

An Analytical Model for Percolation in Small Link Degree Transportation Networks

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ABSTRACT

Microplasmodia of the slime mold *Physarum polycephalum* form a small link degree transportation network in a percolation transition in order to forage. We model this transition analytically within the configuration model of graph theory utilizing all partaking types of nodes. Quite generally, we find that at the percolation transition the formation of a small link degree network is topologically highly constrained and only weakly dependent on environmental factors.

Categories and Subject Descriptors

C.2.1 [Computer-Communication Networks]: Network Architecture and Design—*Network topology*; G.2.2 [Discrete Mathematics]: Graph Theory—*Network problems*; I.2.8 [Artificial Intelligence]: Problem Solving, Control Methods, and Search; I.4.6 [Image Processing and Computer Vision]: Segmentation; J.2 [Computer Applications]: Physical Sciences and Engineering—*Physics, Mathematics and Statistics*; J.3 [Computer Applications]: Life and Medical Sciences—*Biology and Genetics*

General Terms

Theory, Experimentation

Keywords

Physarum polycephalum, graph theory, percolation, analytical methods

1. INTRODUCTION

Physarum polycephalum, a multi-nucleated, unicellular slime mold, forms a tubular vein network for foraging and distribution of nutrients. This transportation network (see e.g. [1]) has been shown to possess the ability to solve complex tasks like maze solving [2], network optimization in terms of path length and efficiency (globally [3,4] and also locally as it was

found to prefer optimized network motifs [5]). Furthermore, *P. polycephalum* is even thought to possess certain learning capabilities [6–8].

In a favourable natural environment *P. polycephalum* is usually found in the plasmodial phase covering areas in the square centimeter range. In contrast, in a liquid shaking culture large plasmodia are torn apart by shear forces, creating homogeneously sized spherical plasmodia on the micrometer scale. These objects are usually referred to as microplasmodia and serve as the fragments from which the networks observed in this study were cultivated following [9], see Figure 1. Construction of a transportation network for foraging

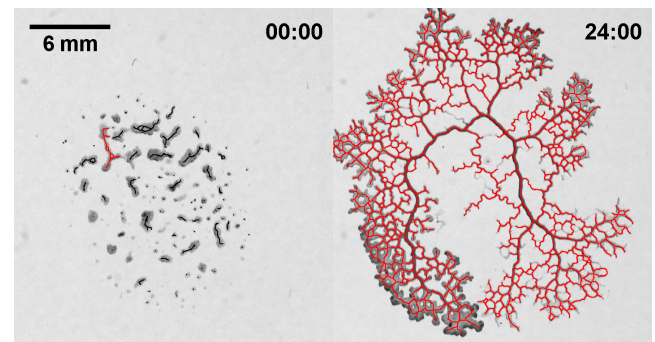


Figure 1: Fragmented (Left Panel) versus connected (Right Panel) configurations of a *P. polycephalum* network. The skeleton is shown as an overlay. The largest component is shown in red, other components in black. Time is given in hours.

from fragments mimics the situation in the reproduction cycle [10] where uni-nuclear cells grow and fuse to form the mature multi-nucleated plasmodium. One may wonder which general rules and sets of external boundary conditions as well as internal biochemical cues work together to orchestrate the formation of the optimal network in a given environment. In fact, it is known that *P. polycephalum* assumes topologically different configurations on homogeneous agar substrates depending on the availability of food and the presence of repellent substances [11]. Given ample resources, *P. polycephalum* is found in a predominantly smooth and disklike shape, whereas high levels of repellent substances induce the formation of a tentacle-like network with long veins. While it may be fruitful to determine the dependence of the network growth dynamics on environmental factors, this study

takes a different standpoint. We ask which topological constraints govern the development of a connected network from disconnected pieces independent from detailed biochemical and other external cues. Indeed, even systems of differing structure, function or abstractness share the common phenomenon called the percolation transition in which a disconnected network spontaneously develops a giant component occupying almost all available nodes, thus changing from a locally to a globally connected structure. The mathematical similarities shared can be described within the field of networks or graph theory. In this investigation the connectivity within the network is described only via nodes and links. We analyzed this process using the configuration model of graph theory [12].

Spatial transportation networks like road or vascular networks tend to have predominantly nodes of small degree with no highly connected central nodes due to either their process of formation or certain spatial constraints like dimensionality and finite vein size. Connectivity tends to be local, i.e., nodes only connect to their spatial neighbours.

Recently [13], we developed an exact mathematical model including nodes up to link degree $k = 3$ describing the percolation transition during the de-novo formation of a *Physarum polycephalum* plasmodial network from fragments. We found that within the configuration model the location of the percolation transition in phase space is independent of experimental details. We will show in this work that an extension of the model is able to incorporate nodes of degree four. We present a well-defined analytical solution for the emergence of a giant component and compare our results to the *P. polycephalum* measurements made in [13].

The additional degree of freedom provided by nodes with link degree $k = 4$ leads to a certain variability in the location of the percolation transition. However, such 4-nodes only occur at a small percentage due to topological constraints, thus leading to only small variations.

In summary, it is the main result of this work that the formation of a foraging network is highly constrained by topology at the percolation transition and only weakly dependent on environmental factors, thus supporting the previous conclusion from [13].

2. MATERIALS AND METHODS

We re-evaluated the 48 experimental growth trajectories from [13] in the context of the four-node-degree model. Briefly, for each sequence, a droplet of liquid-cultured microplasmodia with sizes ranging between 200 – 500 μm was plated on nutrient-containing 1.7%-agar. Network growth was observed under optimal conditions for *P. polycephalum* (darkness, 24 °C, 84 % rel. humidity) with a mounted Canon EOS 500D digital camera. Images were taken every 1 – 2 min for 24 – 60 h depending on the speed of network growth.

A representation of the vein network was obtained via binarization and skeletonization and analyzed with respect to the link degree and connected component size. Nodes of degree higher than four were not considered as they were not observed at a significant percentage. Nodes of degree two were not incorporated as topologically no distinction can be made between a vein and a vein containing a node of degree two. Besides its structure, the internal flow of a transportation network is crucial for an accurate description of its function and may influence the characterization of nodes. While an investigation of the actual flow pattern within the veins, es-

pecially at the 4-nodes, would be beneficial, our purely topological analysis still holds true for the general case. Figure 1 shows two states of a sample sequence recorded 24 hours apart. The skeleton as described above has been overlaid onto the image with the largest component labeled in red.

3. AN EXACT PERCOLATION MODEL

The configuration model describes the structure of graphs with predetermined degree sequences, here given in terms of the node degree fractions p_k , i.e., the probability of a randomly chosen node to be of degree k . This description is especially useful in the case of transportation networks, as the small number of occurring degrees allows for analytical calculations. We are interested in the formation of a connected graph from disconnected pieces in a percolation transition which is described in the configuration model as the spontaneous emergence of a giant component S . It is defined as the probability of a random node to be part of the giant component.

Two general conditions for the degree distributions arise from the configuration model. The self-consistent relation

$$u = \sum_k p_k u^k \quad (1)$$

for the probability $u = 1 - S$ for a node not to be part of the giant component can be understood as follows [12]: If a node is not part of the giant component, all of its neighbours also will not. As a second relation we may use the normalization condition:

$$1 = \sum_k p_k \quad (2)$$

A third condition is only valid in an infinitesimal regime around the phase transition [14]:

$$0 = \sum_k k(k-2)p_k \quad (3)$$

In the case of neglecting the sufficiently small fraction p_4 , the three conditions 1-3 can be used to calculate the remaining fractions $p_{0,1,3}$ at the percolation transition, i.e. $(p_0, p_1, p_3) = (1/3, 1/2, 1/6)$ [13]. If p_4 is included in the calculation, the system becomes underdefined, but allows the expression of these fractions as functions of the fourth. To do so, we solve

$$\begin{pmatrix} 1 & u & u^3 \\ 1 & 1 & 1 \\ 0 & -1 & 3 \end{pmatrix} \cdot \begin{pmatrix} p_0 \\ p_1 \\ p_3 \end{pmatrix} = \begin{pmatrix} u - p_4 u^4 \\ 1 - p_4 \\ -8p_4 \end{pmatrix} \quad (4)$$

in the limit of large graph size at the transition, i.e., $u \rightarrow 1$. We find the expressions

$$p_0 = \frac{1}{3} - p_4 \quad (5)$$

$$p_1 = \frac{1}{2} + 2p_4 \quad (6)$$

$$p_3 = \frac{1}{6} - 2p_4 \quad (7)$$

For $p_4 = 0$, $p_{0,1,3}$ are fixed at the fractions given above. Following equation 7, $p_4 > 1/12$ is topologically impossible at the transition. Thus, the fraction of 4-nodes is necessarily small. Substituting equations 5-7 into the definition of the average link degree, $\langle k \rangle = \sum_k k p_k$ one finds $\langle k \rangle = 1$,

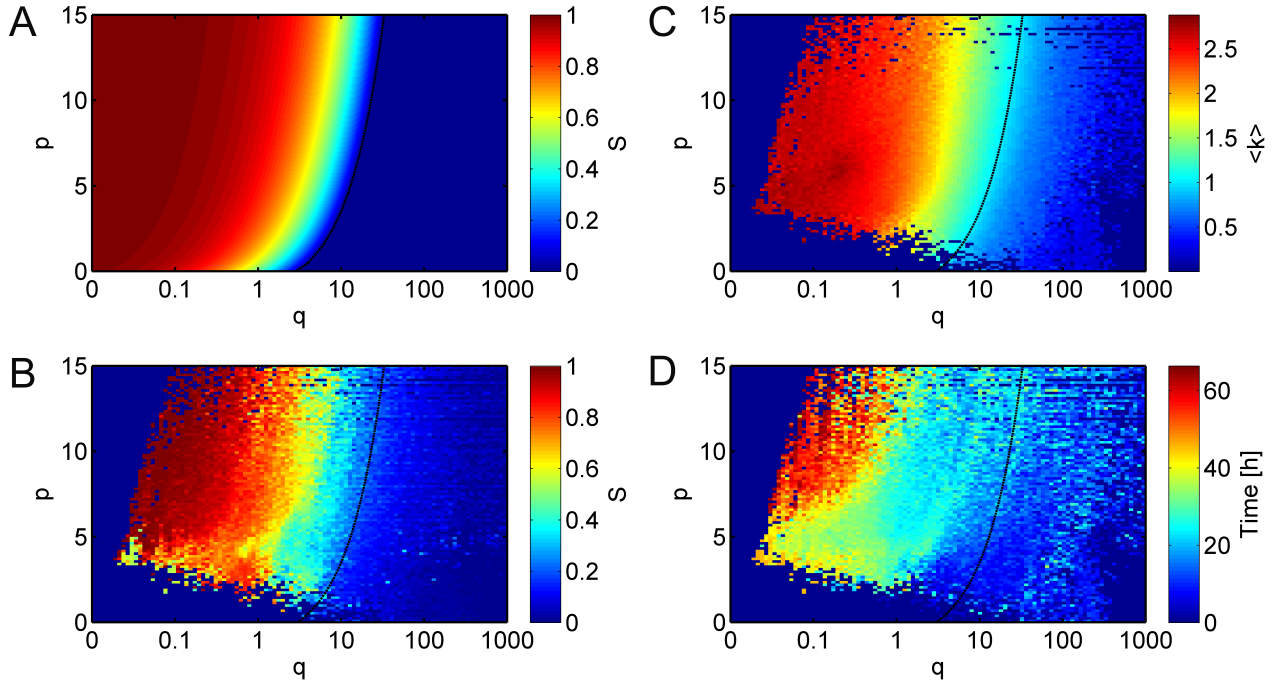


Figure 2: Panel A,B: Largest component $S = 1 - u$ in terms of the fractions $p = p_3/p_4$ and $q = p_0/p_4$. The dashed line marks the percolation transition at $p = 1/2(q - 3)$ in the limit of infinite graph size. Panel A: Theoretical result following equation 11. Panel B: Experimental data obtained from 48 growth experiments. Panel C: Experimental average node degree $\langle k \rangle$. Panel D: Time evolution of the experimental data.

analogously to the simplified case excluding p_4 .

To determine the evolution of the largest component $S = 1 - u$ in terms of the p_k we define the ratios

$$p = \frac{p_3}{p_4} \quad \text{and} \quad q = \frac{p_0}{p_4}. \quad (8)$$

Using equations 5-7 the condition for the phase transition may be expressed as

$$p = \frac{1}{2}(q - 3). \quad (9)$$

Thus, we find a straight line for the phase boundary. The evolution of u is determined by equation 1 which, written out in terms of p and q and employing equation 2, reads

$$0 = u^4 + pu^3 - (1 + p + q)u + q. \quad (10)$$

Note that equations 5-9 only hold at the phase transition and thus do not generally connect p and q , while equation 10 is valid for all combinations of pairs.

Equation 10 is a quartic equation with real coefficients which can be solved using Euler's method. We identified the physically sensible solution as

$$u = \sqrt{z_1} - \sqrt{z_2} - \sqrt{z_3} - \frac{1}{4}p \quad (11)$$

with

$$\begin{cases} z_1 = \left(\frac{p}{4}\right)^2 + \sqrt{-\frac{4}{3}a} \cdot \cos\left(\frac{1}{3}\cos^{-1}\left(-\frac{b}{2}\sqrt{-\frac{27}{a^3}}\right)\right) \\ z_2 = \left(\frac{p}{4}\right)^2 - \sqrt{-\frac{4}{3}a} \cdot \cos\left(\frac{1}{3}\cos^{-1}\left(-\frac{b}{2}\sqrt{-\frac{27}{a^3}}\right) + \frac{\pi}{3}\right) \\ z_3 = -\frac{c}{8z_1z_2} \end{cases} \quad (12)$$

and

$$\begin{cases} a = -\frac{1}{4}q - \frac{1}{16}p(1 + p + q) \\ b = -\frac{1}{64}(1 + q)(1 + 2p + q + p^2) \\ c = -(1 + p + q) + \frac{1}{8}p^3 \end{cases} \quad (13)$$

The solution for $S = 1 - u$ is shown in figure 2(A) in the p - q phase space. The disconnected region ($S = 0$) and the percolated region ($S > 0$) are separated by the relation given in equation 9.

4. P. POLYCEPHALUM PERCOLATION

A disconnected graph consisting primarily of solitary p_0 nodes or tubes limited by p_1 nodes contains only a small fraction of p_3 or p_4 nodes. If a graph becomes more connected, the fractions of p_0 and p_1 will decrease in favour of p_3 and p_4 increasing simultaneously. This leads to a drop in q , eventually forcing the system into the percolated region while much less variation is observed in p .

Figure 2(B) shows the experimental data for S obtained from 48 growth sequences. To accommodate the number of data points a grid with 100×100 bins, using a logarithmic spacing in q , was spanned in p and q and an average value was calculated for each bin. A histogram of the number of values averaged in each bin is shown in 4(B). The same binning was used for all experimental results shown. We find experimental and theoretical data to be in good agreement. Deviations in S can be attributed to the statistical nature of the quantity due to the finite size of the networks observed. While in the limit of infinite graph size S equates to zero before percolation, the finite experimental graphs do

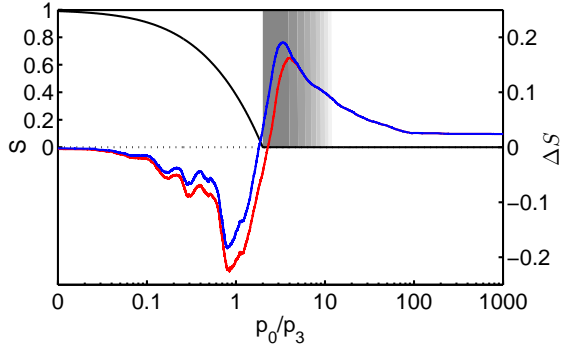


Figure 3: Left axis: Evolution of the largest component in the three-node-degree model (black) [13]. The shaded region illustrates variations in the position of the transition due to non-zero p_4 , its width representing the maximal fluctuation observed and its intensity illustrating the occurrence of a given shift within the experiments. Right axis: Floating average deviations of the three-node-degree (blue) and four-node-degree (red) models from the experimental data. Most significant deviations occur shortly after and prior to percolation while at the transition the system is strongly constrained allowing no large fluctuations.

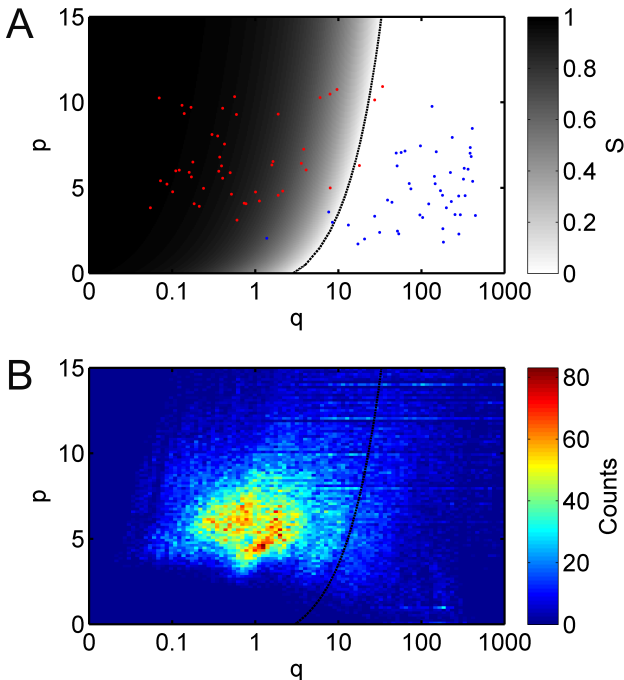


Figure 4: Panel A: Start- (blue) endpoints (red) of all growth experiments. Panel B: Density-histogram of network states. 100 bins were used in p and q with a logarithmic spacing in q .

always have a largest component leading to small but non-zero values in this regime. The ratios p and q are tied to the local topology while S is a global quantity, leading to deviations even in the percolated region. E.g. a finite-sized graph consisting of several equally-sized highly connected components needs only very few strategically placed additional links to form a giant component, even though such a process would lead to small change in p, q .

While in good agreement, the giant component shows the same deviations in both, three- ($S = S_3$) [13] and four-node-degree ($S = S_4$) models. Figure 3 shows the floating average deviations $\Delta S = S_{\text{exp}} - S_i$ of S_3 and S_4 , respectively, from the experimental data computed for both models against the ratio $p_0/p_3 = q/p$. The latter is the driving parameter of the three-node-degree model. The strongest deviations are found on either side of the phase transition. Before the transition, the giant component is finite in the experimental data and thus underestimated by the model. After the transition, S is usually overestimated due to the reasons given above. Using equations 5 and 7 the value of driving parameter at the transition can be tied to p_4 :

$$\frac{p_0}{p_3} = \frac{2 - 6p_4}{1 - 12p_4} \quad (14)$$

For $p_4 = 0$ one finds $p_0/p_3 = 2$, consistent with [13]. If the fraction of p_4 nodes increases, the percolation transition occurs earlier, i.e. p_0/p_3 increases. In figure 3 the shaded region represents the position of the phase transition for p_4 varying from 0 to 0.07. Experimentally, we find $p_4 = 0.026 \pm 0.002$ [13], the error given as σ/\sqrt{N} for $N = 48$ experiments, leading to $p_0/p_3 = 2.68 \pm 0.08$ for the shifted average zero position of the red curve in 3. Analyzing the root-mean-square deviations between the two models at the q, p average values assumed by the experimental data we find $\sqrt{\langle (S_3 - S_4)^2 \rangle} = 0.039$ with a standard deviation of $\sigma = 0.032$.

A quantity tied to the local structure of the whole network and thus less influenced by finite-size effects is the average node degree $\langle k \rangle$ (see figure 2(C)). In a developed state, *P. polycephalum* was found to consist mostly of nodes with degree $k = 3$ [15]. We also find $\langle k \rangle$ approaching value slightly smaller than three as nodes of degree $k = 0, 1$ dominate over nodes of degree $k = 4$ [13] due to exterior growth regions being included in the analysis. At the phase transition (equation 9) we find $\langle k \rangle = 1.027 \pm 0.0027$ (standard deviation $\sigma = 0.011$), a good agreement with the theoretical requirement of $\langle k \rangle = 1$.

5. DYNAMICS OF LINK DEGREES

It is apparent, that any network developing from fragmented to percolated in a series of states has to pass through the percolation transition (See figure 4(A) showing initial and final network states in the p, q phase space.). Even though all states are included in the set described by the configuration model, the theory outlined in this work does not describe the temporal dynamics which are largely dependent on the initial configuration and biological/environmental factors. For example, we found [13] that decreasing the initial density of microplasmidia leads to a delayed percolation while a low availability of nutrients sped up the plasmodial development to quickly increase the searchable area. Similarities in the temporal dynamics between sequences could also be observed in the p, q space. Figure 2(D) shows

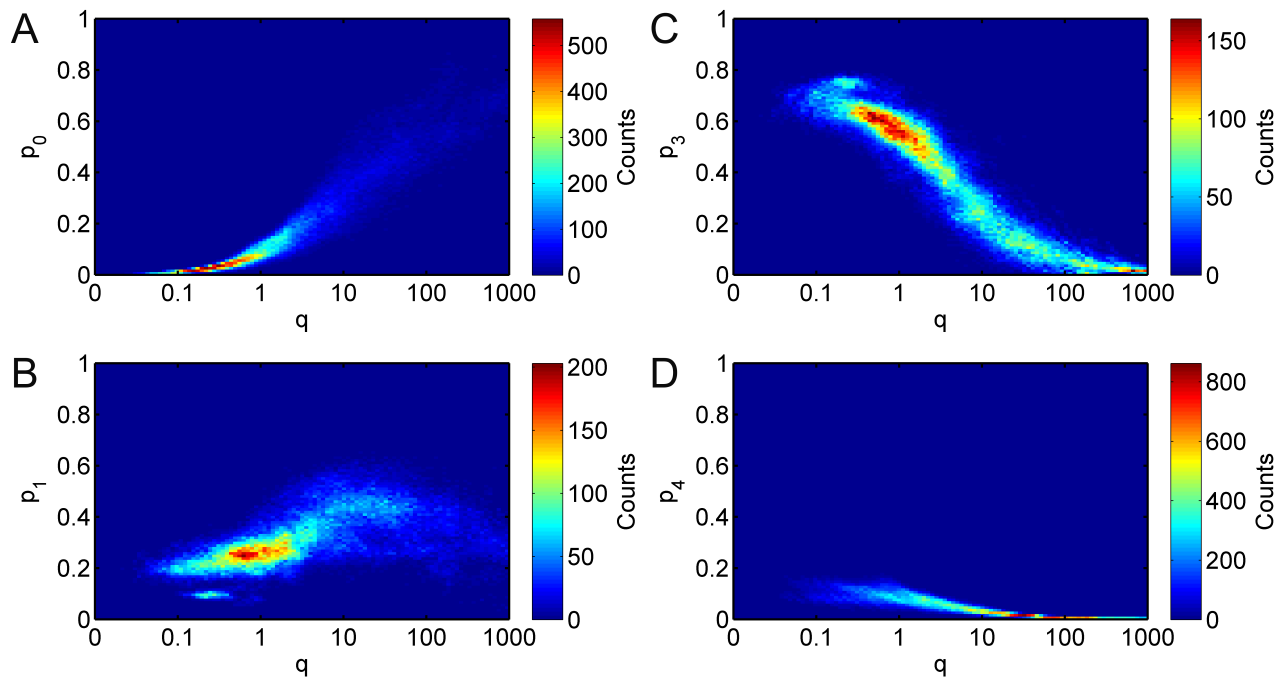


Figure 5: Development of p_k in *P. polycephalum* with respect to q which is decreasing monotonically with time. Panel A: The initially dominant species of p_0 nodes decreases strongly and consolidates with very few solitary nodes remaining. Panel B: Besides p_0 , p_1 are also present in the initial configuration. This fraction has to reach a maximum of about 0.5 at percolation. In the late states, p_1 is mostly found in the circumference of the network thus always being inferior to p_3 . Panel C: p_3 is rare in the initial configuration but becomes the dominant species in the developed network. Panel D: p_4 is almost negligible up until percolation and stabilizes between 0.1 – 0.2 afterwards.

a map of the points-in-time, at which a certain state was reached. While scattered in the non-percolated region and up to the transition, the majority of sequences (27 out of 48) were found to be stabilizing until termination between 30 – 45 h into a region around $(p, q) = (5, 0.5)$ with high number of recorded states (figure 4(B)). Ten sequences were terminated between 45 – 65 h with an increased value for p . The consolidation in q can be understood as a depletion of reachable p_0 nodes which ties further changes in q to changes in $1/p_4$. Figure 5 shows the probabilities p_k as functions of q which is monotonically decreasing and can be seen as the parameter driving the system across the transition. During late stages of network growth we find p_4 to remain at a low value (up to 0.2) while p_3 is found to be dominant at about 0.6 – 0.8, slightly increasing. The increase in p_3 is a geometrical necessity as the *P. polycephalum* network spans an approximately circular area with p_1 nodes only found in the circumferential area. Assuming a constant density of nodes, in a growing network circumferential nodes will always have to give way due to the growing area to circumference ratio. For a detailed description of node link dynamics see the caption of Figure 5.

6. CONCLUSION

We devised an exact percolation model employing all node types relevant for small link degree transportation networks represented by the *P. polycephalum* tubular vein network. We find a description of the transition in a two-dimensional

phase space. The dominant driving parameter turns out to be q , the ratio of 0-nodes to 4-nodes, whereas p , the ratio of 3-nodes to 4-nodes, changes relatively little in comparison given the data set discussed. Since both probabilities, p_3 and p_4 , exhibit a sigmoidal shape as a function of q , as characterized by p , both q and p_0/p_3 play a similar role allowing them to be exchanged. Even though the system is prone to inherit variations in the initial configuration into the late states - in some regions accordingly shows deviations of up to 25% in the development of a giant component - the topological conditions at percolation are found to strongly constrain the available configurational space. Comparison of the four-node-degree model to the simplified three-node-degree model from [13] shows that the essential character of the transition is already covered by the latter, thus justifying the use of the simplified version for practical purposes.

The topological constraints at percolation have implications for the development of a foraging network. An individual organism aims to optimize its network with respect to general search efficiency. Nevertheless, the dynamics of the link degrees, defining the network structure, must pass through percolation. Thus, percolation serves as a common transition distinguishing the developmental phases.

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