Resilience of soil to biological invasion: analysis of spread on networks.

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Abstract
A network model for soil pore volume is presented and applied to the analysis of biological invasion of microorganisms. The pore geometry of two soils with a relatively high or low bulk density were quantified with the use of X-ray tomography and networks were constructed to present the pore space by channels connecting intersecting points. This network was subsequently quantified by the measurement of biologically relevant parameters, such as the distribution of lengths of the links between two nodes, the coordination number of the nodes, and the distribution of the sizes of the links between two nodes. Spread of microorganisms was subsequently considered as a function of these characteristics and embedded into a simple epidemiological model for spread that can be mapped onto percolation theory. We found that the networks display critical behaviour for biological invasions with a greater resilience to invasion for the more densely packed soil. We also found that inherent heterogeneity of soil systems further contributes to resilience to invasion.

Key Words
X-ray tomography, percolation, micro-organisms, epidemiological models, soil structure, modelling.

Introduction
Soil structure is of significant importance for various dynamical processes in soil, including the movement of water, gasses and microorganisms. Several techniques have been used to quantify soil structure and microscopic heterogeneity including serial thin sectioning, but with the rapid advances in the use of X-ray tomography quantification of real structures is becoming increasingly routine. Whereas various transport models have been developed over recent years to cope with transport and the distribution of water and air in heterogeneous soil environments, there is less theoretical understanding of the impact of microscopic heterogeneity on biological invasion. A problem here is that inclusion of biological complexity to capture the growth dynamics in real 3-D structures is computational demanding.

The use of network representations of real soil pore geometries may however offer a way forward. The use of network descriptions of soil has increased over recent years, but this analysis has only recently been extended to consider biological invasions (Perez-Reche *et al.* 2009). The analysis of biological invasions has been studied extensively in human, animal and plant epidemiology (Otten and Gilligan 2006), and this theory can be readily extended to consider the spread of microorganisms on a 3-D complex network.

In this paper we demonstrate how networks can be derived from real 3-D data, and how epidemiological models can be mapped onto these networks to quantify the probability of invasion. We test if thresholds can be found for biological invasions, which would indicate that only small changes to either the soil structure or the ability of microorganisms to move can result in rapid different ecological outcomes. We do the analysis for a soil with a low and a soil with a relatively high bulk density to test the effect of soil structure on the reliance to invasion.

Methods
Sample preparation and X-ray micro-tomography
Soil aggregates (1 − 2 mm) of an arable sandy loam were packed to attain bulk densities of 1.2 or 1.4 Mg/m^3, representing two characteristic examples of a loosely and densely packed field soil, respectively for this soil type. Previously we experimentally quantified the spread of fungi into these soil samples, and full details can be found in Harris *et al*. (2004). We refer to these two soil samples as loosely (1.2 Mg/m3) and densely (1.4 Mg/m3) packed soils hereafter. We scanned these samples with a Metris X-TEK Benchtop micro-tomography system (Johnson *et al*. 2009), using a molybdenum target, X-ray source settings of 155 kV and

25 μA, and an aluminum filter (0.25 mm) to reduce beam-hardening artefacts. 2-D radiographs were collected at 1169 angular positions and then reconstructed using a filtered back projection algorithm with a resolution of 74 μm. Both 3-D volumes were then imported into VGStudioMax v.1.2.1 (Volume Graphics) and converted into 260×525 8-bit TIFF image stacks with voxel-thick slices. Binary data sets were created by thresholding the grey-scale image stacks in ImageJ. The choice of the threshold parameter was based on the 3-D statistical analysis of the histogram region corresponding to the pore-solid interface.

Derivation of the network from X-ray CT data sets

The procedure to derive a network from the soil data is described by Perez-Reche *et al*. 2009. In short, all the pores were processed by a thinning algorithm (Costa and Cesar 2002; Viana *et al*. 2009), required to reduce each object (pore) to a respective 1-voxel skeleton. The skeleton is a thin structure located at the most central parts of the respective original shape. The skeleton retains all the topological features of the original shape (e.g. branching structure and cycles). The skeletonized pores were then mapped onto a network as follows. The skeleton is a set of intersecting curves with some dead ends (where the skeleton terminates). Each intersection point and all dead ends were associated with the nodes of the network (Viana *et al*. 2009). The pore space around the skeleton between two nodes is called a channel or link (edge) between two nodes. The axis of the channel thus coincides with the skeleton. Various network characteristics were calculated that can be important for biological invasion including (1) fraction included in the largest connected cluster, (2) the number of links attached to each node, (3) the arc-length of the channels and (4) the bottleneck diameter of each channel.

Biological invasion on networks

We considered the spread of micro-organisms through soil represented by a network. Specifically we analysed invasive spread through the network from a single site. We start from an arbitrary selected node in the network, and consider the spread to a neighbouring node as a stochastic process with a specified probability, and from then on the same rules are followed with the exception that the microorganisms do not move back. Under these rules we can derive models that are identical to those used in epidemiology and fall under a SIR (susceptible-infected-removed) class of models. These models can subsequently be mapped onto percolation by associating the probability to spread along a channel with the bond probability.

The biological invasion was assumed to be a Poisson process with a rate of spread along a link dependent on a typical velocity of motion and the length of the link. As this would lead to the entire networks to be invaded with infinite time, something which is unlikely to happen with limited resources, we introduced an available time for invasion. In our approach we assume a local clock for colonization of each successive pore (link). Under these assumptions, the probability of invasion of a neighbouring node, transmissibility, depends on the channel characteristics and varies from channel to channel throughout the network. We consider two situations: the first one takes an average transmissibility (T) over the entire network; the second one takes the value calculated for each link and therefore better reflects the soil heterogeneity. For further analysis we assume that the values for the velocity and the finite time are the same for each channel which leads to the concept of a local invasion scale (k). The local invasion scale has the meaning of a typical channel length such that channels which are longer than the local invasion scale are likely to be closed and those that are shorter are likely to be open for invasion.

Results

An example of visualization of loosely packed soil samples is provided in Figure 1, together with an example of a derived network. In constructing the network and to enhance visibility, isolated pores with volume smaller than 104 voxels were discarded. This has negligible impact on the topology of the resulting network on which we perform our analysis. In the loosely packed soil, the largest connected cluster percolated through the sample comprising 10183 nodes connected by 11369 channels, but the more dense packed soil did not have a cluster spanning the entire soil sample and the largest cluster contained only 2613 nodes connected by 2823 channels. We restricted our analysis of biological invasion to this largest connected cluster.

We characterised our networks according to properties that are likely to affect the spread of microorganisms, such as the node degree distribution. The networks were rather sparsely connected with mean degrees of 2.23 and 2.13 for the loosely and densely packed soil, respectively. The arc-lengths of the links differed for both soils with the more densely packed soil having fewer short as well as fewer very long pores. Further analysis

of the lengths revealed that the majority of the links did not deviate much in length from the shortest possible path between two nodes. A final property that is relevant for biological invasion is the bottleneck diameter of each link, with the more densely packed soil having smaller bottle neck diameters, hence more links that could become restrictive for spread.

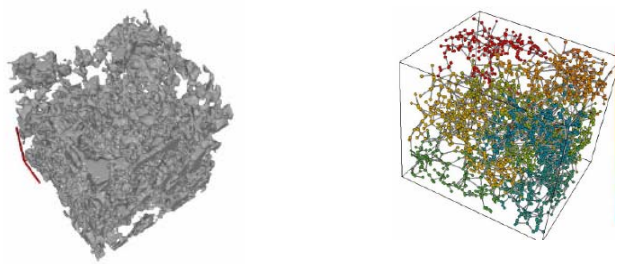

Figure 1. An example of a pore volume visualized with X-ray tomography (left) and its representation as a network (right).

Biological invasion

The probability to invade the largest cluster shows a threshold like behaviour with increasing local invasion scale (k) and with increasing transmissibility (T) (Figure 2). The probability to invade the soil sample (P_{inv}) increases non-linearly with increasing local invasion scale, with a critical value (the absence of a sharp threshold is due to finite-size of the sample) of approximately 15 and 35 for densely and loosely packed soil, respectively. This indicates that the densely packed soil is more resilient to biological invasion due to the fact that pore sizes are smaller, which means that the local invasion scale must be larger in order to 'activate' more channels to achieve the same level of invasion.

The probability of invasion also changes with the transmissibility T, which is analogous to the bond probability for percolation. For small transmissibility the probability of invasion is close to 0, and the value where it increases significantly from zero is the invasion threshold. The values for this probability are relatively high: approximately 0.81 and 0.96 for the dense and loosely packed soil, as compared with for example 0.25 on a simple cubic lattice. This is a consequence of the low node coordination number of these networks. Variability in transmissibility made the networks more resilient to invasion. This indicates that correlations in transmissibility play a significant role in the spread as for random variables the two probabilities should have coincided. Correlations reduce the transmissibility for a given value and thus make real soil networks more resilient to invasion.

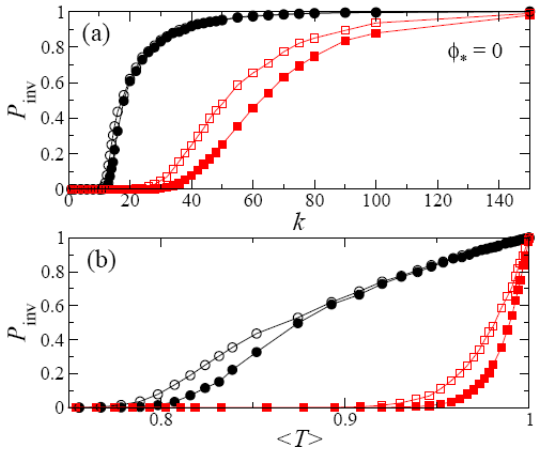

Figure 2. The probability of invasion versus a local invasion length-scale (k) and versus the transmissibility (T) in networks representing loosely packed (circles) or densiely packed (squares) soil on homogeneous (closed) and heterogeneous (open) networks (from Perez-Reche *et al*. 2009).

Conclusion

We have presented a network based on real data for soil structure and used this to analyse biological invasion in soil. The main idea is to reduce the complex geometry of the porous network to a network which is topologically equivalent to the original pore space. We demonstrated how epidemiological models can be

used to analyse the ability of organisms to invade the soil volume. With this approach biological spread became a critical phenomenon which either can or cannot invade the soil sample depending on the values of the control parameter. This will enable a quick assessment of the ability of organisms to invade a soil sample based upon simple biological parameters such as the critical pore diameter for spread. We have also demonstrated that soil networks are significantly heterogeneous in topology and that this makes them more resilient to invasion. Finally we demonstrated that increase in bulk density has a considerable impact on pore networks and makes a soil more resilient to biological invasion.

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