Ecological Indicators 60 (2016) 54–63

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Spatial metrics as indicators of biodegradation benefits from bacterial dispersal networks

Thomas Banitz[a,*], Karin Frank[a,c,d], Lukas Y. Wick[b], Hauke Harms[b,c], Karin Johst[a]

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

ARTICLE INFO

Article history:
Received 14 August 2014
Received in revised form 2 June 2015
Accepted 9 June 2015

Keywords:
Microbial ecosystem service
Fungal networks
Bioremediation
Spatial metrics
Simulation model
Nonparametric correlation

ABSTRACT

Ecological dynamics often show intricate variations in response to different spatial configurations of environmental conditions. For instance, efficient turnover of natural or anthropogenic compounds in soils strongly depends on the bioavailability of these compounds to metabolically active bacteria. Experimental and modelling studies have highlighted that fungal networks may considerably enhance bioavailability by facilitating bacterial dispersal. Therefore, such dispersal networks may play a key role in many soil processes, for example, in contaminant degradation. Particularly, simulation studies revealed that the spatial configurations of networks may be a crucial factor determining the bacterial access to contaminants. Since these spatial configurations are typically complex and not precisely known, suitable metrics describing them in an aggregated manner are required for assessing expected biodegradation benefits from different bacterial dispersal networks. Using a spatially explicit microbial model we randomly created various dispersal network configurations and simulated the resulting bacterial degradation of organic compounds. We investigated numerous spatial metrics for characterizing the manifold network configurations, and identified appropriate metrics based on nonparametric correlation measures. Our results show that single metrics can approximately indicate biodegradation performance, and that well-chosen combinations of two metrics offer very good assessments. Thus, our analysis provides characteristics to focus on when dealing with real fungal networks in future practical applications in environmental management. Moreover, the protocol we employed for deriving the appropriate metrics is suited to be adapted to other ecological studies of functional responses to spatial environmental characteristics, for instance, changes in ecosystem services or biodiversity aspects due to habitat loss and fragmentation.

1. Introduction

The turnover of natural or anthropogenic soil compounds by microbial activity has a strong impact on terrestrial ecosystems, for instance, affecting soil health, carbon storage, trace gas production, or provision of plant nutrients (Madigan et al., 2008; Schmidt et al., 2011). Regarding organic contaminants, bacterial degradation is an important ecosystem service with a high potential for resource-efficient in situ bioremediation (Höhener and Ponsin, 2014). In water-unsaturated soils, however, a low bioavailability of contaminants to bacteria often impedes the biodegradation performance (Harms and Wick, 2006; Semple et al., 2007). Searching for means to enhance this bioavailability, experimental studies have shown that networks of mycelia (e.g. formed by fungi or oomycetes) may strongly facilitate the dispersal of bacteria and, thus, their access to contaminants (Ellegard-Jensen et al., 2014; Furuno et al., 2010; Knudsen et al., 2013; Kohlmeier et al., 2005; Wick et al., 2007). The mechanism underlying the dispersal facilitation is the provision of continuous liquid films around the mycelia. Moreover, many mycelial fungi are well-adapted to typical heterogeneities in water-unsaturated soils, such as air filled pores or patchy distributions of nutrients and water (Allen, 2007; Boswell et al., 2007; Ritz and Young, 2004; Wösten et al., 1999). Therefore, promotion of fungal networks that provide a dispersal infrastructure for contaminant degrading bacteria is promising for the development of novel bioremediation approaches to be applied in soil management (Harms et al., 2011; Schamfuß et al., 2013).

The positive impact of bacterial dispersal networks on biodegradation performance was verified by a spatially explicit simulation model established in accordance with laboratory experiments

* Corresponding author. Tel.: +49 341 2351708; fax: +49 341 2351473.
E-mail address: thomas.banitz@ufz.de (T. Banitz).

http://dx.doi.org/10.1016/j.ecolind.2015.06.021
1470-160X/

(Banitz et al., 2011a, 2012). This model describes the growth and dispersal of bacteria, and the resulting substrate consumption, which corresponds to the ecosystem service of contaminant biodegradation. Simulations with simple grid-like bacterial dispersal networks implied that their explicit spatial configurations may strongly influence the resulting benefits for biodegradation (Banitz et al., 2011a, 2011b, 2013). As natural fungal networks are typically much more complex (Boswell et al., 2007; Heaton et al., 2012), understanding which aspects of these spatial configurations govern the effects on biodegradation performance is a precondition for efficiently making use of fungal networks in future applications.

Here, we therefore extend the above-mentioned simulation model to create a wide variety of dispersal network configurations and analyze their impact on bacterial substrate consumption. We investigate a large number of implicit spatial metrics, each characterizing the diverse explicit network configurations. This includes the metrics provided by the *Fragstats* software (McGarigal et al., 2001; McGarigal and Marks, 1994) and several additional eligible metrics. We develop a protocol to study these metrics' suitability as indicators of the biodegradation benefits created by the dispersal networks. Utilizing nonparametric correlation coefficients, we first examine the metrics separately and second in combination.

A question of particular interest is whether the relevant aspects of the networks can be subsumed by implicit measures in the form of spatial metrics, or whether the specific explicit spatial configurations are decisive. Here, the developed protocol enables us to find particular combinations of two implicit metrics that can serve as very good indicators of biodegradation performance, irrespective of the networks' explicit spatial configurations. These combined indicators are also robust to changes in the time horizon over which biodegradation performance is assessed. Thus, we derive relevant characteristics for developing enhanced bioremediation approaches based on the establishment of suitable fungal-bacterial associations in contaminated soil.

2. Methods

2.1. Simulation model and environmental conditions applied

We used the spatially explicit simulation model of bacterial colony growth (Banitz et al., 2011a), in which bacteria take up organic substrate, allocate this uptake to energy-demanding tasks, disperse, grow and reproduce, and the substrate diffuses. The process of bacterial dispersal is modelled as diffusion. The resulting overall consumption of substrate over certain time horizons represents the bacterial degradation of organic contaminants. The model was parameterized to laboratory experiments of *P. putida* PpG7 (NAH7) bacterial colonies spreading in Petri dishes (diameter 88 mm) on minimal medium agar at 30 °C using homogeneously distributed glucose as a growth substrate (Banitz et al., 2012). The bacterial maximum growth rate was set to 0.347/h (approximated from PpG7 growth on liquid minimal medium containing 2 g/l glucose as sole energy source, method described by Wick et al., 2001). We always applied spatially homogeneous abiotic conditions with concentrations of 0.1 g/l initial substrate and 5 g/l agar (i.e. unfavourable bacterial dispersal conditions; Banitz et al., 2011a). At the beginning of the simulation runs, the bacteria were placed in the centre of the two-dimensional circular simulation area (diameter 88 mm) consisting of quadratic grid cells (side length 1 mm).

2.2. Bacterial dispersal networks

The dispersal-facilitating effect of fungal networks was modelled with corridors (i.e. linear assemblages of grid cells) of high bacterial diffusivity. Such dispersal corridors had been introduced in grid-like spatial configurations in earlier studies (e.g. Banitz et al., 2011a). To account for the spatial variety of natural dispersal networks within our simplified modelling framework, we generated manifold different network configurations as follows: We randomly selected the number (1–40) of dispersal corridors placed on the simulation area. For each of these corridors, length (11–51 mm), midpoint location (grid cell coordinates), and orientation (horizontal or vertical) were selected randomly too (cf. example network configurations, Fig. 1). To increase the diversity of examined spatial configurations, we also generated networks with the additional restriction that the midpoints of the dispersal corridors forming the network all lie in one half of the simulation area (e.g. Network 1 in Fig. 1). Thus, the second half of the simulation area remained almost free of grid cells belonging to the dispersal networks. In all simulations performed, the substrate was neither degraded nor translocated by the networks.

2.3. Metrics of spatial configurations of dispersal networks

A variety of implicit metrics can be considered for characterizing the different explicit spatial configurations of dispersal networks. Therefore, we investigated the suitability of the following spatial metrics (cf. Table 1 for symbol descriptions):

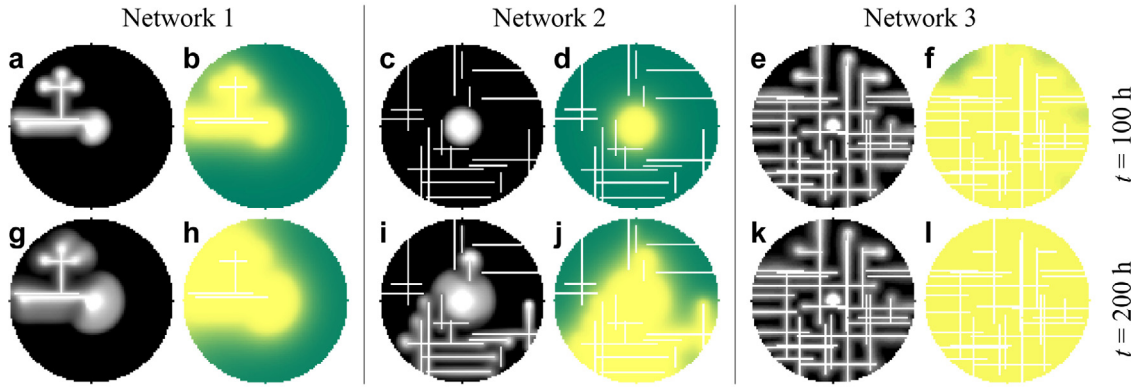

Fig. 1. Simulation results for three exemplary, randomly created spatial configurations of dispersal networks (Networks 1–3; cf. titles; dispersal corridors visualized in white). (a–f) After 100 h. (g–l) After 200 h. (a, c, e, g, i and k) Spatial patterns of bacteria. Bacterial concentrations are indicated by grey shading, increasing from black (no bacteria) to white. (b, d, f, h, j and l) Spatial patterns of substrate. Substrate concentrations are indicated by colour shading, decreasing from green (0.1 g/l) to yellow (0 g/l). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)