Modelling functional resilience of microbial ecosystems: Analysis of governing processes

Sara König [a, b, d, *], Anja Worrich [b, c], Florian Centler [b], Lukas Y. Wick [b], Anja Miltner [c], Matthias Kästner [c], Martin Thullner [b], Karin Frank [a, d, e], Thomas Banitz [a]

[a] UFZ — Helmholtz Centre for Environmental Research, Department of Ecological Modelling, Permoserstraße 15, 04318 Leipzig, Germany
[b] UFZ — Helmholtz Centre for Environmental Research, Department of Environmental Microbiology, Permoserstraße 15, 04318 Leipzig, Germany
[c] UFZ — Helmholtz Centre for Environmental Research, Department of Environmental Biotechnology, Permoserstraße 15, 04318 Leipzig, Germany
[d] Institute for Environmental Systems Research, University of Osnabrück, Barbarastraße 12, 49076 Osnabrück, Germany
[e] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

ARTICLE INFO

ABSTRACT

Functional stability of microbial ecosystems subjected to disturbances is essential for maintaining microbial ecosystem services such as the biodegradation of organic contaminants in terrestrial environments. Functional responses to disturbances are thus an important aspect which is, however, not well understood yet. Here, we present a microbial simulation model to investigate key processes for the recovery of biodegradation. We simulated single disturbances with different spatiotemporal characteristics and monitored subsequent recovery of the biodegradation dynamics. After less intense disturbance events local regrowth governs biodegradation recovery. After highly intense disturbance events the disturbance pattern's spatial configuration is decisive and processes governing local functional recovery vary depending on habitat location with respect to the spatial disturbance pattern. Local regrowth may be unimportant when bacterial dispersal from undisturbed habitats is high. Hence, our results suggest that spatial dynamics are crucial for the robust delivery of the ecosystem service biodegradation under disturbances in terrestrial environments.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Microbial ecosystem functioning and services are highly relevant in many ecosystems as they are known to be determinants for various aspects of human well-being (Millennium Ecosystem Assessment, 2005). Therefore, the supply of these microbial ecosystem services ought to be sufficiently robust, even in face of changing environmental conditions. This underpins the importance of 'functional resilience' of ecosystem services, measured in terms of resistance and recovery of their performance in response to certain disturbances, and the urgency of understanding its determinants (Biggs et al., 2012). An important regulating ecosystem service provided by microorganisms is the removal of organic pollutants by bacterial degradation. In terrestrial ecosystems, especially in highly dynamic environments such as soil which is constantly exposed to fluctuating conditions and disturbances (Young and Crawford, 2004; Dechesne et al., 2010), the ability of the microbial ecosystem to maintain the ecosystem function of biodegradation is essential.

The types of disturbances and their effects on microorganisms are diverse. Some disturbances in soil such as a contamination with toxic chemicals or the immigration of predators may reduce bacterial biomass. Others such as drought may decrease their activity with respect to motility or metabolism. Bioturbation as another common disturbance may further reduce the bioavailability of substrate due to a change of the connectivity between pores in the soil system (Botton et al., 2006; Shade et al., 2012). Several studies analysed the change in microbial 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). For instance, Kim et al. (2013) showed a high sensitivity of soil bacterial community composition and biodiversity to a physical disturbance with a lethal effect on parts of the community. Similarly, many comparable studies have concentrated on the structural resilience

---

in terms of abundance and community composition of the considered microbial ecosystem to a certain disturbance. By contrast, functional responses to disturbances have rarely been addressed, although they have recently come more and more into focus. For instance, Berga et al. (2012) examined the changes in both, community structure and functionality, in response to salinity disturbances with different intensities and frequencies. They found changes depending on the disturbance strength, and recovery rates varying with the type of function (Berga et al., 2012). In other fields of ecology, several studies are already dealing with the response of ecosystem functions to disturbance events (e.g. see Oliver et al., 2015a; for a review). However, little is known about the influence of disturbances on the ecosystem function biodegradation and the key factors for its recovery. Understanding functional resilience requires knowledge on the underlying mechanisms at play in an ecosystem and on their dynamic responses to a disturbance.

Computational simulation models are an established approach for analysing dynamics and mechanisms of ecosystems. Such models provide the opportunity to observe spatiotemporal dynamics and to examine the responsible mechanisms in detail. In environmental microbiology, modelling approaches are successfully used for understanding and predicting system behaviour (Murphy and Ginn, 2000; O'Donnell et al., 2007; Esser et al., 2015). In particular, reactive transport models have been used for the simulation of biogeochemical processes in porous media at different scales (Murphy and Ginn, 2000; Centler et al., 2010; Gharasoo et al., 2012; Monga et al., 2014), addressing, for example, effects of bioclogging (Thullner and Baveye, 2008; Brovelli et al., 2009), microbial dormancy (Stolpovsky et al., 2012) or microbial motility (Banitz et al., 2012; Gharasoo et al., 2014). For the simulation of biofilms, individual-based models as well as population-based models were used (Matsushita et al., 2004; Picioreanu et al., 2004; Korth et al., 2015).

The present study addresses the dynamic response of biodegradation to certain disturbances which has not been tackled by modelling so far. We present a methodology for systematically assessing the functional resilience of biodegradation to disturbance events of different intensities and spatial patterns of occurrence. Core is the spatially explicit numerical model *eColony* for bacterial colony growth under disturbances which is an extension of an earlier established model (Banitz et al., 2011a, b). The model is used to simulate versatile disturbance scenarios to reveal insights into (i) key factors for functional resilience of biodegradation, (ii) the temporal dynamics of functional recovery after disturbances of varying intensities, (iii) the relative importance of involved processes including bacterial growth and bacterial dispersal, and (iv) possible indicators for the recovery behaviour derived from the spatial pattern of occurrence of the disturbance itself.

2. Methods

2.1. Simulation model eColony

2.1.1. Model description

We present a population-based, spatiotemporally explicit ecological model (named *eColony*) for simulating the functional recovery of biodegradation after certain disturbance events. The model is an extension of a model developed by Banitz et al. (2011a) in which a consumer-resource-system consisting of bacteria degrading substrate (representing the biodegradation of organic pollutants) is described via reaction-diffusion equations. The model operates on a two-dimensional circular simulation area of 88 mm diameter consisting of rectangular habitats of size 1 mm^2 with reflective boundaries. The spatiotemporal dynamics of both bacterial and substrate concentrations are approximated with a finite

difference method (Banitz et al., 2011a). The model was implemented in the programming language Delphi. One simulation time step of 1 min includes the following processes: substrate uptake by bacteria, uptake allocation to energy-demanding tasks, bacterial dispersal, growth, and substrate diffusion.

We implemented a constant substrate input representing ongoing substrate dissolution, which is controlled by the maximum solubility of the substrate (similar to Keymer et al., 2006; Centler et al., 2011). In each simulation step the substrate is refilled depending on the difference between a given maximal ($C_{s,max}$) and the current (C_s) substrate concentration within a habitat with λ as the substrate input parameter (cf. Eq. (2)). Based on this substrate input, a (spatially homogeneous) undisturbed reference state is defined at which the substrate input matches exactly the uptake of the bacteria in the system and this uptake matches exactly their maintenance (Table 1). Thus, the bacterial population in the undisturbed reference state remains constant as it continuously receives sufficient energy for maintenance but not for growth and dispersal.

2.1.2. Equations

With respect to the depicted extensions, the dynamics of bacterial colony growth and substrate degradation are described by the extended reaction-diffusion equations:

$$\frac{\partial C_x}{\partial t} = \nabla(D_x(C_x, C_s)\nabla C_x) + (q(C_s)Y_G - a - d(C_x, C_s))C_x, \tag{1}$$

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

where C_x is the concentration of bacteria ($g_x mm^{-2}$) and C_s the concentration of substrate ($g_s mm^{-2}$). D_x and D_s are the diffusion coefficients of bacteria and substrate ($mm^2 h^{-1}$), q is the specific substrate uptake rate of bacteria ($g_s g_x^{-1} h^{-1}$), calculated according to $q = q_{max}\frac{C_s}{C_s + K_s}$ with q_{max} as maximum specific uptake rate ($g_s g_x^{-1} h^{-1}$) and K_s as half-saturation constant ($g_s mm^{-2}$). Y_G the growth yield coefficient ($g_x g_s^{-1}$), a the specific maintenance rate (h^{-1}), d the specific dispersal cost, expressed as biomass decrease rate (h^{-1}), and λ the substrate input rate parameter (h^{-1}). Note that D_x and d are variables depending on the substrate concentration (cf. Banitz et al., 2011a, 2012). An overview of parameter values used in the simulations is given in Table 1.

2.2. Disturbance scenarios

Initial bacterial concentration C_x and substrate concentration C_s were homogeneously set to the undisturbed reference state concentrations in the whole system (Table 1). Disturbance events were introduced as a drastic reduction of bacterial biomass within a randomly picked disturbance area. The biomass concentration in the disturbed area was set to a fraction of the undisturbed reference state concentration (Table 1) with

$$C_x = \varepsilon \times C_x^*, \tag{3}$$

with parameter $\varepsilon < 1$ indicating the survivorship. ε was varied between 10^{-9} (highest disturbance intensity) and 10^{-2} (lowest disturbance intensity) in logarithmic steps. The bacteria in the remaining area were not directly affected by the disturbance event.

We used the midpoint displacement algorithm developed for creating random fractal landscapes (e.g. Saupe, 1988) to generate the disturbance patterns. The disturbed area was defined by the parameters relative size p and fragmentation parameter H (cf. Banitz et al., 2011b). The relative size p was set to 50% of the simulation