Motifs of Growth and Fusion Govern *Physarum polycephalum* Network Formation

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ABSTRACT

Physarum polycephalum, grown from fragments on an agar surface, forms a planar transportation network with exclusively low node degrees in a percolation transition. The dynamics of such a process can be captured by a rate equation reflecting basic events, such as growth and fusion of fragments. This work was presented at PhysNet 2015.

Categories and Subject Descriptors

C.2.1 [**Computer-Communication Networks**]: Network Architecture and Design—*Network topology*; G.2.2 [**Discrete Mathematics**]: Graph Theory; J.2 [**Computer Applications**]: Physical Sciences and Engineering—*Physics, Mathematics and Statistics*; J.3 [**Computer Applications**]: Life and Medical Sciences—*Biology and Genetics*

Keywords

Physarum polycephalum, graph theory, percolation

1. INTRODUCTION

The unicellular slime-mold *Physarum polycephalum* forms an extended vein network which serves as a foraging strategy [1] and for the distribution of nutrients between food sources and exterior cell body parts. The oscillatory mechanism acting as a driving force is called shuttle streaming and organizes as a peristaltic wave [2]. Remarkable characteristics of the *Physarum* network include maze-solving, network optimization [1, 3, 4] and apparent learning [5, 6].

We are interested in the topological transitions of a *P. polycephalum* network when grown from fragments. During previous studies [7,8], we disrupted plasmodia by shear to create disconnected microplasmodia [9]. Those solitary amoeba reunite upon encountering each other when placed in patches on a 2-dimensional agar substrate. Given abundant nutrients, microplasmodia fuse in a percolation transition directly into an extended network [7].

Our methodology has proven suitable for an investigation of concepts such as centrality and efficiency. Recently, we employed an efficiency measure to distinguish between phases of network formation in *P. polycephalum*, concluding that organization until peak efficiency precedes extension and search [8]. Furthermore, we found central nodes, as characterized by shortest path accumulation, to be correlated with transport-heavy veins, providing further evidence that *P. polycephalum* functional organization follows shortest path principles even in an environment free of constraints.

The topological transition can be described in the framework of graph theory [10], employing purely topological quantities as driving parameters. However, this description does not yet require detailed knowledge of the temporal dynamics of the process. The present work aims at integrating a mathematical model for dynamics of growth and fusion, which are the central processes during network formation, with the topological description of percolation to pave the way for a more physiological explanation.

2. THE FRAMEWORK OF NODE DEGREES

We treat *P. polycephalum* networks as graphs, i.e., a set of nodes and undirected links. Depending on the number of neighbours connected to a selected node, this node may be assigned a node degree k. As our networks are embedded in a plane and connectivity is local, node degrees are usually small. We define the fraction $p_k = N_k/N$ of the number of nodes N_k of degree k to the overall number of nodes in the network N where $k = 0 \dots 4$.

Previously [7,8], we have analytically described random graph percolation within this framework by integrating it with the configuration model of graph theory [11]. In our previous work we did not include the degree fraction p_2 as it is irrelevant in a purely topological description. However, for the spatio-temporal dynamics of network formation, p_2 can no longer be neglected as the number of p_2 nodes in a link may be used to represent its length.

Similarly to [7, 8], development of a giant component S can be modelled [12] with respect to p_2, employing the parameters $u = p_0/p_2$, $v = p_3/p_2$ and $w = p_4/p_2$. When p_4 is sufficiently small, $w \approx 0$ and solutions simply equal roots of a second degree polynomial, with the physically significant solution being

$$S = 1 + \frac{v+1}{2v} - \sqrt{\left(\frac{v+1}{2v}\right)^2 + \frac{u}{v}} \qquad (1)$$

in the percolated regime. S is shown in fig. 1, panel B, for an

BICT 2015, December 03-05, New York City, United States

DOI 10.4108/eai.3-12-2015.2262452

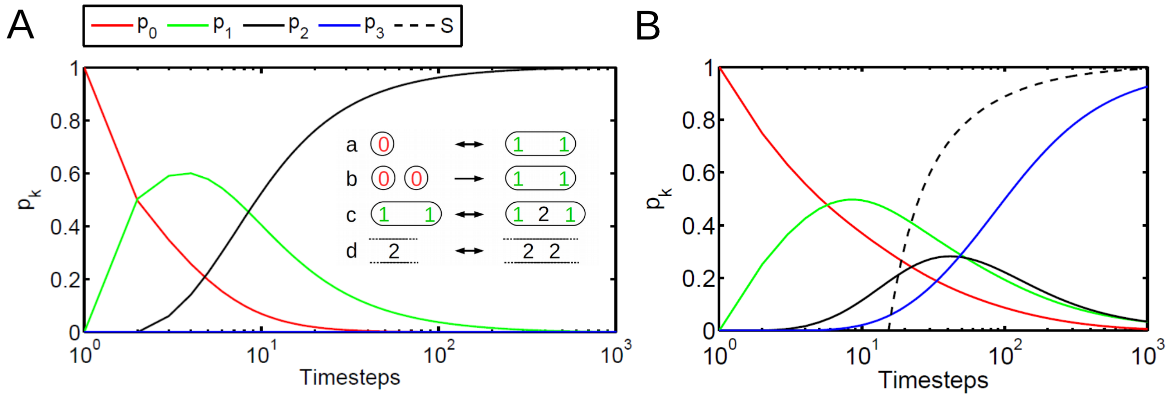

Figure 1: Modelling Percolation Dynamics. Solid lines show an iterative solution of the rate equation assuming solitary p_0 nodes only as initial conditions. To demonstrate the general dynamics of the system, rate constants were set to be equal to either unity or zero in both panels. A: Given a limited set of possible transitions (shown as an inset) with no possible transition to form p_3 nodes, the system cannot reach a percolated state. B: Enabling all possible transitions produces a percolating system, stabilizing into a p_3 dominated state. The dashed line shows the statistic fraction of nodes connected in a giant component.

exemplary evolution of the p_k obtained from the dynamics described in the next section.

3. A RATE EQUATION FOR DEGREE DYNAMICS

In our studies on percolation, we treat network formation from fragments. In such a setting, the dominant mechanisms of network progression are fusion of objects and growth. Also present but less pronounced, are secondary mechanisms such as hole formation, separation and retraction, the latter two gaining in importance in a percolated network. Investigating these processes in detail unveils that only a limited number of basic processes involving a low number of constituents is required for a description of network formation. We will term those basic processes motifs of growth or fusion, respectively. For example, two p_0 nodes may fuse into an elongated object with two connected p_1 nodes. To illustrate the significance of growth, the aforementioned object could extend along its longer axis, leading to the emergence of a p_2 node in its center (see fig. 1, panel A, inset). More complex motifs can be introduced in a similar fashion.
Based on the assumption that the probability for such a motif is dependent only on the availability of its constituents, the dynamics of the number of nodes indeed follow from a simple rate equation [12], which can be solved numerically using an appropriate Euler scheme.
Exemplary solutions of this equation are shown in fig. 1. Panel A shows a dynamic limited to the motifs a-d as shown in the inset, starting out with a set of p_0 nodes. Thus, by definition, the dynamic is not allowed to produce p_3 nodes. As a consequence, the system evolves into a set of elongating tubes and cannot reach a percolated state.
Panel B features dynamics of a percolating system involving all necessary motifs for producing p_3 nodes. However, the relative probabilities of transition were set to be equal. As a result, the system is dominated by p_3 nodes; whereas a stabilizing fraction of p_3 and p_2 nodes would be expected in the final network based on [8]. Such a result requires further fine-tuning of rate constants, which indeed can be accessed experimentally [12].

4. REFERENCES

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