance. However, the type of disturbance should also be considered. The observed impact of the disturbance pattern's spatial configuration on functional resistance applies to disturbances that affect some but not all pores, such as toxic chemicals released to the system or drought events decreasing the water potential. In case of disturbance events that affect the whole system homogeneously, such as temperature fluctuations, the particular pore network structure is likely to be less relevant.

Similarly, our simulation study shows that the biodegradation benefits provided by bacterial dispersal networks also depend on the spatial configuration of the disturbance pattern. Thus, also the potential of such networks to enhance biodegradation performance under recurrent disturbances may vary for different soil types. We suggest that further studies with the focus on microbial functional resistance to disturbance regimes in soil systems should involve the influence of different pore network structures.

4.4.4 *Model potentials and limitations*

We used a population-based model describing the dynamics of bacterial growth, dispersal and substrate biodegradation in a simplified manner. In particular, we assumed that the disturbance events recur always in the same area, directly reducing the bacterial biomass in the disturbance area without any effect to the undisturbed area. These assumptions on the applied recurrent disturbance regimes reduce the complexity compared to such disturbance events in natural systems. Thus, we excluded influences of additional environmental factors such as substrate limitation or inhibition of dispersal due to decreased soil moisture. We also simulated one aggregated bacterial population and thus cannot infer conclusions for effects on intrapopulation heterogeneities or community structure which were described in previous studies to influence the functional stability [Fernandez et al., 2000; Griffiths et al., 2001; Botton et al., 2006]. Moreover, we assumed that the dispersal networks are not altered under disturbances.

However, in case of diffusive transport, as in our study, specific pore space geometries have only little influence on spatiotemporal bacterial distribution [Gharasoo et al., 2014] and the use of simplified models focusing on the interaction of specific processes was shown to be beneficial for understanding the dynamics of microbial systems [King et al., 2010; Banitz et al., 2011a; Centler et al., 2011; Stolpovsky et al., 2011; Kaiser et al., 2014]. Using the model to systematically vary the disturbance regimes regarding spatial fragmentation and return interval length, we were able to identify general phenomena that may have a high relevance for microbial ecosystem functioning under recurrent disturbances. Particularly, spatial explicitness of the simulation model enabled us to analyse the spatiotemporal biodegradation dynamics on different scales and to assess the influence of the disturbance pattern's spatial configuration on functional resistance.

When determining the influence of dispersal networks also a variation of their spatial configuration may be of interest [Banitz et al., 2016]. However, the applied dispersal networks are a good representation for well-connected mycelial networks that cover the entire system. Networks that are sparser or have less coverage may have less beneficial effects, whereas denser networks may lead to even higher improvements. But it is unlikely that dispersal networks with different spatial configurations would significantly alter our findings regarding their potential for improved functional resistance to recurrent disturbances, and regarding the spatial and temporal disturbance characteristics determining this potential. Following the 'virtual lab' approach, we were able to simulate a wide range of spatially heterogeneous disturbance events occurring in arbitrary but constant return intervals which is hardly realizable in laboratory experiments. Thus, this study underlines the advantages of simplified modelling for gaining insights into microbial systems and their functions.

5

EMERGENCE OF FUNCTIONAL COLLAPSE AND ITS PREVENTION

5.1 INTRODUCTION

As was shown in Chapter 4, microbial ecosystems can be functionally resistant against a given disturbance regime and able to maintain an ecosystem service despite recurrent disturbance events. Depending on the spatial configuration of the disturbance, areas of continuous activity of disturbed and undisturbed habitats were formed contributing to the biodegradation performance and, thus, enhancing the functional stability. However, these results were obtained assuming a disturbance that occurs always in the same area whereas other 'safety areas' were never disturbed. If the disturbance occurs with different spatial configurations at each new disturbance event, such 'safety areas' do not exist which is likely to result in a lower functional resistance of the microbial ecosystem. This may lead to a functional collapse of the system under recurrent disturbances, i.e. a permanent loss of the ability to maintain its function (Fig. 5.1). This is especially the case if the time between recurrent disturbance events is too short for a full functional recovery of the microbial ecosystem. As a result, its functional performance constantly declines and reaches a threshold below which the desired ecosystem service is not provided anymore [Kennedy et al., 2013; Rocha et al., 2014]. This, of course, has drastic consequences for the ecosystem but also for various aspects of human well-being as the specific ecosystem service is not delivered any more.

In soil, environmental conditions are continuously fluctuating causing recurrent disturbances affecting the ecosystem and its services. Such disturbances may occur with different spatial distributions and frequencies, depending on the type of disturbance. Some disturbances occur homogeneously in a certain area like an increase or decrease in temperature [Yuste et al., 2011; Rousk et al., 2012]. Others are directly linked to the specific pore structure such as drought stress and, thus, affecting the same area with each disturbance event [Or et al., 2007; Dechesne et al., 2010]. Depending on the pore size distribution, the disturbance area may be highly heterogeneously distributed. However, the distribution of the pores is not completely static and may alter due to various factors. For instance, soil organisms like earth worms change the pore network when they move within the soil. Growing roots of plants may also influence the spatial pattern of the pore network [Jenny, 1994; Harms and Wick, 2006].

Anthropogenic factors may also affect the pore network distribution in soil, for instance, mixing of soil due to agricultural reasons or forest management activities [Curran and Howes, 2011; Ödman et al., 2012; Gasch et al., 2014]. Moreover, some disturbance types may occur regularly but vary in disturbance size or area. The affected area resulting from contamination with toxic chemicals, for instance, depends on the current saturation of the soil system and thus varies in size [Edwards, 2002]. The toxicants will also not enter the ecosystem at exactly the same place each time resulting in a variation of the disturbance area.

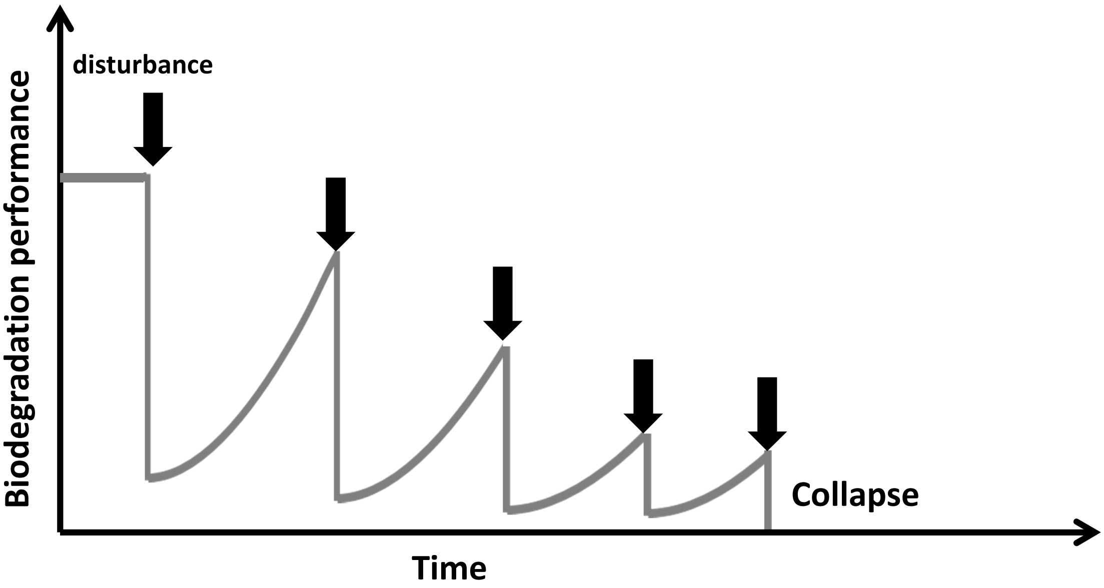


Figure 5.1: Scheme of functional collapse: The system collapsed after some disturbance events and, in consequence, the biodegradation performance is not maintained during periodic disturbances

The preceding arguments directly lead to the question of the key factors of functional resistance and resilience of biodegradation in the case of disturbances with varying temporal and spatial occurrence. In this chapter, we are particularly interested in the role of the ecological processes in the microbial ecosystem for its capacity to buffer the effects of the disturbance events. As was shown in Chapter 3, different processes are responsible for the functional recovery in different phases after a single disturbance event, depending on the spatial configuration of the disturbance. Thus, the relevance of these ecological processes (e.g. bacterial growth, bacterial dispersal) should also be analysed regarding their importance for the functional response to recurrent disturbances, the capacity to buffer and the risk of functional collapse.

Within this chapter, the main focus is on identifying key factors for buffering the functional effects of recurrent disturbances with varying spatial occurrence and for controlling the emergence and mitigation of functional collapses. We are particularly interested in (i) identifying key factors determining the probability of the emergence of a functional collapse, (ii) uncovering the relative role of the disturbance characteristics and the mentioned ecological processes in this context and (iii) assessing the relevance of dispersal networks for mitigating collapses and enhancing functional resistance of biodegradation.

5.2 METHODS

The initial conditions for bacterial biomass and substrate concentration were again set according to the reference state (Tab. 2.1), and the surviving fraction ε was set to 10^{-9}.

In contrast to the simulations in Chapter 4, the disturbance event occurred with the same spatial characteristics (area and degree of fragmentation) but each with a different explicit spatial disturbance pattern for simulating stochastic disturbance events.

The disturbance return interval is again constant. Thus, a disturbance regime consists of a set of different disturbance patterns with a particular constant degree of fragmentation (fixed value of H = -1, 0, 0.5 or 2) occurring in a constant frequency (fixed length of the disturbance return interval between 5 and 250 h). Following an ensemble approach, we applied several such disturbance regimes equivalent in degree of fragmentation but with different sets of disturbance patterns.

For analysing the influence of ecological factors we also varied the parameter values determining bacterial growth and bacterial dispersal. The maximum specific growth rate μ_{max} was varied equivalent to generation times of 2, 5, or 10 hours. The maximum bacterial diffusion coefficient $D_{x,max}$ was varied for simulating different dispersal conditions: a low diffusion coefficient representing dispersal in unfavourable conditions as in Chapter 3 and 4 (cf. Tab. 2.1), and two higher diffusion coefficients for representing dispersal in more favourable conditions (e.g. due to higher water availability). Furthermore, for each of these ecological scenarios and each disturbance regime simulations were performed in absence and in presence of dispersal networks with the structure already introduced in Chapter 4 (Fig. 4.2). The varied parameters are summarized in Table 5.1. All these simulation scenarios were performed until the overall degradation activity permanently reached zero, which defined the collapse of the system, or until a maximum simulation time of 50000 h was reached. We calculated the total degraded substrate over the first 2000 hours after the begin of the simulations and compared the results to the undisturbed steady state situation as a measurement for the functional resistance to the recurring disturbance events. We determined the influence of dispersal networks by calculating the difference of the total degraded substrate in scenarios with and without dispersal networks.

Fragmentation parameter H (-):	-1, 0, 0.5, 2
Disturbance return interval (h):	5-250
Max. specific growth rate μ_{max} (h^{-1}):	0.0639, 0.1386, 0.347
Max. bacterial diffusion coefficient $D_{x,max}$ ($cm^2 s^{-1}$):	5.9E-07, 5.03E-06, 1.55E-05
Dispersal networks (-):	without, with

Table 5.1: Varied parameters of this chapter

5.3 RESULTS

5.3.1 *Relevance of disturbance characteristics*

Recurrent disturbances with varying spatial patterns substantially decrease the biodegradation performance (examples given in Fig 5.2). Under frequent disturbances (i.e. disturbance return interval of 20 hours), this decrease is often very fast resulting in a functional collapse (e.g. after approximately 320 hours in Fig. 5.2a). Thus, the microbial ecosystem is able to handle 16 disturbance events before collapsing in this example. For less frequent disturbances (i.e. disturbance return interval of 80 or 150 hours), the system is functionally resistant and does not collapse within 2000 hours simulation

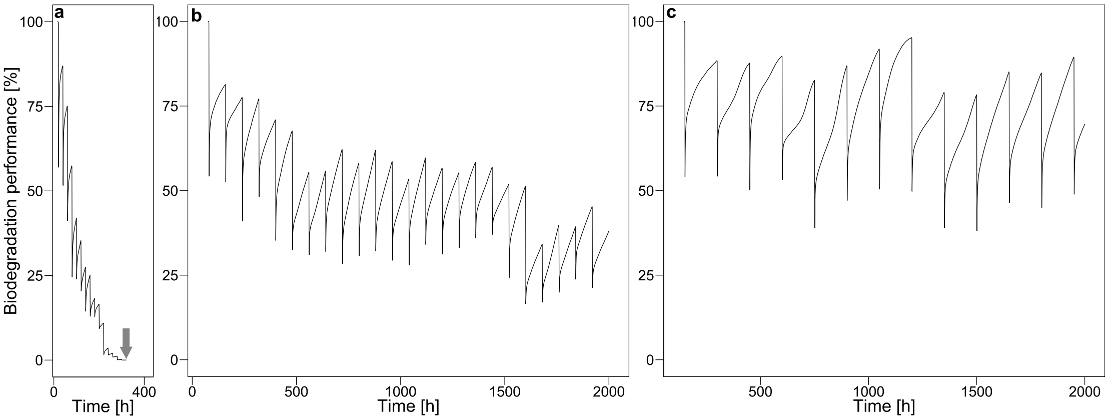


Figure 5.2: Biodegradation performance over time under recurrent disturbances with moderately fragmented disturbance regimes (H=0.5) and disturbance return interval of 20 (a), 80 (b), and 150 (c) hours. Grey arrow indicates functional collapse. The maximum specific growth rate μ_{max} was 0.1386 h^{-1}, the maximum bacterial diffusion coefficient $D_{x,max}$ was 5.9033E-07 cm^2s^{-1}, dispersal networks were not applied.

time under the specific disturbance regimes (Fig. 5.2b, c). In these examples, the system buffers 25 or 13 disturbance events, respectively, without a functional collapse. This suggests that the number of disturbance events that can be handled without collapse is not fixed. Rather, longer return intervals may increase this number and might also strongly reduce the probability that a functional collapse occurs at all.

Systematically varying the disturbance return interval for different fragmented disturbance events reveals a clear relationship between the disturbance return interval length and the time to collapse (Fig. 5.3). The longer the disturbance return interval, the longer is the time to collapse. However, for how long biodegradation performance is maintained depends on the degree of fragmentation of the disturbance pattern as well. For less fragmented disturbance patterns, the time to functional collapse is often short even if the disturbance return interval length is large (see symbols for H = 0.5, and H = 2 in Fig.5.3). We can identify thresholds of the disturbance return interval for functional collapse for the different degrees of fragmentation of the disturbance pattern. Under most fragmented disturbances, the system buffers already a disturbances returning with an interval of 30 hours. If the disturbance pattern is less fragmented with parameter $H = 0$, the threshold is at 55 hours and, with $H = 0.5$, at 90 hours. Under non-fragmented disturbances, the threshold for functional collapse is at a disturbance return interval of 125 hours. However, the time to collapse is already very long in the scenarios near the threshold for moderately and non-fragmented disturbances, the degradation in the system takes place up to approximately 25000 hours before collapse.

A similar relationship is found between the degree of fragmentation and the functional resistance of biodegradation within 2000 hours simulation time (Fig. 5.4). With increasing disturbance return interval, the system buffers the recurrent disturbances better in two respects: the emergence of collapse is prevented and the biodegradation performance is enhanced. However, as before the degree of fragmentation of the disturbance patterns is important too. With decreasing fragmentation (i.e. increasing values

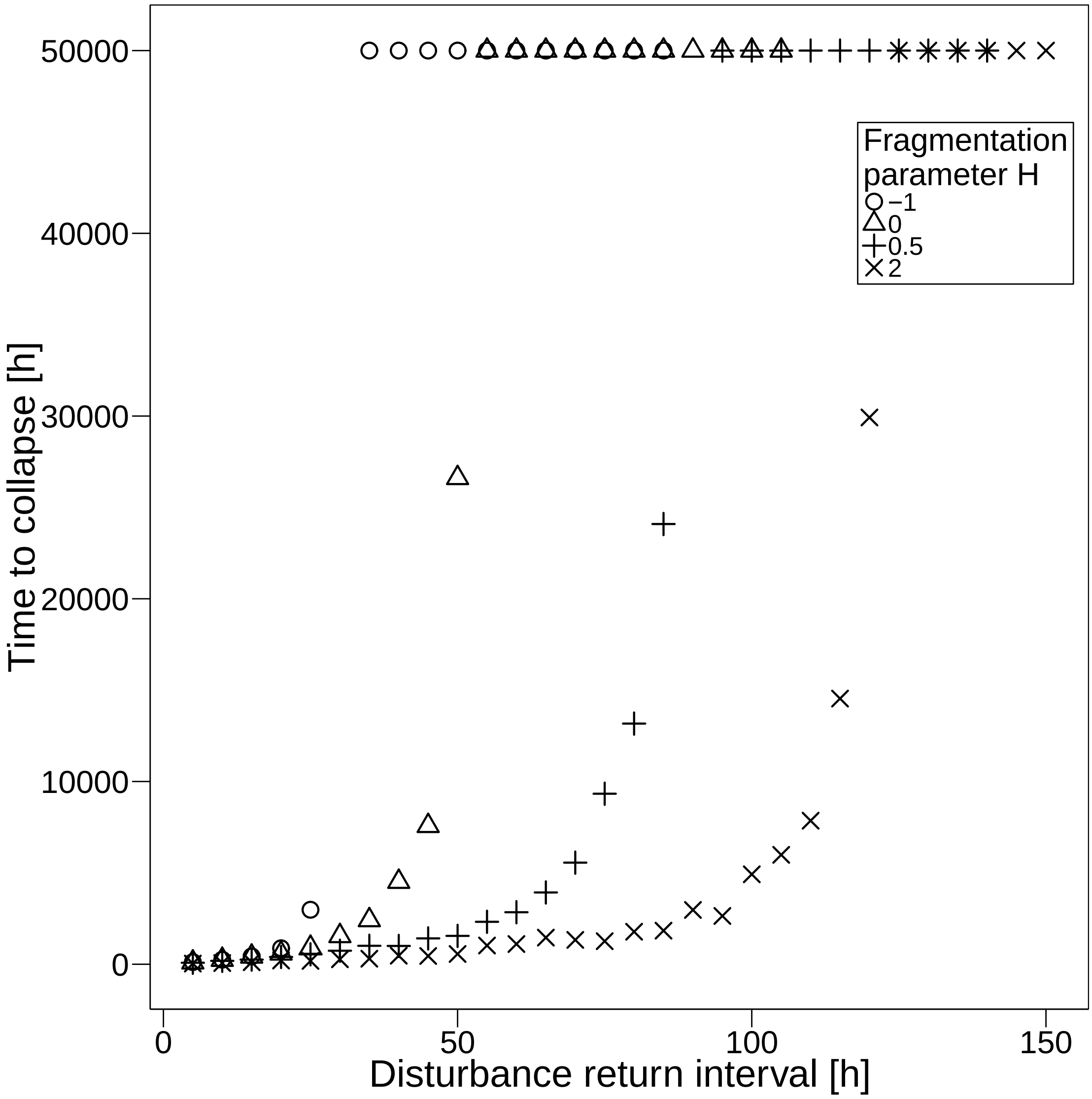


Figure 5.3: Time to collapse under disturbance regimes with fragmentation parameter H of -1, 0, 0.5, and 2 of the disturbance pattern and disturbance return interval of 5-150 hours in steps of 5 hours. Symbols show mean values of 5 simulation runs with maximum specific growth rate μ_{max} of 0.1386 h^{-1} and maximum bacterial diffusion coefficient $D_{x,max}$ of 5.9033E-07 cm^2s^{-1}. Degradation activity up to the maximum simulation time of 50000 hours without collapse are visualized by markers at 50000 hours.

of H), the resistance of the biodegradation performance decreases as well. If the disturbance patterns are highly fragmented (Fig. 5.4, $H = -1$), only highly frequent disturbance events cause a functional collapse and reduce biodegradation performance to less than 20 % of the undisturbed reference scenario. Disturbance return intervals of 25 hours or longer prevent a collapse and biodegradation performance exceeds 50 %. In particular, the difference between a disturbance return interval of 20 and 25 hours is very pronounced. Under moderately fragmented disturbances, this change is smoother and the threshold disturbance return interval, below which collapses may occur, is longer. For lowest fragmentation of disturbance patterns (Fig. 5.4, $H = 2$), a

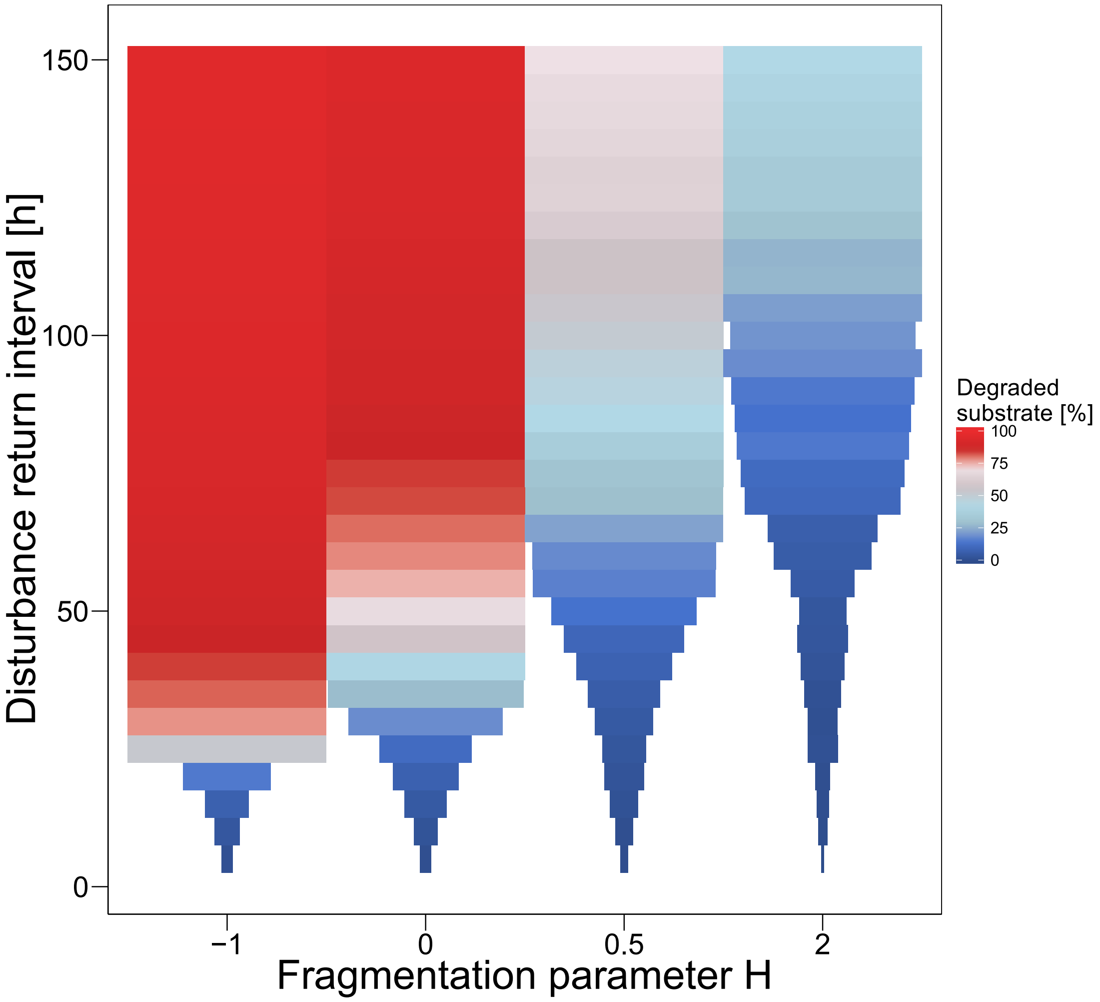


Figure 5.4: Degraded substrate within 2000 hours of simulation time under disturbance regimes with disturbance patterns occurring with four different degrees of fragmentation ranging from highly to non-fragmented (cf. Tab. 5.1), and disturbance return intervals from 5 to 150 hours in steps of 5 hours. Width of boxes indicate time to collapse in relation to 2000 hours of simulation time (i.e. small boxes indicate early collapse, full boxes indicate no collapse). Boxes show mean values of 10 simulation runs with maximum specific growth rate μ_{max} of 0.1386 h^{-1} and maximum bacterial diffusion coefficient $D_{x,max}$ of 5.9033E-07 $cm^2 s^{-1}$.

functional collapse occurs up to a disturbance return interval of 100 hours and the maximum biodegradation performance is only approximately 40 %, which is reached for the longest disturbance return interval of 150 hours. Thus, functional resistance under recurrent disturbance events with a varying spatial occurrence depends on both the disturbance return interval and the degree of fragmentation of the applied disturbance patterns.

5.3.2 *Relevance of ecological processes*

For assessing the influence of changes in the ecological processes bacterial growth and bacterial dispersal, we systematically varied the maximum specific growth rate μ_{max} and maximum bacterial diffusion coefficient $D_{x,max}$ (see Tab. 5.1) and analysed their effects on the functional resistance for selected disturbance regimes characterized by the four considered degrees of fragmentation H = -1, 0, 0.5, or 2 and five different disturbance return intervals of 20, 50, 80, 150 and 250 hours (Fig. 5.5). The figure reveals that the relative importance of the two ecological processes for the functional resistance is not universal, but dependent on the characteristics of the disturbance. Three zones of different effects can be distinguished: The first zone is characterized by high functional resistance and no risk of collapse, regardless of the details of the ecological processes (mostly red subplots in Fig. 5.5). This happens in case of disturbances with high to moderate fragmentation and return intervals above 80 hours. The second zone is a transition zone with a noticeable dependence of the functional resistance on both ecological processes, and an emergence of functional collapse in some disturbance regimes (subplots with colors varying in x- and y-direction in Fig. 5.5). This happens within a critical range of disturbance return intervals and this range shifts to higher values (longer return intervals) with decreasing fragmentation. The remaining third zone is characterized by the emergence of functional collapses and a very low functional resistance, independent of the details of the ecological processes (dark blue subplot in Fig. 5.5). This happens when disturbance return intervals are short and the degree of fragmentation is low, resulting in such harsh conditions that cannot be buffered by the system anymore. These findings on the influence of changes in the ecological processes are also reflected by the schemes with the values of the standard deviation over the outcomes for the different disturbance scenarios (Fig. 5.6). Here, a low standard deviation indicates that a change in the ecological parameters has no considerable influence on the biodegradation performance. This is the case in the two extreme Zones 1 (high resistance) and 3 (low resistance). Only in the transition zone 2, the tested variations of ecological processes can substantially alter the biodegradation performance. This is the case for disturbance regimes with a moderate effect on the microbial ecosystem: there is not enough time to fully recover within the disturbance return intervals, but the effects are also not sufficiently severe for completely inhibiting recovery. In these scenarios with moderately intense disturbance regimes, the biodegradation performance is most sensitive towards variations in the process bacterial growth: mean biodegradation performance can be enhanced by 80 % just by increasing the maximum specific growth rate μ_{max} from the lowest to the highest inspected value (bottom left subplot in Fig. 5.5). Accordingly, varying the growth rate leads to a high standard deviation under moderately intense disturbance regimes, indicating an influence of bacterial growth on the biodegradation performance in those scenarios (Fig. 5.6b). The highest standard deviation in scenarios where the diffusion coefficient is varied is approximately 10 % (Fig. 5.6c), which is much lower than the standard deviations assessed for the scenarios where the growth rate is varied (up to 41 %). However, for certain disturbance regimes in combination with a specific value of μ_{max}, also the dispersal ability may strongly influence biodegradation performance (Fig. 5.6c). For instance, if the disturbance return interval is rather short (20 h), the dis-

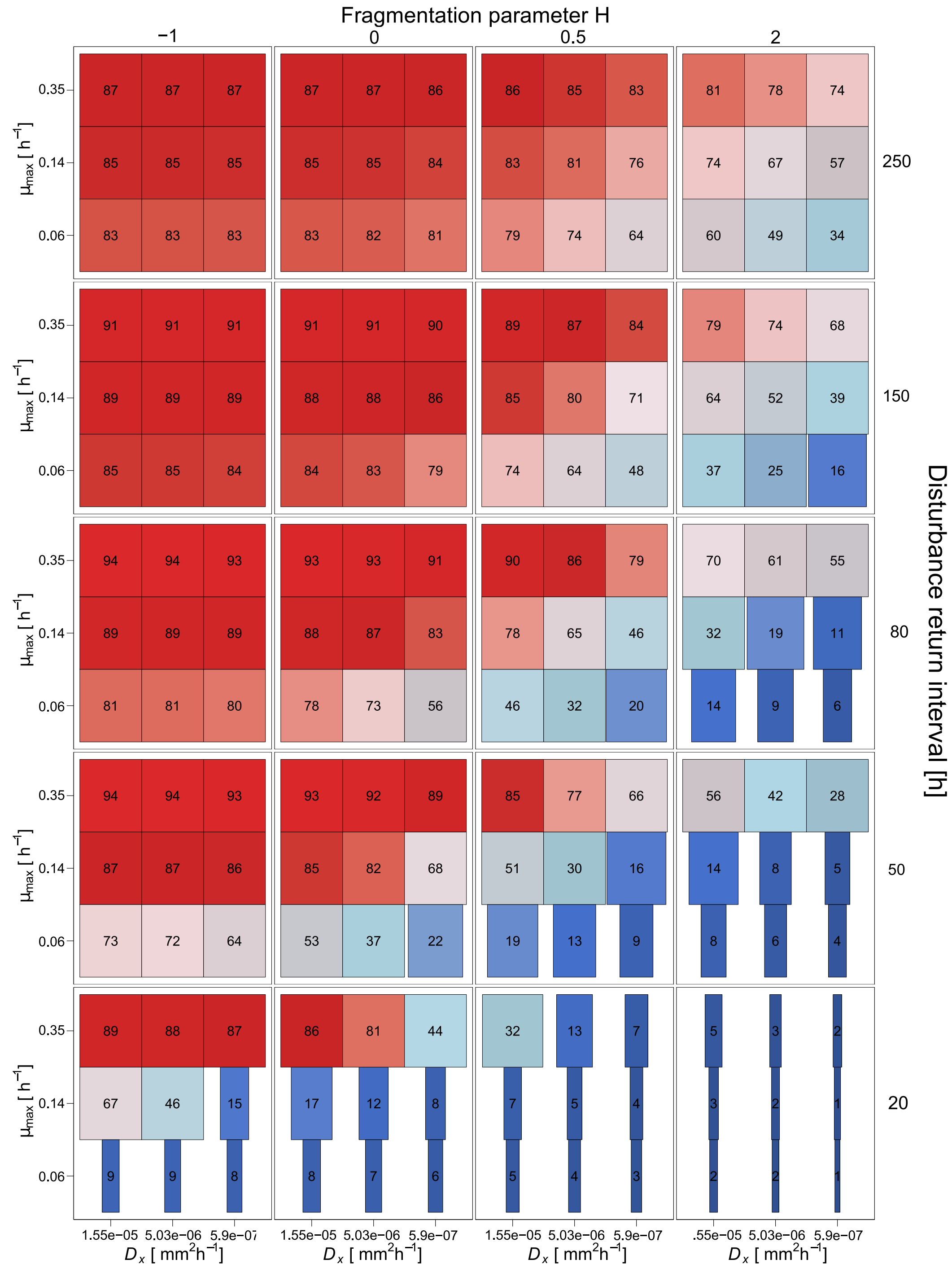


Figure 5.5: Degraded substrate within 2000 hours of simulation time under disturbance regimes with disturbance patterns occurring with four different degrees of fragmentation ranging from highly to non-fragmented (cf. Tab. 5.1), and disturbance return interval of 20, 50, 80, 150 and 250 hours. Within each small plot separated maximum specific growth rate μ_{max} and maximum bacterial diffusion coefficient $D_{x,max}$ are varied according to Table 5.1. Width of boxes indicate time to collapse in relation to 2000 hours of simulation time. Boxes show mean values of 40 simulation runs.

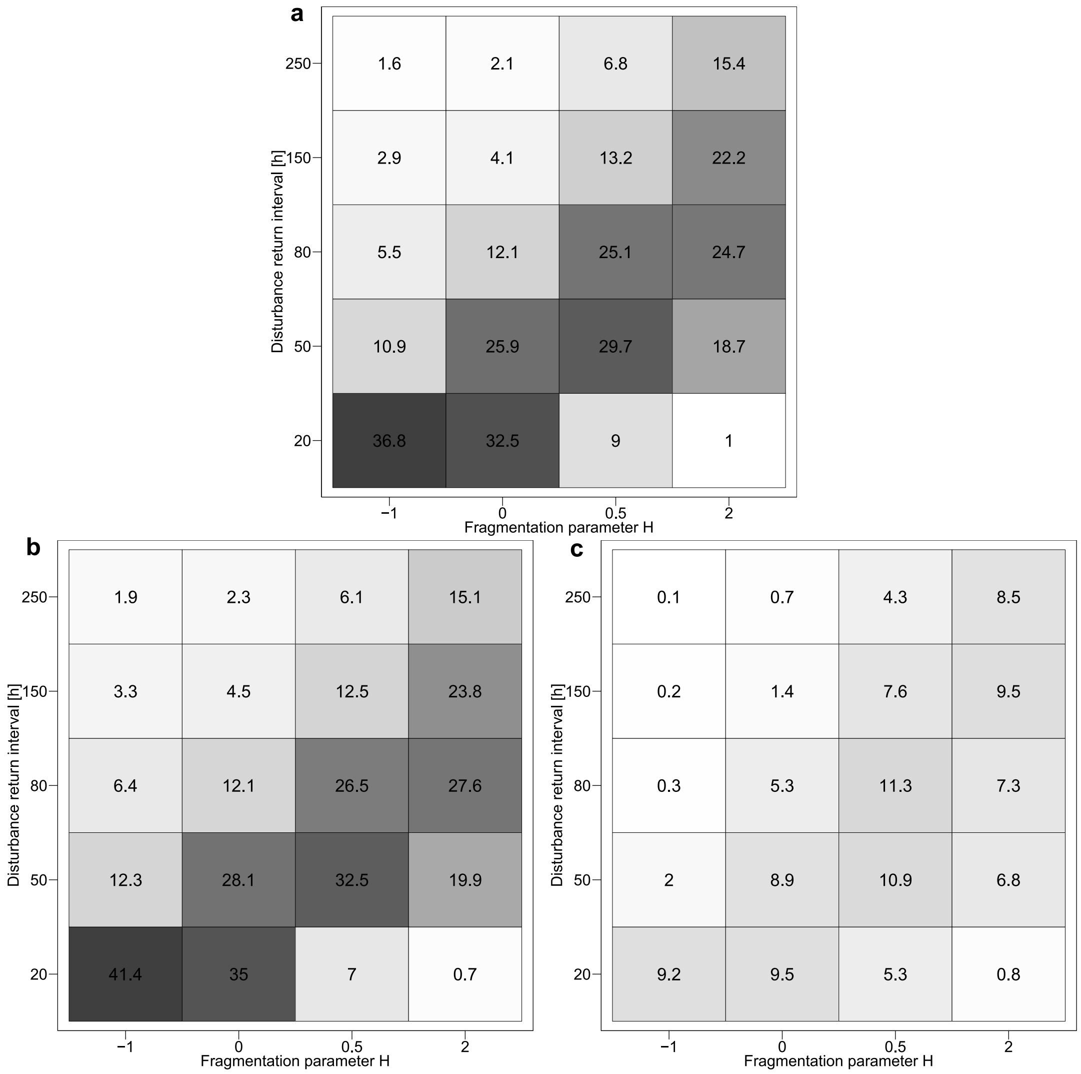


Figure 5.6: Standard deviation (SD) of degraded substrate for each small plot of Figure 5.5 within 2000 hours of simulation time under disturbance regimes with disturbance patterns occurring with four different degrees of fragmentation ranging from highly to non-fragmented (cf. Tab. 5.1), and disturbance return interval of 20, 50, 80, 150 and 250 hours. Boxes show SD values of simulations for each disturbance regime of 40 simulation runs indicating the influence of (a) all ecological processes (SD of simulations with variation of both ecological processes), (b) growth (mean of SD of simulations with varying growth rate) , and (c) dispersal (mean of SD of simulations with varying diffusion coefficient) on the functional resistance.

turbance patterns are highly fragmented (H = -1) and growth is moderately fast (μ_{max} = 0.1386), mean biodegradation performance is raised by 52 % in scenarios with the highest tested bacterial diffusion coefficient compared to the lowest bacterial diffusion coefficient (bottom left subplot in Fig. 5.5).

Thus, ecological processes, especially growth, are a key factor for functional resistance under moderately disturbed scenarios, but not under severe or weak disturbance regimes. In such cases, a variation of ecological processes makes no difference in the biodegradation performance and, in consequence, the specific disturbance regime is the only crucial factor here.

5.3.3 *Relevance of dispersal networks*

Depending on the disturbance return interval and the degree of fragmentation, dispersal networks either do not alter the collapse time, delay a functional collapse, or completely prevent it (Fig. 5.7). If the disturbance return interval is short, dispersal networks have substantial influence on the collapse time. With increasing disturbance return interval, dispersal networks may delay the time to collapse for all degrees of spatial fragmentation. The highest benefit is determined under non-fragmented disturbance events (Fig. 5.7d). Here, a clear delay of collapse time of approximately 500 hours is observable already in scenarios with a disturbance return interval of 35 hours. For longer return intervals, this delay can reach up to 40000 hours. And if the disturbance return interval is longer than 95 hours, dispersal networks completely prevent the functional collapse.

Furthermore, dispersal networks increase the biodegradation performance mainly in disturbance scenarios belonging to transition zone 2 and in cases where the maximum bacterial diffusion coefficient is low (Fig. 5.8). Here, the dispersal of the bacteria is significantly enhanced and, thus, the biodegradation performance is increased by 28 %. Again, it depends on the specific disturbance regime whether the dispersal networks lead to an increased buffer capacity. Highest benefits from dispersal networks occurred under moderate disturbance scenarios, the system benefits most from dispersal networks, but only for specific combinations of ecological parameter values. Most disturbance regimes, under which an increase of functional resistance due to dispersal networks is reported, are related to those under which an influence of bacterial dispersal is already observed (cf. Fig. 5.6c). However, under some disturbance regimes, an increase of the bacterial diffusion coefficient from 5.9E-07 to 1.55E-05 cm^2s^{-1} increases the biodegradation performance, whereas a further increase of the dispersal ability due to dispersal networks does not enhance the functional resistance. Altogether, we observed only few scenarios where dispersal networks strongly enhance the resistance of biodegradation performance to recurrent disturbances.

Moreover, in some scenarios with a short disturbance return interval dispersal networks indeed exceed the time to collapse , but do not substantially increase the biodegradation performance. For instance, under disturbance regimes with high degree of fragmentation and a disturbance return interval of 20 hours, with a moderate growth rate and a low diffusion coefficient, dispersal networks almost double the mean time to collapse (cf. Fig. 5.7a), but increase the degraded substrate only from 15 to 19 % (bottom left subplot in Fig.5.8).

5.4 DISCUSSION

5.4.1 *Thresholds for functional collapse*

With our simulations, we were able to identify thresholds at which functional collapses emerge under recurrent disturbances with varying spatial occurrence. If the

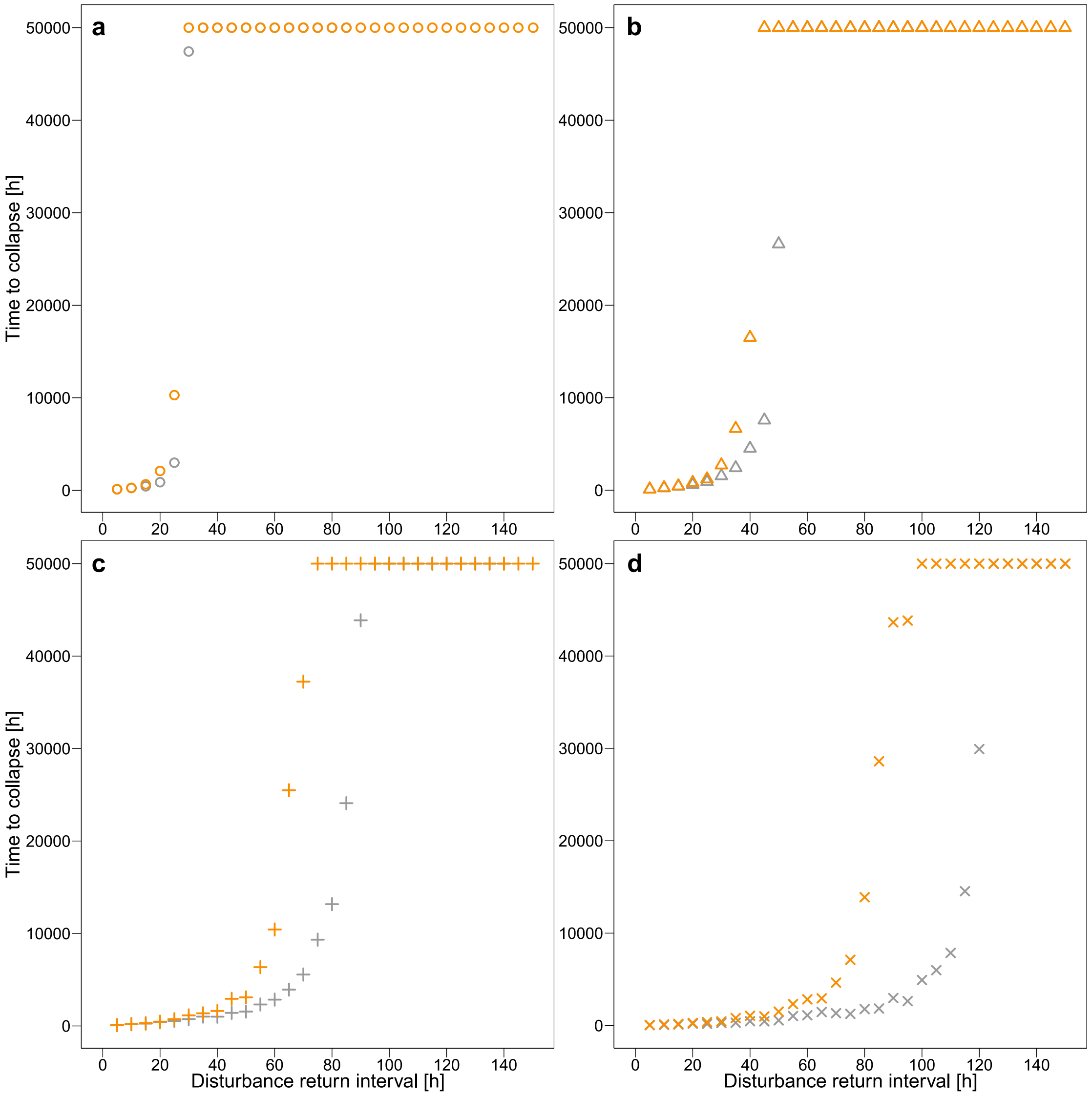


Figure 5.7: Time to collapse in scenarios with (orange) and without (grey) dispersal networks under disturbance regimes with fragmentation parameter H of -1 (a), 0 (b), 0.5 (c), and 2 (d) of the disturbance pattern and disturbance return interval of 5-150 hours in steps of 5 hours. Symbols show mean values of 5 simulation runs with maximum specific growth rate μ_{max} of 0.1386 h^{-1} and maximum bacterial diffusion coefficient $D_{x,max}$ of 5.9033E-07 cm^2s^{-1}. Degradation activity up to the maximum simulation time of 50000 hours without collapse are visualized by markers at 50000 hours.

disturbance return interval is shorter than a certain threshold, the system is not able to maintain its biodegradation performance and collapses. However, these thresholds depend on the degree of fragmentation of the disturbance pattern. If the disturbance pattern is highly fragmented, a disturbance return interval of longer than 30 hours is buffered without a functional collapse. Here, the distance between disturbed and undisturbed habitats is low and, thus, the disturbed habitats are completely recolonized in a short time. The disturbed area can recover before the next disturbance occurs, so that the system is able to cope with a renewed disturbance event. Under less frag-

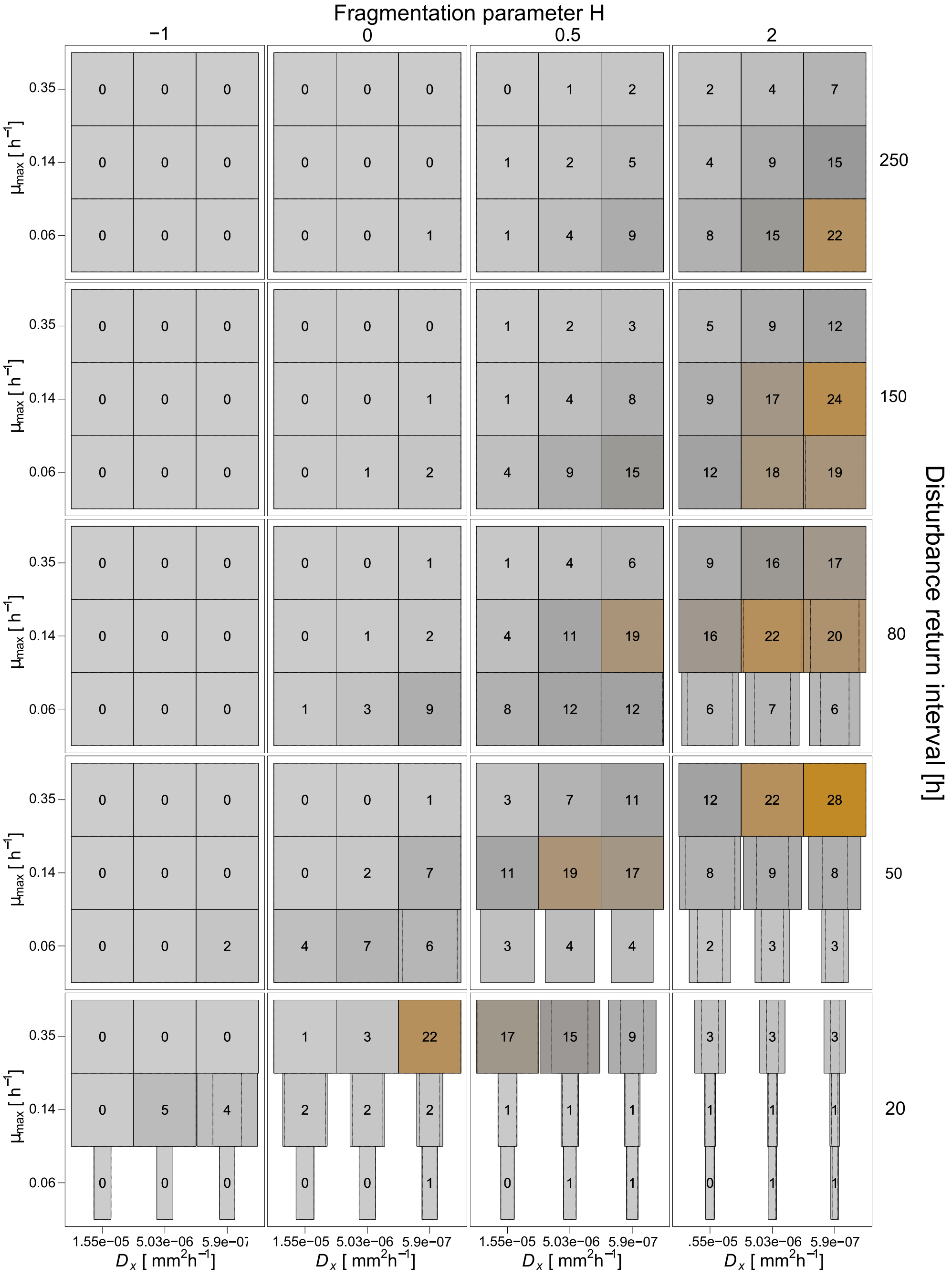


Figure 5.8: Difference in degraded substrate with and without dispersal networks within 2000 hours of simulation time under disturbance regimes with disturbance patterns occurring with four different degrees of fragmentation ranging from highly to non-fragmented (cf. Tab. 5.1), and disturbance return interval of 20, 50, 80, 150 and 250 hours. Within each plot separated maximum specific growth rate μ_{max} and maximum bacterial diffusion coefficient $D_{x,max}$ are varied according to Table 5.1. Width of boxes indicate time to collapse in relation to 2000 hours of simulation time in scenarios with (solid line) and without dispersal networks (dashed line). Boxes show mean values of 40 simulation runs.

mented disturbances, the mean distance between disturbed and undisturbed habitats is enlarged such that the system needs more time for recolonizing the entire disturbance area. In consequence, the required return interval for which disturbances can be buffered without collapsing is longer. When the next disturbance occurs before the system has completely recovered, the effects of the disturbance events are cumulated. The new disturbance pattern likely includes habitats which where undisturbed during the previous disturbance. This increases the effective number of almost uncolonized habitats: disturbed habitats from the previous disturbance, which are not yet recolonized, and disturbed habitats from the current disturbance event. Therefore, the number of habitats which do not substantially contribute to the ecosystem service biodegradation increases with each new disturbance event.

In ecology, collapse of population in the sense of extinction is widely discussed. There is already a long debate on the influence of spatially correlated environmental fluctuations on extinction thresholds and the chances to cope with them through enhancing dispersal [Bascompte and Sole, 1996; Frank and Wissel, 1998; Palmqvist and Lundberg, 1998; Ovaskainen et al., 2002; Frank, 2005]. This is also discussed with regard to the spatial occurrence of the disturbance [Keymer et al., 2000; Thomas, 2000; Johst and Drechsler, 2003; Banitz et al., 2008; Liao et al., 2015]. Liao et al. [2015] identified the spatial correlation of the disturbance as an important factor influencing the extinction probability under recurrent disturbance events for locally dispersing populations. Using a spatially explicit simulation model, they showed that extinction of a population got more likely if the disturbance is highly correlated, which is in accordance with our findings. Spatially correlated disturbances as driving force for functional collapses are much more seldom addressed. For instance, a cumulative effect of recurrent disturbances resulting in a functional collapse was also shown in an experimental study assessing the influence of the frequency of drying-rewetting cycles to microbial activity [Ho et al., 2015].

In the present study, dispersal networks alter the thresholds for functional collapse, depending on the degree of fragmentation of the disturbance patterns. For any tested degree of fragmentation, the system is able to buffer more frequent disturbance events in simulations with dispersal networks than in simulations without dispersal networks. With decreasing fragmentation of the disturbance patterns, the benefit of dispersal networks in terms of the time to collapse increases. Thus, the shift of the threshold is most distinct under non-fragmented disturbances. As described, in those scenarios, the mean distance between disturbed and undisturbed habitats is long, such that the system is not able to recolonize all disturbed habitats within shorter disturbance return intervals. The effects of the next disturbance event then cumulate with the effects of the previous disturbance event, which results in a collapse after several disturbance events. Dispersal networks help overcoming the long distance between the undisturbed and the disturbed habitats. In consequence, the bacteria are able to quickly recolonize the disturbance area and, thus, to buffer more frequent disturbances than without dispersal networks. Furthermore, dispersal networks delay the time to collapse under some disturbance regimes. A functional collapse is not completely prevented, but the time to collapse is increased, such that the system is longer maintaining the biodegradation function.

5.4.2 *Key factors for functional resistance*

Certainly, a collapsed system is not maintaining ecosystem functioning anymore, which indicates a low functional resistance. Factors preventing a functional collapse, thus, increase the stability. However, even more important to understand are the key factors increasing the effective biodegradation performance under recurrent disturbances with varying spatial occurrence.

Within this study, we tested the influence of these ecological processes bacterial growth and bacterial dispersal on the functional resistance of a microbial ecosystem. Our simulation results show that an enhancement of the ecological processes can improve the biodegradation performance, but only under moderate disturbance regimes denoted by a certain trade-off range between a short return interval but high fragmentation and a long return interval but low fragmentation (Fig. 5.6a). Outside of this range the disturbance regime is either too severe, such that the functional resistance of the system is low regardless of the specific ecological processes of the bacteria. Or the disturbance regime is weak, such that the disturbances are buffered quite well and the function is maintained in all tested scenarios, irrespective of how fast the bacteria grow or disperse. Looking at both ecological processes, the rate of bacterial growth proved to be more important for the functional resistance than the velocity of bacterial dispersal. A higher growth rate allows for a faster recolonization and functional stabilization of the disturbed habitats. In those habitats, bacteria do not only significantly contribute to biodegradation, the bacterial biomass is also high due to faster growth. These bacteria are the source for recolonizing the disturbed habitats after the next disturbance event and, thus, keeping the overall bacterial biomass on a sufficient level for maintaining the biodegradation function. Here, structural stability in terms of bacterial biomass appears to be highly correlated with functional stability. The correlation of functional and structural stability of microbial ecosystems was analysed in previous studies [Fernandez et al., 2000; Botton et al., 2006; Allison and Martiny, 2008]. However, the results differ depending on the specific ecosystem and considered function indicating that there is no universal answer to the question whether structural and functional stability are linked.

Faster bacterial dispersal helps to recolonize disturbed habitats, which are farther away from the undisturbed habitats. However, the benefit due to an increased dispersal is lower than due to an enhanced growth rate.

In summary, the processes bacterial growth and bacterial dispersal are important factors for functional resistance under recurrent disturbance events with varying spatial occurrence, depending on the disturbance regime. We showed that the disturbance return interval and the fragmentation of the applied disturbance pattern have the strongest influence to the resistance of the biodegradation performance. With increasing disturbance return interval and increasing degree of fragmentation, the functional resistance of the microbial ecosystem is also increased. This relationship was also described for recurrent disturbances without a variation in the spatial occurrence of the disturbance pattern (cf. Fig. 4.7, Sec. 4.4.1).

Only under certain conditions, dispersal networks can increase the resistance of the biodegradation performance to recurrent disturbances of varying spatial occurrence by helping to overcome the distance of undisturbed to disturbed habitats and, thus, fasten the recolonization. Again, we show a dependence on the disturbance regime. Under certain moderately intense disturbance regimes, the biodegradation performance is significantly increased by dispersal networks, especially if the disturbance pattern is less fragmented and the diffusion coefficient of the bacteria is low. Similar to the influence of the tested ecological processes, dispersal networks have no or very little influence in scenarios with a very high or very low disturbance severity.

Moreover, we showed that dispersal networks shift the threshold for collapse and, thus, prevent a collapse under certain disturbance regimes, but do not always substantially enhance the biodegradation performance in these scenarios. Here, one aspect - the time to collapse - indicates an increased functional resistance due to dispersal networks, whereas the assessed biodegradation performance indicates no benefit. In those scenarios, the biodegradation performance is maintained without collapsing, but on a very low level. In consequence, the time to collapse alone is no indicator for the functional resistance under recurrent disturbances. Thus, it may be appropriate to define some minimum biodegradation performance level. We may then refer to a system as 'functional resistant' if this minimum level is constantly exceeded under recurrent disturbances.

5.4.3 *Implications for management strategies*

With the applied simulations, relevant factors for managing contaminated soils were identified regarding two aspects: ecological properties of the microbial ecosystem and the disturbance regime. First, as we have shown the relevance of bacterial growth, strategies for enhancing growth may be applied to soil systems which are exposed to recurrent disturbance events. Examples for such strategies are an additional supply of nutrients, an increase of oxygen concentration in the soil water or the increase of plant roots, which enhance bacterial growth by producing several exudates acting as a carbohydrate source for the bacteria [de Lorenzo, 2008; Niti et al., 2013; Srivastava et al., 2014]. Applications enhancing bacterial dispersal such as dispersal networks may also enhance the functional resistance. However, we have shown that bacterial dispersal is only in a few scenarios a key factor and, thus, dispersal enhancing strategies may not always be effective.

The second aspect is the influence of the disturbance regime. For managing contaminated soil, especially manipulating the fragmentation of the disturbance may be of high interest. The spatial occurrence of many types of disturbances in soil are related to the pore size network, such as release of toxic chemicals or salt stress. Those disturbances are highly fragmented, if the soil is highly fragmented. Thus, manipulating the soil structure such that it is more fragmented, for instance by tilling, may enhance the functional stability and prevent a functional collapse.

6

SYNTHESIS AND OUTLOOK

6.1 MAIN RESULTS

In the present thesis, several aspects on microbial ecosystems, their dynamic response to disturbances and their functional stability were addressed which were not fully understood so far (Fig. 6.1). This was done using an important microbial ecosystem service, namely 'biodegradation', as case study. By the mean of the *eColony* modelling framework developed in Chapter 2 we were able to derive a number of important principle insights. In the following, the main results are summarized and discussed considering the outcomes of the three performed studies of the Chapters 3, 4, and 5.

6.1.1 *Key factors for functional stability*

One of the major objectives of all three studies presented in this thesis was the identification of key factors influencing the functional stability of the modelled microbial ecosystem. Basically, the influencing factors can be categorized in (i) *ecological factors*, meaning abiotic and biotic properties of the microbial ecosystem itself, and (ii) *disturbance characteristics*, described by the intensity, frequency and spatial pattern of occurrence of the disturbance.

i) *Ecological factors*

   It was shown that ecological processes of microbial ecosystems are key factors for maintaining or recovering the biodegradation performance after single or repeatedly recurring disturbance events. Thus, the specific properties of the bacterial population are influencing both functional resilience and resistance.

   Bacterial growth is essential for 'self-recolonization' of disturbed areas and facilitates the functional recovery after disturbances, especially in disturbed areas with a high distance to the undisturbed area (Fig. 3.5). In such habitats, bacterial growth is particularly necessary for recovering the biodegradation performance. Thus, it is also a limiting factor for complete long-term recovery when exposed to clustered disturbance patterns resulting in a high amount of habitats with a high distance to the undisturbed area. The importance of bacterial growth for the functional resistance to recurrent disturbance events depends on the specific disturbance regime (Fig. 5.5). Under disturbance regimes with a high severity characterized by low fragmentation and high frequency, the functional resistance is low, independent of how fast the bacteria are able to grow. Under weakly severe disturbance regimes, the system is able to buffer the disturbance events regardless whether the bacteria are growing fast or slow. Under moderately severe disturbance regimes, however, bacterial growth is an important factor for the functional resistance. Here, an accelerated 'self-recolonization' due to bacterial growth allows for coping with an even increasing frequency of disturbances.

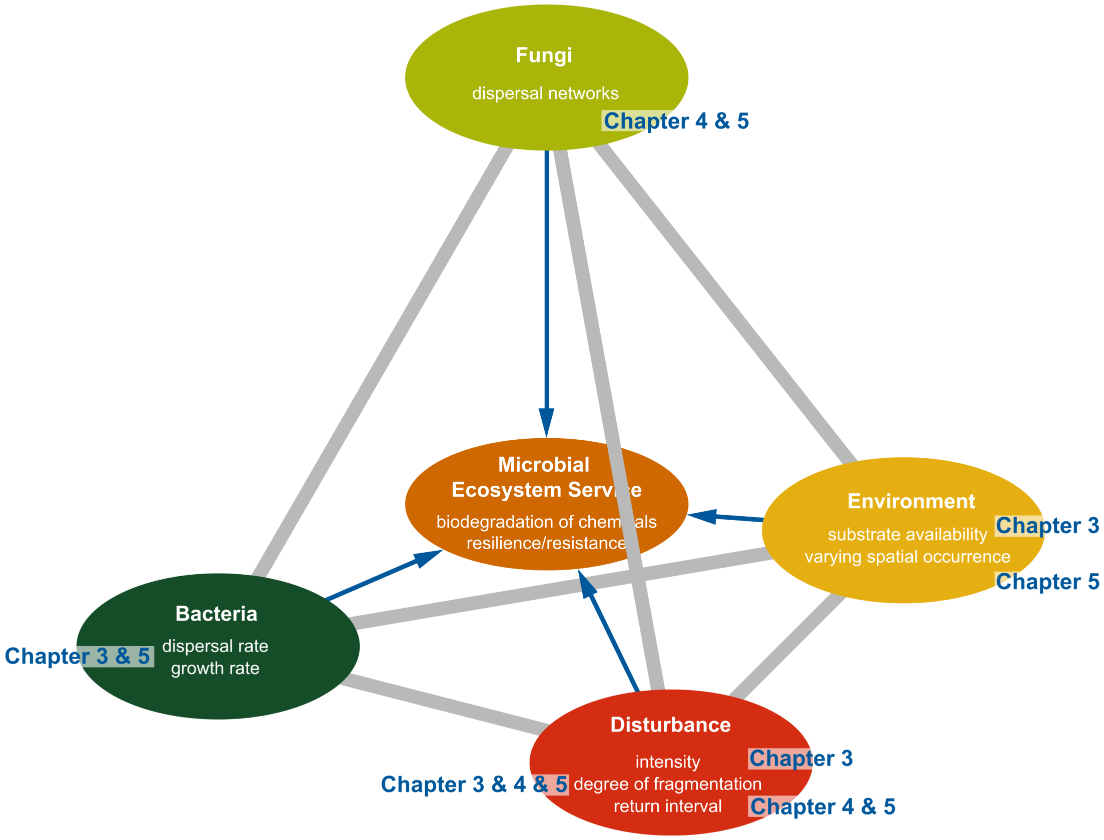


Figure 6.1: Conceptual relationships and specific aspects analysed within this thesis.

Bacterial dispersal is also a key factor for functional resilience as well as for functional resistance. The ability to disperse within the disturbed system allows faster recolonization of disturbed areas and, in consequence, an increased biodegradation performance. Particularly, in the first recovery phase after a disturbance event, biodegradation performance is driven by dispersing microorganisms in disturbed areas at the edge to undisturbed areas (Fig. 3.6). Thus, a higher dispersal rate leads to a better functional recovery shortly after a disturbance. This is especially important for the functional resistance under highly frequent recurrent disturbances. If the disturbance return interval is short, bacterial growth is still in its lag-phase, and the biodegradation performance is only maintained due to bacterial dispersal. However, this is not true for very short disturbance return interval lengths. Here, the effects of the disturbances are that fatal, that an increase in dispersal ability can not enhance the biodegradation performance.

The *mobility of the substrate* or the pollutant is a further key process. A high diffusion coefficient of the specific compound increases the contact probability of bacteria and substrate and, thus, the functional stability of the system. Similar to the spatial process bacterial dispersal, substrate mobility increases the biodegradation activity especially shortly after a disturbance. Unconsumed substrate from disturbed areas diffuses to undisturbed or disturbed areas which have already been recolonized. Therefore, the total biodegradation performance is increased.

ii) *Disturbance characteristics*

The intensity of the disturbance in terms of remaining biomass in the disturbed area affected the biodegradation recovery time as well as the shape of the recovery dynamics (cf. Fig. 3.3, 3.7). As expected, the more biomass survives a particular disturbance event, the faster the biodegradation performance is recovered and, thus, a higher (structural) resistance of a microbial ecosystem enhances the functional resilience. However, the remaining biomass also influences the importance of the ecological processes: after less intense disturbances, bacterial dispersal is the limiting process, whereas after highly intense disturbances bacterial growth and bacterial dispersal are both limiting factors in different recovery phases.

Within all three studies, the characteristics of the disturbance regarding the spatiotemporal pattern of occurrence were found to strongly influence the functional stability of the microbial ecosystem. With an increasing *degree of fragmentation* of the disturbance pattern, the biodegradation performance faster recovered after a single disturbance event and persisted on a higher level under recurrent disturbances. Moreover, a high fragmentation of the disturbance prevents the emergence of a functional collapse. Thus, both functional resilience and resistance are influenced by the degree of fragmentation of the disturbance. It was shown, that the key aspect of this relationship is the mean distance Δ of disturbed habitats to the next undisturbed habitat (cf. Fig. 3.7c, d; 4.6). A high fragmentation of the disturbance results in a very low value of Δ and, thus, the distance the bacteria have to overcome for recolonization of the disturbed area is short. Contrarily, if the disturbance pattern is less fragmented and, therefore, the mean distance is high, the time needed for recolonizing the entire disturbed area increases. In consequence, functional recovery after disturbances is slowed down, causing also a lower functional resistance when affected by recurring disturbance events.

However, how much the functional stability is impaired due to a lower degree of fragmentation depends on the *disturbance return interval* as well. A short disturbance return interval, i.e. highly frequent disturbance events, decrease the functional resistance and increase the probability for collapsing. A higher disturbance return interval increases the time the system has for recovering its function between two disturbance events and, thus, enhancing the functional resistance. However, the rate of functional recovery depends again on the degree of fragmentation. Therefore, the system can buffer a more frequent disturbance better if the spatial occurrence is highly fragmented.

Certainly, the described key factors are often combined, and the interplay between those aspects enhances the functional stability even more. For instance, a microbial ecosystem consisting of microorganisms with a good dispersal ability may be very resistant against highly fragmented recurring disturbances.

Furthermore, the presented results of this thesis show a high relationship between functional resistance and resilience. How good a system recovers its function (i.e. how resilient the system is) depends on how much it was affected by the disturbance (i.e. how resistant it is). On the other hand, how good a system can buffer recurrent disturbances depends on how fast it recovers the function between the disturbance events.

6.1.2 *Influence of dispersal networks*

Dispersal is identified as one of the main factors for the functional resilience and resistance of biodegradation under disturbances, but only under certain preconditions. Therefore, only in these cases, mechanisms enhancing bacterial dispersal can facilitate the functional stability of biodegradation. Dispersal networks proved to be a buffer mechanism in most scenarios, as shown in Chapter 4 and 5. The increased dispersal of the bacteria causes a better connectivity between more distant disturbed habitats and the undisturbed area under recurrent disturbance events (cf. Fig. 4.4). Thus, dispersal networks attenuate the negative effect of a lower degree of fragmentation of the disturbance pattern. Bacteria disperse faster within the disturbed system and are able to reach habitats during a disturbance return interval which remain uncolonized in scenarios without dispersal networks. This increases the biodegradation performance mainly in habitats with a very low activity up to a mean biodegradation performance and, with this, enhances the functional resistance. Moreover, a functional collapse under recurrent disturbances varying in the spatial occurrence is preventable due to dispersal networks in some scenarios (Fig. 5.7).

However, it was shown that, under highly fragmented disturbance events, the system is not further benefiting from dispersal networks regarding its functional stability. In these scenarios, the functional resistance is high in absence and presence of dispersal networks because the mean distance of disturbed to undisturbed areas is low. This shows that dispersal networks are not automatically of key importance for functional stability but in situations where the microbial ecosystem is 'at the edge'.

Moreover, in some scenarios the biodegradation performance was even lower in presence of dispersal networks (Fig. 4.8). This was observed under frequent recurrent disturbance events with a highly fragmented pattern. In these cases, dispersal networks mediated 'highways to hell'. Bacteria dispersed from 'safe' undisturbed habitats into the disturbance area and were removed during the next disturbance event. This phenomenon of mistakenly preferred habitats with worse conditions is widely discussed in ecology as 'ecological trap' [Rich et al., 1994; Kristan, 2003; Weldon, 2006; Hale and Swearer, 2016]. However, the disadvantage in the total performance of the entire system was very low and resulted from a negative, local effect of the dispersal networks in single habitats.

6.1.3 *A question of scale*

As discussed in Section 6.1.1 some of the main key factors for functional stability are spatial aspects: bacterial dispersal, substrate diffusion, and the presence of dispersal networks as ecological infrastructure, as well as the spatial occurrence of the disturbance events in terms of the mean distance of disturbed to undisturbed habitats. For identifying these aspects, the analysis of the spatiotemporal dynamics was essential (Ch. 3, 4). Observing the biodegradation performance in single habitats allowed for determining the limiting factor for recovering the function after a disturbance event of the habitats in relation to its relative position within the system (Fig. 3.5). Moreover, the spatially explicit analysis enabled the identification of activity areas in which the biodegradation performance is maintained under recurrent disturbance events (Fig. 4.4).

Generally, in single habitats the local biodegradation performance may highly differ from the global performance. At the interface between disturbed and undisturbed area, the biodegradation performance is shown to be higher than in other areas of the system, especially shortly after a disturbance. Thus, the functional stability depends also on the observed scale: some habitats are more resilient and/or resistant then others, depending on their location with respect to the disturbance pattern. Moreover, it was shown that dispersal networks decrease the local biodegradation activity in undisturbed habitats to the benefit of the activity in the disturbed habitats. Bacteria in undisturbed habitats, that are directly connected to dispersal networks, disperse fast to the disturbed areas. In consequence, the local biodegradation performance decreases in such habitats (Fig. 4.4e, f). In these cases, the explicit spatial configuration of the disturbance pattern, i.e. the distribution and the relative position of the disturbed habitats, proved to highly influence the functional stability. However, for the functional stability of the system the overall biodegradation performance is crucial. We showed with our simulation results, that the functional stability in terms of the recovery rate after single disturbance events or the mean global biodgeradation performance can be estimated using aggregated spatial metrics such as the mean distance between disturbed and undisturbed habitats. But, of course, the global biodegradation performance depends on the local biodegradation performance of all habitats within the system. Thus, it is important that a worse local functional stability of single habitats is compensated by habitats with a high functional stability.

6.2 IMPLICATIONS FOR NATURAL SYSTEMS AND MANAGEMENT APPLICATIONS

The terrestrial environment is continuously exposed to fluctuating conditions with different effects. Understanding the response of the microbial ecosystem and its functional stability is important for managing microbial ecosystem services such as biodegradation. Several implications for the stability of biodegradation in natural systems under lethal disturbance events, for instance initiated by toxic chemicals, derive from the described results of this thesis.

We identified indicators which may help estimating the functional stability of microbial ecosystems and, thus, optimize management strategies. With an aggregated spatial metric of the disturbance pattern - the mean distance of disturbed to undisturbed habitats - the functional resilience in terms of the recovery time after single disturbances as well as the functional resistance under recurrent disturbance events can be determined. In soil, the area affected by disturbances may be considerably influenced by the spatial characteristics of the soil texture with different pore size distributions and connectivity. Thus, with knowledge about the soil characteristics, a first approximation about the response of the soil microbial ecosystem to disturbances may be possible. Furthermore, the results regarding the degree of fragmentation of the disturbance pattern may be a hint under which conditions a change of the soil structure, for instance via tilling, increase the stability and the efficiency of the ecosystem service. Soil tilling is already known as a process increasing biodegradation by enhancing the oxygen concentration [Rhykerd et al., 1999; Gogoi et al., 2003; Couto et al., 2010]. Our results indicate that a mixing of soil may be even more advantageous as it increases the degree of fragmentation of the pore network. However, disrupting the soil structure may also have negative effects on the microbial ecosystem, for instance, by destroying the network of mycelial hyphae or changing community composition [Young and Ritz, 2000].

The disturbance regime characteristics also affect the importance of the ecological processes. Under highly intense and moderately or less fragmented disturbances, dispersal is important for functional recovery and, thus, dispersal enhancing management strategies such as the application of dispersal networks provided by fungal hyphae may help increase the functional stability. Under highly fragmented disturbances, dispersal is no key factor and dispersal networks can, in turn, even decrease the functional resistance. Here, management strategies may not need to involve dispersal enhancing applications. Growth proved to be an important process for the long time functional recovery and for buffering moderately intense recurrent disturbance events. Thus, under such specific recurrent disturbance regimes, strategies for improving growth conditions such as the additional supply with nutrients may further enhance functional stability.

6.3 APPLIED METHODOLOGY

The studies within this thesis aimed at gaining principle understanding of determinants of functional stability of microbial ecosystems and their biodegradation performance rather than understanding a specific case study. Therefore, a 'virtual laboratory approach' was applied with the model *eColony* used for the simulations that are combined with a range of generic scenarios and different analyses. This methodology has certain advantages, but reveals also limitations.

6.3.1 *Model potentials*

Using a modelling approach for addressing the specific research questions has several advantages. The applied numerical modelling approach allowed for comparing varying parameters and analysing their influence on the functional stability. This was essential for the different analyses made in this thesis, for instance, the mechanistic analysis of functional resilience (Sec. 3.3.2), determining the influence of the disturbance patterns' degree of fragmentation or of dispersal networks.

As discussed in Section 6.1.3, the spatiotemporal observation of the biodegradation performance proved necessary for understanding functional stability and the underlying mechanisms. The developed spatially explicit model allowed for monitoring the biodegradation dynamics at the global and the local scale. Using an ensemble approach for generating sets of disturbance regimes, we were able to identify under which conditions the explicit spatial configuration of the disturbance pattern is influencing the functional stability. On the other hand, we assessed the predictive power of aggregated spatial metrics characterizing the disturbance pattern for determining the stability behaviour under disturbances. Despite a low complexity in its spatial explicitness (e.g. no pore network), the simulation results lead to better understanding of the relevance of spatial aspects.

The applied methodology allowed for the analysis of a wide range of different scenarios with variations in ecological processes as well as in disturbance characteristics which is hardly realizable in laboratory experiments. In particular, the heterogeneous occurrence of the disturbance pattern is not easily applicable in laboratory conditions. Most experimental studies are limited to the observation of temporal changes in function or structure. Here, numerical modelling fill an important gap in stability analysis of microbial ecosystems.

Moreover, we show with our results that the analysis of microbial ecosystems, especially when combined with simulation modelling approaches, can help for testing concepts and theories on general ecology. Several examples for this derived from the conducted studies, for instance, debates on 'ecological implications of fragmentation', 'dispersal and survival in fragmented landscapes', or 'emergence of functional collapse' [Settele et al., 1998; Frank and Wissel, 1998; Palmqvist and Lundberg, 1998; Johst and Drechsler, 2003; Heinz et al., 2006; Lindenmayer and Fischer, 2013]

6.3.2 *Model limitations*

A model is always a simplified version of some specific aspects of the real world. For developing a simulation model, certain assumptions have to be made with a focus on the research question that should be answered. In the case of *eColony*, the microbial ecosystem and the applied disturbance regimes were described in a simplified manner. The microbial ecosystem was assumed as one aggregated bacterial population and, thus, excluded possible effects due to specific properties of different species. Furthermore, the model did not consider evolutionary processes, i.e. properties of the bacteria were not altering over time. Influences of additional environmental factors such as substrate limitation or inhibition of dispersal due to decreased soil moisture were excluded. For generating a comparable steady state situation, a constant substrate input was assumed. Thus, substrate for the bacteria was always available up to a maximum concentration, which is certainly not in accordance with the situation in an environmental system. Simplifications were also made regarding the applied disturbance events reducing the complexity compared to such events in natural systems. The effect was a reduction of biomass only within the disturbance area without any impact on bacteria outside this area, although they were directly in contact with the disturbed area. Moreover, the disturbance events had no effect on the properties of the bacteria, i.e. their dispersal ability or growth rate.

Dispersal networks were basically assumed as an abiotic factor for enhancing bacterial dispersal. However, in natural systems fungal mycelia, which should be represented by the dispersal networks in the model, are a biotic part of the microbial ecosystem. Thus, they may also be affected by disturbances and may lose the potential as a stabilizing factor.

Regarding the soil environment, the explicit occurrence of pore networks were excluded. As spatial aspects were identified as important key factors for functional stability, the distribution and composition of pores in soil are presumably also highly relevant.

6.3.3 *Outcome visualization*

When using a complex modelling approach for simulating different scenarios varying in several parameters, the interpretation of the results requires a reasonable design of the simulation scenarios, but also appropriate analyses and visualizations of the simulation results. Within this thesis, several different types of visualizations were applied for gaining insights into the dynamics and underlying mechanisms of the examined model system. For instance, plotting a transect over several habitats with increasing distance to undisturbed areas revealed the relevance of the habitats' relative position for their contribution to functional resilience (Fig. 3.4). The ranges over biodegradation performance recovery for ensembles of different explicit spatial configurations of the disturbance patterns were displayed with polygon plots allowing for testing the influence of the explicit spatial configuration on functional stability (Fig. 3.7a, b). Using spatial metrics in the data analyses, such as the mean distance of disturbed to the next undisturbed habitats, allowed for identifying indicators of functional stability (e.g. Fig. 4.6). With tileplots, we were able to visualize the outcome of a huge amount of simulations with different parameter combinations, for instance, analysing the functional resistance to recurring and spatially varying disturbance events (e.g. Fig. 5.5). Representing the biodegradation performance by the color key, and the time to collapse by box width enabled us to combine these two different aspects of functional resistance within single plots (Fig. 5.4, 5.5). Overall, the use of these and other types of visualizations facilitated understanding the dynamic responses of the modelled microbial ecosystem dynamics to different disturbance regimes and addressing the specific research questions in this thesis.

6.4 OUTLOOK

The microbial soil system and its ecosystem services are influenced by many factors (Fig. 1.4). Some were analysed in this thesis and the results are contributing to a better understanding of functional stability of microbial ecosystems in soil. However, for determining the response of such a complex environment to changing conditions and disturbances, many more aspects may be analysed in future research. Therefore, respective investigations in simulation models but also laboratory experiments are needed, and a continuous interplay may lead to a wider comprehension of how to manage the soil microbial ecosystem for optimizing ecosystem service provision.

6.4.1 *Bacteria*

In general ecology, the relationship between biodiversity and stability has been widely discussed in the past [Peterson et al., 1998; Loreau et al., 2003; Balvanera et al., 2006; Steudel et al., 2012]. It was shown that a large number of species enhances the stability of an ecosystem under changing conditions [Darwin, 1859; MacArthur, 1955; Holling et al., 1995; Peterson et al., 1998]. In microbial ecology, community structure was also already described as a potential key factor for functional stability in several experimental studies [Buckling et al., 2000; Fernandez et al., 2000; Griffiths et al., 2001; Botton et al., 2006; Allison and Martiny, 2008; Fetzer et al., 2015]. In consequence, considering the microbial ecosystem as a union of several bacterial species with different properties is important for completely understanding the functional response to disturbances in real soil environments. In the presented model version, bacteria are assumed as one aggregated population with the same properties, which was sufficient for the specific research objectives. However, for further studies, the implementation of several bacterial species differing in their properties should be considered. Several modelling studies already exist addressing the development of models explicitly including microbial communities [Stolyar et al., 2007; Larsen et al., 2012; Ebrahimi and Or, 2014; Kaiser et al., 2014]. For instance, Kaiser et al. [2014] developed a spatially explicit simulation model for examining the dynamics of a microbial population consisting of different functional groups during litter decay.

Concerning functional stability analysis, it is important to know if the different species are equally contributing to the specific ecosystem service, if they are competing with each other and if they are varying significantly in their properties regarding ecological processes and individual resistance to disturbances. For example, rapidly dispersing species may recolonize disturbed areas faster than slower species, which may be important for the community composition in this area [Wolf et al., 2015]. On the other hand, in disturbed areas highly distant from undisturbed areas species with a high growth rate may outmatch species with a good motility, especially when they also differ in their resistance to the specific disturbance. Several interesting research question in the context of functional stability may be analysed with a microbial simulation model of different species or species groups: When one species becomes extinct, is the ecosystem service simply delivered by some other species at the same level? What combination of species with varying properties is optimal for overall functional stability of the ecosystem? Is the functional stability even increased due to disturbances affecting competing species, which are not contributing to the ecosystem service of interest? How important is the spatial distribution of the different species for functional stability? However, microbial modelling on community level is a hard challenge. The high number of different species in natural soil systems has to be classified in functional groups, and is even than quite high [Faust and Raes, 2012]. How much functional groups and how fine they are classified in detail, should be proved for each research question individually. Moreover, stochastic processes on individual level play an important role in community dynamics [Zhang et al., 2016]. Including stochasticity for individual processes requires individual-based modelling, which is a time-consuming attempt for modelling microbial communities in terms of the explicit consideration of several different species.

6.4.2 *Fungal networks*

In terms of total biomass, fungi are the most dominant organisms in the soil environment and also highly resistant against fluctuating conditions [Harms et al., 2011; Barnard et al., 2013]. Fungi are shown to interact with bacteria and plant roots (Sec. 1.1.4), transport nutrients and water and are actively changing the soil structure [Ritz and Young, 2004; Furuno et al., 2010; Guhr et al., 2015]. Furthermore, fungi are delivering several ecosystem services such as biofertilization, biodegradation or prevention of nutrient loss [Pellegrino and Bedini, 2014; Cavagnaro et al., 2015; Zafra and

Cortes-Espinosa, 2015]. Despite the high resistance of fungi compared to bacteria, they may also be affected by disturbances in terms of abundance or ecological processes [Maestre et al., 2015]. Thus, fungi are an important aspect for functional stability of soil microbial ecosystems regarding both direct and indirect contribution to the function of interest.

6.4.2.1 *Fungi as transport network*

The ability of fungal mycelia to act as dispersal networks for bacteria proved to be a buffer mechanism for the stability of the ecosystem service biodegradation (Sec. 6.1.2). However, fungi are also able to take up and transport substances through their hyphaes over larger distances than possible by substance diffusion [Jacobs et al., 2004; Furuno et al., 2012; Schamfuss et al., 2013]. Within this thesis, substrate diffusion was shown to be a key factor for functional stability as the bioavailability is enhanced when substrate is more mobile. Thus, the ability of fungal networks acting as 'pipelines' for transporting substrate may be an additional stabilizing factor and should be considered in functional stability analyses.

Besides the substance translocation, fungi are also able to transport water [Egerton-Warburton et al., 2007; Plamboeck et al., 2007; Guhr et al., 2015]. This is especially interesting for the functional response to drought events. Guhr et al. [2015] showed that fungi actively redistributing water from moist into dry soil and, thus, increasing the water potential in the dry soil. This may be an important buffer mechanism for functional stability due to an enhancement in the conditions for bacteria. The potential of fungi to act as 'water pipelines' is an interesting aspect for further modelling studies addressing the response of microbial ecosystems to drought. With a spatially explicit model, the spatial distribution of water due to fungi under heterogeneous, unsaturated conditions in soil may be analysed, for example, considering different pore networks. Including this in a model for simulating bacterial degradation under drought stress may allow for determining the buffer capability of the 'water pipeline' function of fungi.

In real soil systems, the discussed three functions of fungi (transport of bacteria, substances and water) are supposedly not isolated and may even occur simultaneously. This should be considered in terms of combining all three functions within a model and comparing the influence to the functional stability.

6.4.2.2 *Fungi as degrader*

Some fungi in soil are actively degrading pollutants themselves such as polycyclic aromatic hydrocarbons (PAHs), alkanes, pesticides, or biphenyls [Pointing, 2001; Harms et al., 2011; Winquist et al., 2014]. Thus, fungi may also directly influence the stability of biodegradation in soil systems by contributing to the ecosystem service actively. As already discussed, fungi are more resistant against fluctuating conditions and can, with their ability to transport substrate and water, supply also hyphae under worse conditions with nutrients. Nevertheless, degrading fungi are not often applied for bioremediation. Compared to degrading bacteria, fungi have some disadvantages for practical use, for instance, a lower growth rate of fungi, less mobility in aqueous environments and a strict oxygen demand [Harms et al., 2011; Niti et al., 2013]. However, under some conditions fungi may be more efficient degraders of pollutants such as in dry soils or under recurrent disturbances. Therefore, for optimizing functional stability in bioremediation strategies, the use of both microorganisms shall be proved, maybe even in combination.

6.4.3 *Soil environment*

Beyond biotic factors and aspects of the disturbances, also the heterogeneous soil environment should be considered in stability analysis. Biotic and abiotic processes are interacting with the surrounding environment and, thus, the response to disturbances depends also on the characteristics of the soil environment.

6.4.3.1 *Pore size distribution*

As described in Section 1.1.3 soils are composed of different particle types with varying sizes resulting in completely different compositions of the pore network. The spatial occurrence of most disturbances in soil highly depends on the pore size distribution which is more or less fragmented and, thus, the disturbance is also varying in its fragmentation. Within the model presented in this thesis, the pore network is not explicitly implemented. Nevertheless, the fragmentation of the disturbance pattern was identified as one of the main key factors for functional stability (Sec. 6.1.1). Although the spatial explicitness is described in a simplified manner, the degree of fragmentation proved to be essential. Moreover, the mean distance between disturbed and undisturbed habitats was shown to be an indicator for the recovery time after disturbances as well as for the functional resistance under recurrent disturbances. In consequence, the explicit implementation of pore network structures is of high interest for understanding the functional stability of microbial ecosystems in real soil systems. Different modelling approaches exist for dealing with the challenge of simulating heterogeneous pore networks in previous studies [e.g. Thullner and Baveye, 2008; King et al., 2010; Gharasoo et al., 2012; Raoof et al., 2013; Qin and Hassanizadeh, 2015]. For instance, King et al. [2010] developed a pore network model for investigating the interplay between microbial dynamics and chemical transport in a sandy aquifer. They coupled differential equations for describing the concentration of microbial biomass and a chemical within the single pores with a spatially explicit implementation of the pore network. Qin and Hassanizadeh [2015] investigated solute transport and biofilm growth under various conditions with a 3-D pore network model including heterogeneities in pore sizes. Gharasoo et al. [2012] coupled a pore network model simulating diffusive transport with an earlier established numerical tool for modelling kinetics of arbitrary size and complexity [c.f Regnier et al., 2002; Centler et al., 2010]. With the resulting model called PNBRS, the reactive transport of solutes in heterogeneous porous media was simulated. Ebrahimi and Or [2014] developed a 3D - pore network model with an explicit implementation of the water content and analysed microbial dispersal under unsaturated conditions with an individual-based approach. Furthermore, the shape and spatial distribution of community composition as well as biogeochemical processes associated with microbial activity were determined [Ebrahimi and Or, 2015].

6.4.3.2 *Upscaling*

The explicit implementation of the pore network space is certainly a good representation of the actual situation in soil systems. However, the complex spatial informations needed are very detailed and, thus, the maximum scale which can be modelled is limited due to computer capacity. For analysing on larger scales, which are of interest for management implications, an upscaling approach is necessary.

Upscaling approaches aim to replace a spatially heterogeneous domain with an effective homogeneous domain without loosing relevant information [Vereecken et al., 2007]. Using an upscaling approach for implementing the response of microbial ecosystem functions to disturbances may be of high interest for tackling different research questions and for deriving implications for management strategies. For instance, optimal conditions regarding water content or nutrient availability for functional stability of microbial ecosystems may be determined for different types of soil. The specific soil structure may then act as an indicator for managing contaminated soil. Such a model may also have predictive power, for instance, regarding the dynamics of natural attenuation under future disturbance events or estimating the persistence of chemicals under recurrent disturbance events.

6.4.3.3 *Properties of pollutants*

An important factor for the efficiency of biodegradation is the bioavailability of the substrate or pollutant [Ehlers and Luthy, 2003]. The bioavailability depends on the conditions in the surrounding environment, i.e. the water content, as well as on the specific properties of the compound such as the water solubility. As described in Section 1.1.1, several organic compounds occur as pollutants in the terrestrial environment such as pesticides or polycylic aromatic hydrocarbons (PAHs). Those compounds may differ drastically in their properties regarding water solubility, partition coefficients or biodegradability. Thus, for analysing the stability of biodegradation of a specific compound, its properties have to be taken into account. For predicting the response to disturbances of biodegradation of different chemicals with a modelling approach, a classification into groups regarding the important properties such as the diffusion coefficient or bioavailability may be useful. However, pollution in soil systems often consists of a mixture of several pollutants with different properties. Here, the availability of more than one resource may be a benefit for the bacteria as they have more carbon sources to degrade, but on the other hand, one of the compounds can also inhibit the biodegradation for instance due to a high toxicity [Tilman, 1980]. Some modelling approaches have already included the presence of more than one resource, for instance, for analysing stoichiometric constraints of microbial decomposers [Cherif and Loreau, 2007; Kaiser et al., 2014]. However, the influence of chemical mixtures to the functional stability of microbial soil systems has not yet been analysed. May [2014] showed in a modelling study that the biodegradation efficiency can be increased due to an additional substrate depending on the spatial distribution of the compound and their concentrations as well as on the specific uptake strategy. Thus, determining the response of the biodegradation performance to disturbances in presence of more than one substrate may be an interesting approach also for identifying further management strategies for bioremediation.

6.4.4 *Disturbances*

Stability in terms of resilience and resistance is always a question of which aspect of the system, and to what type of disturbance [Grimm and Wissel, 1997; Hodgson et al., 2015]. How stable is one aspect of the ecosystem to one specific disturbance? Therefore, the specific disturbance has to be defined for analysing functional stability.

Soil as a very dynamic environment affected by many types of environmental disturbances such as temperature change, drought, erosion, flood events, or plant succession. Moreover, disturbances induced from anthropogenic sources may influence the soil system due to excessive land-use, pollution with pesticides, or excavation [Abbott and Abbott, 1989; Maynard, 2006]. In natural systems, several disturbance types may occur simultaneously resulting in combined effects on the ecosystem. For completely understanding the dynamics of ecosystem services under changing conditions, an analysis of the response to disturbances with different effects is necessary. As summarized in Section 6.1.1, the disturbance characteristics are highly relevant for the functional stability of microbial ecosystems. Depending on the type of disturbance, the characteristics differ in several aspects regarding frequency, duration, spatial occurrence and effects. Disturbances may occur very often (minutely, hourly), more moderately (daily, weekly), very seldom or only once. They may also differ in duration: a very short discrete event referred to as pulse disturbance, press disturbances lasting minutes to hours and a permanent event may be defined as stress. The spatial occurrence may also be an important aspect to consider. Is the disturbance homogeneously affecting the system or heterogeneously, for instance, depending on the spatial distribution of the pore network? Moreover, the specific effects of the disturbance to the microbial ecosystem has to be considered. The disturbance event may directly reduce the bacterial biomass, inhibit growth or dispersal, or limit the substrate availability. For simulating the response of microbial functions to different disturbances it would be important to include those characteristics rather than specific disturbance types or its source. Therefore, the disturbance types may be classified with regard to their characteristics.

Most disturbance types have several potential disturbance characteristics. For instance, drought events may occur on different temporal scales: as a permanent stress or in drying-rewetting cycles varying in frequency. Temperature changes within the day and night shift in many climate zones, but may also alter permanently. The duration and frequency of disturbances with anthropogenic source are hardly predictable. However, a high frequency may cause cumulative effects of the disturbance, when the system has not enough time to recover [Sec. 6.1.1; Berga et al., 2012; Kim et al., 2013; Ho et al., 2015]. Different disturbance return intervals and durations should be thus tested, which is easily realizable in modelling studies.

However, for implementing disturbances in a model attempt, most important to know is the spatial occurrence and the effects. Addressing disturbances occurring in dependence on pore network such as drought or toxic pollution, the explicit implementation of the pore network structure may be important [Wang and Or, 2012; Ebrahimi and Or, 2014]. For disturbances with a homogeneous or selective occurrence, this may not be necessary. On the other hand, for simulating the response of the ecosystem the explicit pore distribution may be important, as the biological interaction depends on it. For disturbances with a selective spatial occurrence, such as a reduction of biomass due to predators, the pore sizes can be highly relevant, for instance, if the predator is larger in size than the bacteria. However, the question is how much knowledge is gained by increasing the complexity when implementing explicit pore networks compared to the disadvantages of a higher complexity in a model system. For homogeneously distributed disturbances on a large spatial and temporal scale, for example temperature increase in a complete region and over a long time, the high complexity in spatial explicitness may result in a very high computing time, which is not in relation to the additional knowledge on the small spatial scale. Thus, whether, in further modelling studies, the pore network structure is explicitly implemented should be a decision based on the disturbance type that should be analysed.

The second important aspect to be considered is the direct effect to the microbial ecosystem. Here, experimental work is needed for assessing the effects of the different types of disturbances. Some disturbances affect the mobility of bacteria and substrate such as drought. Worrich et al. [2016] showed a decline in dispersal and growth of the soil bacterium *Pseudomonas putida KT2440* with decreasing water potential in a laboratory system and, in consequence, also a decrease of biodegradation performance. Other disturbances reduce the biomass directly due to toxic effects or predation. It is also possible that disturbances alter the specific properties of the bacteria, and those changes may last beyond the disturbance event.

However, in experimental studies usually the resistance to one disturbance or during a stress period is analysed, more seldom the recovery of an ecosystem service after stress events or under the influence of periodic disturbances. For simulating the response to such disturbances, an individual-based model may be appropriate. If each bacterial cell is modelled as an entity, the individual shift in response to disturbances can be simulated as well as evolutionary processes such as adaption [Ferrer et al., 2008; Shade et al., 2012; Cabrol et al., 2016].

If the simulated microbial ecosystem consists of different bacterial species (Sec. 6.4.1), some of these species may be more resistant than others and, thus, the effects of a specific disturbance differs for individual bacteria cells. The community composition may shift in response to a disturbance but the functional stability of the whole microbial ecosystem is still high, or, in turn, the community is unaffected in its composition but the ecosystem service is affected [Fernandez et al., 2000; Fierer and Schimel, 2003; Bressan et al., 2008; Bissett et al., 2013].

APPENDIX

A

A.1 APPENDIX OF CHAPTER 4

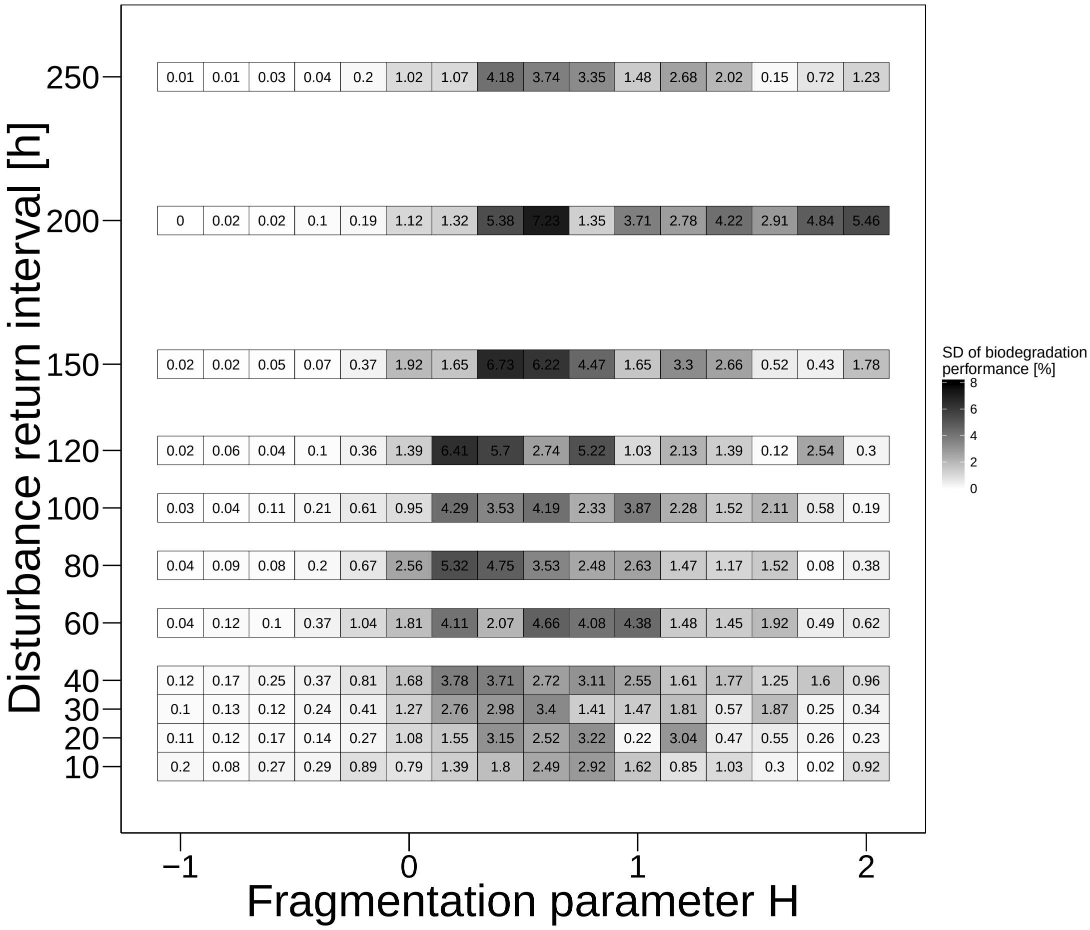
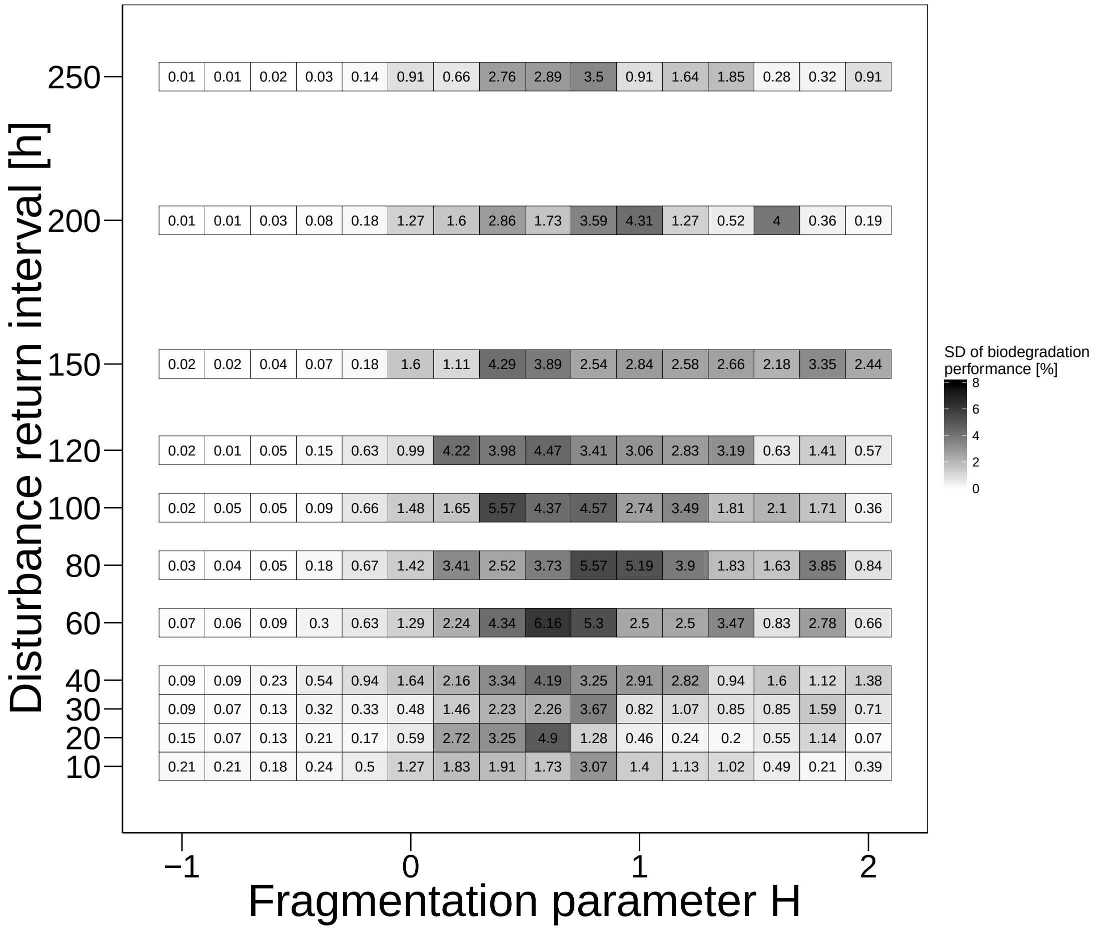


Figure A.1: SD of mean biodegradation performance in quasi-steady state without dispersal networks indicating functional resistance for different disturbance return intervals and degrees of fragmentation (cf. Fig. 4.7 a). Boxes show sd values of 10 simulation runs.



250	0.01	0.01	0.02	0.03	0.14	0.91	0.66	2.76	2.89	3.5	0.91	1.64	1.85	0.28	0.32	0.91
200	0.01	0.01	0.03	0.08	0.18	1.27	1.6	2.86	1.73	3.59	4.31	1.27	0.52	4	0.36	0.19
150	0.02	0.02	0.04	0.07	0.18	1.6	1.11	4.29	3.89	2.54	2.84	2.58	2.66	2.18	3.35	2.44
120	0.02	0.01	0.05	0.15	0.63	0.99	4.22	3.98	4.47	3.41	3.06	2.83	3.19	0.63	1.41	0.57
100	0.02	0.05	0.05	0.09	0.66	1.48	1.65	5.57	4.37	4.57	2.74	3.49	1.81	2.1	1.71	0.36
80	0.03	0.04	0.05	0.18	0.67	1.42	3.41	2.52	3.73	5.57	5.19	3.9	1.83	1.63	3.85	0.84
60	0.07	0.06	0.09	0.3	0.63	1.29	2.24	4.34	6.16	5.3	2.5	2.5	3.47	0.83	2.78	0.66
40	0.09	0.09	0.23	0.54	0.94	1.64	2.16	3.34	4.19	3.25	2.91	2.82	0.94	1.6	1.12	1.38
30	0.09	0.07	0.13	0.32	0.33	0.48	1.46	2.23	2.26	3.67	0.82	1.07	0.85	0.85	1.59	0.71
20	0.15	0.07	0.13	0.21	0.17	0.59	2.72	3.25	4.9	1.28	0.46	0.24	0.2	0.55	1.14	0.07
10	0.21	0.21	0.18	0.24	0.5	1.27	1.83	1.91	1.73	3.07	1.4	1.13	1.02	0.49	0.21	0.39

Figure A.2: SD of mean biodegradation performance in quasi-steady state with dispersal networks indicating functional resistance for different disturbance return intervals and degrees of fragmentation (cf. Fig. 4.7 b). Boxes show sd values of 10 simulation runs.

A.2 APPENDIX OF CHAPTER 5

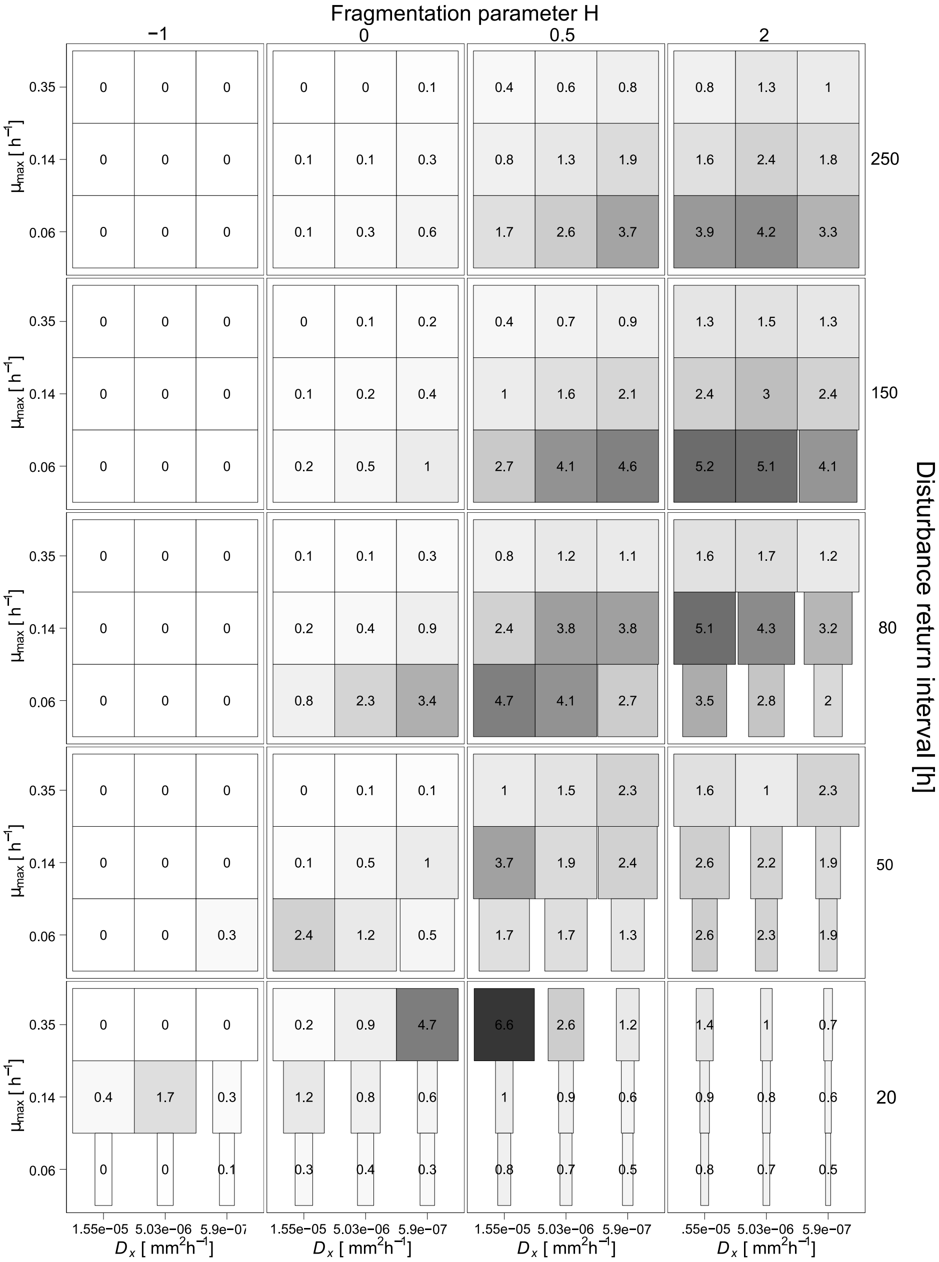


Figure A.3: SD of degraded substrate within 2000 hours of simulation time under disturbance regimes with disturbance patterns occuring with four different degrees of fragmentation ranging from highly to non-fragmented (cf. Table 5.1), and disturbance return interval of 20, 50, 80, 150 and 250 hours. Within each 3x3 tile plot separated by thick lines maximum specific growth rate μ_{max} and maximum bacterial diffusion coefficient $D_{x,max}$ are varied according to Table 5.1 (cf. Fig. 5.5). Boxes show sd values of 40 simulation runs.

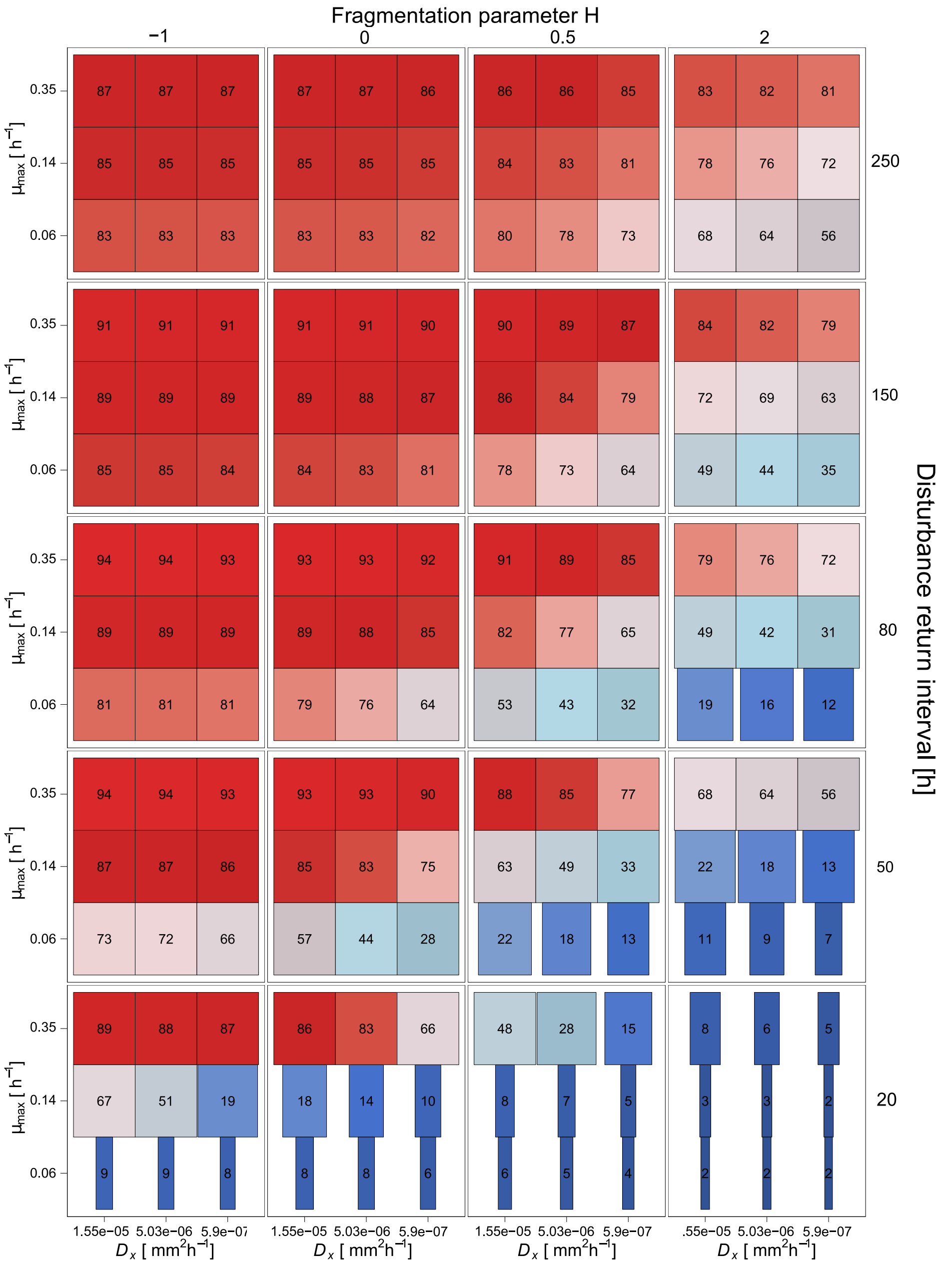


Figure A.4: Degraded substrate within 2000 hours of simulation time in scenarios with dispersal networks under disturbance regimes with disturbance patterns occuring with four different degrees of fragmentation ranging from highly to non-fragmented (cf. Table 5.1), and disturbance return interval of 20, 50, 80, 150 and 250 hours. Within each 3x3 tile plot separated by thick lines maximum specific growth rate μ_{max} and maximum bacterial diffusion coefficient $D_{x,max}$ are varied according to Table 5.1. Boxes show mean values of 40 simulation runs.

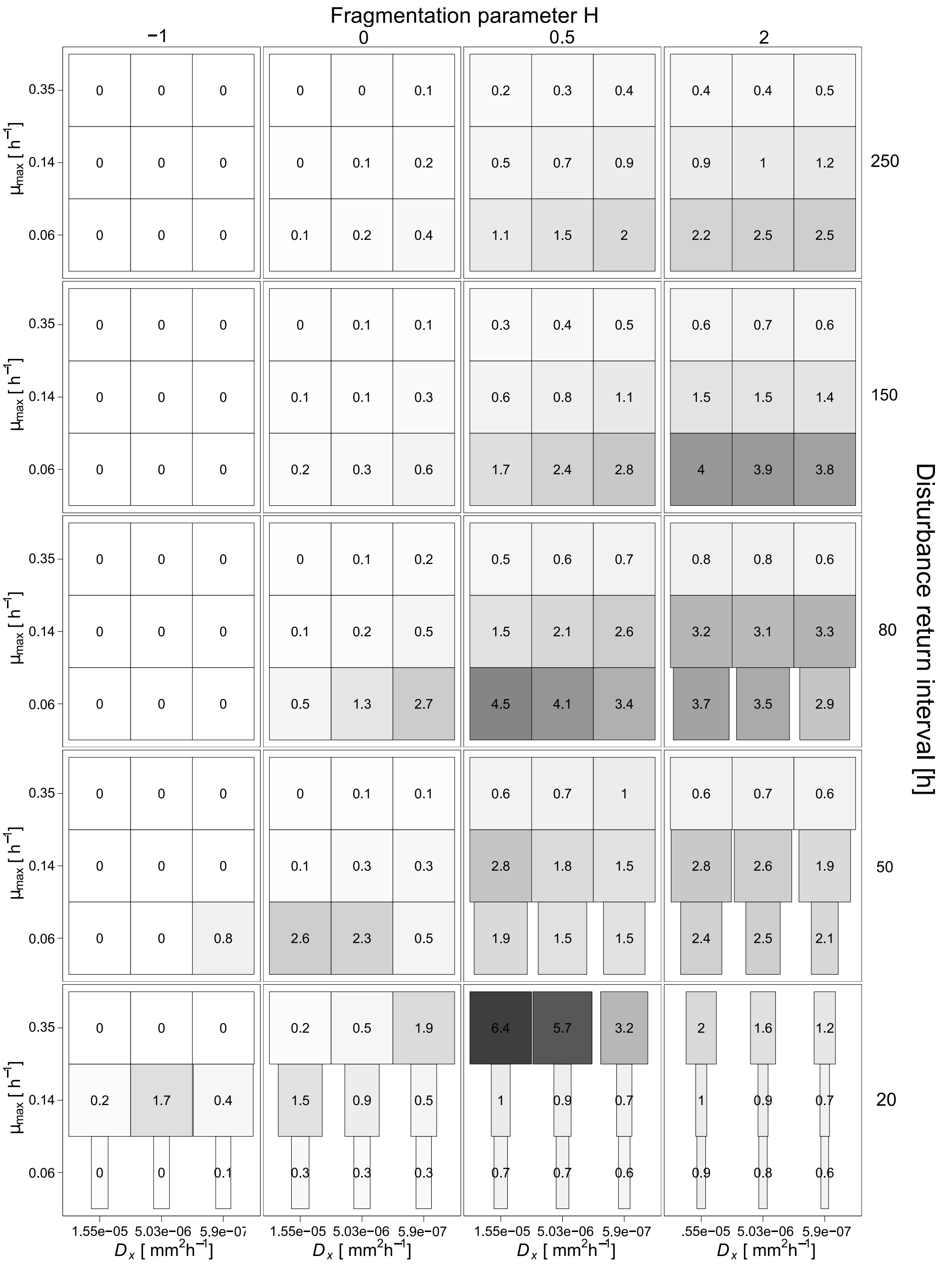


Figure A.5: SD of degraded substrate within 2000 hours of simulation time in scenarios with dispersal networks under disturbance regimes with disturbance patterns occuring with four different degrees of fragmentation ranging from highly to non-fragmented (cf. Table 5.1), and disturbance return interval of 20, 50, 80, 150 and 250 hours. Within each 3x3 tile plot separated by thick lines maximum specific growth rate μ_{max} and maximum bacterial diffusion coefficient $D_{x,max}$ are varied according to Table 5.1. Boxes show sd values of 40 simulation runs.

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LIST OF SYMBOLS

Symbol	**Description**	**Unit**^{a}
α	bacterial dispersal reduction factor	-
∂	partial derivative symbol	-
Δ	mean distance of disturbed to undisturbed habitats	mm
∇	gradient in space	mm^{-1}
∇^2	Laplace operator in space	mm^{-2}
ε	fraction of surviving bacterial biomass	-
φ_{min}	minimum dispersal fraction	-
λ	substrate input rate parameter	h^{-1}
μ_{max}	maximum specific growth rate	h^{-1}
a	specific maintenance rate	h^{-1}
$\widetilde{a}$	energy cost for maintenance	$g_s g_x^{-1} h^{-1}$
C_s	substrate concentration	$g_s l^{-1}$
C_s^*	initial substrate concentration	$g_s l^{-1}$
C_x	bacterial concentration	$g_x l^{-1}$
C_x^*	initial bacterial concentration	$g_x l^{-1}$
d	specific dispersal cost	h^{-1}
d_{max}	specific maximum energy cost for dispersal	h^{-1}
$\widetilde{d}_{max}$	maximum energy cost for dispersal	$g_s g_x^{-1} h^{-1}$
D_s	substrate diffusion coefficient	$cm^2 s^{-1}$
D_x	bacterial diffusion coefficient	$cm^2 s^{-1}$
$D_{x,max}$	maximum bacterial diffusion coefficient	$cm^2 s^{-1}$
$D_{x,max}^{dn}$	maximum bacterial diffusion coefficient along dispersal networks	$cm^2 s^{-1}$
DA	set of disturbed habitats	-
$\lvert DA \rvert$	number of disturbed habitats	-
H	degree of fragmentation of disturbance pattern	-
i	Cartesian coordinate (in x-direction)	mm
j	Cartesian coordinate (in y-direction)	mm
k	Cartesian coordinate (in x-direction)	mm
K_s	half-saturation constant	$g_s l^{-1}$
l	Cartesian coordinate (in y-direction)	mm
p	relative abundance of disturbance pattern	-
q	specific substrate uptake rate	$g_s g_x^{-1} h^{-1}$

Symbol	**Description**	**Unit**[a]
q_{max}	maximum specific substrate uptake rate	$g_s g_x^{-1} h^{-1}$
t	time	h
t_{dist}	time point of disturbance event	h
UA	set of undisturbed habitats	-
Y_G	growth yield coefficient	$g_x g_s^{-1}$

[a] g_x-grams of dry biomass, g_s-grams of substrate

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