Spatial network optimization with a model of the *physarum polycephalum*

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In this report we look at one of the one of the main models that have been proposed to understand and simulate the network optimization behavior of the myxomycete (slime mold) *physarum polycephalum*. The networks resulting from this optimization are examples of spatial networks, and as such they present some typical characteristics like a peaked degree distribution, and fluctuations in betweenness centrality-degree correlations. We look at metrics of transport efficiency, and compare them with some experimental results. Finally, we discuss applications of the model as a null model of road networks, and as an algorithm for linear optimization.

Spatial networks | biological networks

The *physarum polycephalum* slime mold has recently attracted a lot of attention for its surprisingly "smart" behavior. More specifically, despite its simplicity, this organism has been shown to solve mazes [1], optimize networks [2], perform basic computation [3, 4], and even show some learning capabilities [5] In fact, the variety of problems that the *P. polycephalum* appears to solve is so large [6], that it has become popular as a new platform for unconventional computing [3, 7–9], and it has also inspired new classes of algorithms [10, 11].

Early experiments on the network optimization capabilities of the *P. polycephalum* were conducted by Nakagaki [1] in 2000, who found that the slime mold could consistently find the shortest path through a maze connecting two sources of food. Later studies showed that when several food sources were placed on an arrangement that simulated the relative locations of major cities in a country, the slime mold would develop a network structure which was similar to the real road network in the respective countries [3]. When this experiment was conducted for the cities in the neighbourhood of Tokyo, the slime mold network, which took about 26 hours to develop, rivaled the Tokyo rail network in terms of transport efficiency (average shortest path length), cost (total length), and robustness (fault tolerance) [2].

To understand how the slime mold can achieve this, it is important to understand its basic physiology. The *P. polycephalum* is a large amoeba-like single cell organism. More specifically, it forms a large syncytial plasmodium, that is, a single mass of protoplasm surrounded by a single cell membrane, which contains many nuclei [12].

Crucially, nutrients and chemical signals travel macroscopic distances through the body of the slime mold, by flows of the protoplasm, which (in its vegetative state) are mainly localized in tube-like structures called pseudopodia [1]. The network of these corresponds to the observed networks in the experiments described above. Indeed, the fact that we are dealing with a distribution network optimized by evolution over millions of years, may explain the resemblance with man-made transportation networks, as both network types share

similar needs, and similar structures [13].

Finally, the flow through these tubes is not steady, but fluctuates and changes directions in different parts of the network, on the time scale of minutes; this is called protoplasmic shuttle streaming [14].

All these empirical observations have guided the development of the mathematical models that try to simulate the slime mold's behavior. In particular, the growth of the network is assumed to be guided by the protoplasmic flow through the network. The way this is modeled is discussed in the next section.

Mathematical model

There are several approaches that have been proposed in the literature to model the adaptive and pattern formation behavior of the *physarum polycephalum*. Two of the main ones are the following:

The approach proposed by Tero [2, 14] begins with a mesh of thin tubes that span the region occupied by the slime mold. Food sources are placed at selected nodes, and act as both sources and sinks, alternating these roles in time. The protoplasmic flux through the network is computed using simple fluid dynamic equations, and a positive feedback is assumed between the flux through a tube and the growth of its diameter. This is the approach which we are going to focus on in this report.

The approach developed by Jones [15] is a multi-agent reaction-diffusion model, where the "agents" (or particles) represent both the gel (sponge-like matrix) and sol (protoplasm). These diffuse in a lattice, and interact by direct steric hindrance and by depositing *chemoattractants* at visited locations, which can later attract other particles. The model also includes rules for the growth and shrinkage of the population based on local density of particles, as well as rules for representing food sources and other environmental features.

Significance Statement

Biological networks offer some of the best examples of spatial networks (networks with spatial constraints), and their optimality has inspired new models for network design. The *physarum polycephalum*, a single-celled slime mold, grows highly optimal spatial networks to distribute food. In this report, we use a mathematical model that simulates this organism's behavior, to explore the properties of the resulting networks, and discuss some of its applications.

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The model produces interesting results, and its stochastic nature is desirable because real *P. polycephalum* networks show non-determinism in their formation [2].

It is worth mentioning that Tero's model can also have stochastic properties. One way is via the random selection of source/sink nodes at each time step. This seems to affect the time evolution, but the final steady state is barely affected. Another way is via the initial conductances assigned to the edges of the mesh. This seems to have effects both in the time evolution and the steady state network, although the effect seems to depend on the choice of growth function (introduced below) [14]. Some choices make the steady state network independent of the initial conditions, but the convergence is then quite slow.

We chose a growth function that gave fast convergence, for a certain choice of initial conditions. If one is willing to sacrifice the fast convergence, introducing randomness in the initial conditions may be a way to define a random graph ensemble of networks, which may more closely model the real non-deterministic *P. polycephalum* networks.

The model we are going to use is the one proposed by Tero. As mentioned above, the starting point is a mesh of thin tubes, that represents the thin film observed in experiment when the slime mold has just invaded an agar-covered region. This was implemented by a uniform grid, whose points were disturbed randomly (by no more than a quarter of the grid size to either side). The mesh of tubes is then formed by the Delaunay triangulation of these points. The width of these tubes is initiated all the same and small[1].

An extra set of nodes is then added, at locations chosen uniformly at random (or they may be chosen manually) to represent the food sources (FSs). The flux through each of the tubes is then calculated by assuming that the flow is laminar and it follows the Hagen-Poiseuille equation:

$$Q_{ij} = \frac{\pi r_{ij}^4 (p_i - p_j)}{8\eta L_{ij}} = \frac{D_{ij}(p_i - p_j)}{L_{ij}} \qquad [1]$$

where Q_{ij} is the flux through the tube connecting i and j, r_{ij} is the radius of the tube, and L_{ij} is its length. D_{ij} is a measure of the tube's conductivity (if nodes i and j are not connected, we define $D_{ij} = 0$). The dependence of the flow on length is one of the ways these network is constrained by space. At every node i (except the source and sink nodes), flux conservation is obeyed, so that $\sum_j Q_{ij} = 0$. At the source node, a, $\sum_j Q_{aj} = I_0$, and at the sink node b, $\sum_j Q_{bj} = -I_0$, where I_0 is the magnitude of source/sink flow.

The linear system given by combining Eq. 1 with the flux conservation equations, where the unknowns are the pressures, is equivalent to the system for a resistor network, where the unknowns are the voltages. The quantity D_{ij}/L_{ij} is then analogous to the electrical conductance, and $\pm I_0$ to the current of a current source/sink. This system can thus be manipulated to obtain (see for example [17]):

$$\mathbf{Lp} = \mathbf{I} \qquad [2]$$

where $L_{ij} = \delta_{ij}s_i - W_{ij}$ is the (weighted) combinatorial graph Laplacian. $W_{ij} = D_{ij}/L_{ij}$ (where $W_{ij} = 0$ when $i = j$) is the weight matrix, and $s_i = \sum_j W_{ij}$ is the corresponding

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[1] Homogeneous initial conditions gave the best results, and fastest convergence; sufficiently large deviations from this generally didn't converge in the simulation. This may be related to the initial state dependence found for simple networks [14, 16]

weight strength. p_i is the pressure of node i, and $I_i = 0$ except when $i = a, b$ for which $I_{a,b} = \pm I_0$. As we can only solve for the pressure differences, **L** is singular, and we work with the corresponding reduced quantities, given by removing the first row of Eq. 2, and the first column of **W**.

The crucial assumption in the model is that the evolution of the matrix D_{ij} is given by the equation:

$$\frac{dD_{ij}}{dt} = f(|Q_{ij}|) - D_{ij} \qquad [3]$$

where $f(x)$ is a monotonically increasing function of its argument (called the growth function), which here we assume is:

$$f(x) = \frac{x^\gamma}{1 + x^\gamma} \qquad [4]$$

This is based on the the idea that plasmoid tubes that carry a large flux tend to stretch and widen and thus carry more flux, while plasmoid tubes that carry little flux shrink in diameter (as ensured by the second term in Eq. 3). In [14], the authors offer empirical justification, as well as a proposed biomolecular mechanism for this behavior. However, the actual form of the growth function isn't defined by their model, and other sigmoid functions may be used. Furthermore, forms like $f(x) = x^\mu$, $\mu > 0$ are also used [10]. This freedom is an issue with the model, and a deeper understanding of the molecular mechanism constraining the form of $f(x)$, should be sought. Alternatively, growth functions that give desired analytical properties (say for an optimization algorithm) may be chosen.

We solve Eq. 3 by the explicit Euler method. After each time step, two of the food source nodes are chosen at random to be the source and the sink for updating the flux matrix Q_{ij}. This simulates the protoplasmic shuttle streaming seen in the real system.

Results and discussion

The above model was implemented in `MATLAB` code, and run with values $\gamma = 1.15$, $I_0 = 0.2$, as these were found to give the best match with the real physarum network (although under constraining illumination) [2]. The initial grid linear size was 30.

Basic properties of the network. A typical network, at time step $t = 2000$ is shown in Fig. 1. The planarity of the network is apparent. One could think that this may be due to the underlying mesh being planar (a triangular tessellation). However, from simulations I found that adding shortcuts to the mesh, giving a decidedly non-planar underlying graph still produced planar graphs, as long as the length dependence was kept in Eq. 1.
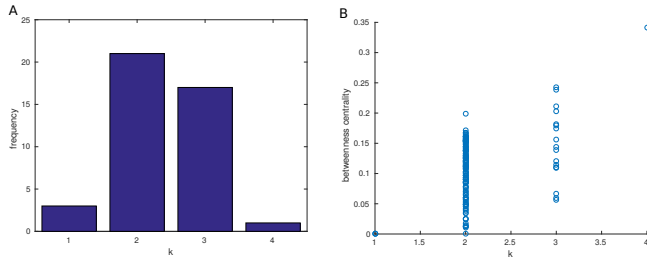
The degree distribution of this network is seen in Fig. 2**A**, which shows a clearly peaked distribution (with a maximum of two). Peaked degree distributions are typical of planar spatial networks, as both the constraints of links not crossing, and the higher cost (and lower probability) of longer links, suppress high degree nodes [13]. Both of these are present here, and so we certainly expect a peaked degree distribution.

Fig. 2**B** shows a plot showing the node betweenness centrality versus the degree for all nodes in the core network. While, as one would expect, there is a general trend for the betweenness centrality to increase with the degree, there is also
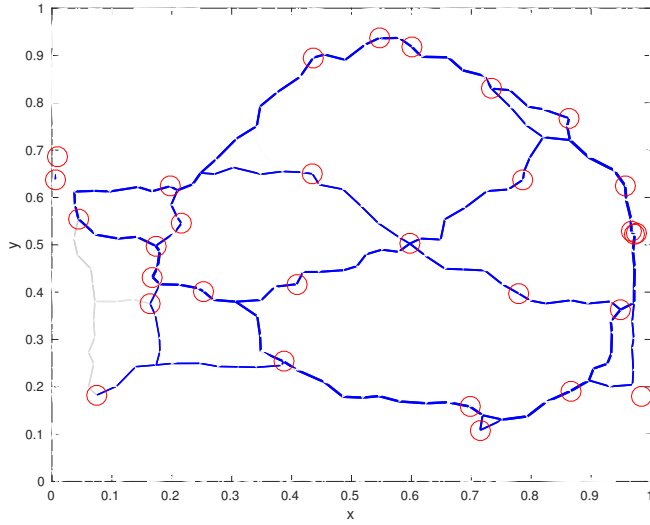
Fig. 1. Food distribution network at time step $t = 2000$. The 50 FSs are represented by red circles centered on the corresponding nodes. Tubes with a thickness greater than 10% of the maximum thickness are shown in blue, while the others are shown in a nonlinear grayscale with darker colours corresponding to thicker tubes. The network formed by the blue edges, together with the nodes they connect, and the food sources, will be referred to as the *core network*. Most tubes are invisible because their thickness is too low. The thickness of the line in the figure is also linearly related to the thickness of the actual tube.

Fig. 2. A Degree distribution for the network in Fig. 1, including only the degrees of the FSs (and any Steiner points in the core network, if any), as the degrees along the tube are fundamentally mesh-dependent. **B** Betweenness centrality (normalized to 1) versus degree, for the same network.

very large fluctuations for each degree. These are also typical of spatial networks and are usually caused by the competition between spatial constraints (which makes paths tend to visit nodes towards the barycenter of the network), and topological constraints (that makes path tend to visit high degree nodes) [13].

Growth and efficiency of the network. This network does not only offer interesting behaviour as a spatial network, but also as a temporal network [18]. The network in this model evolves in time until it reaches an steady state [2]. However, real physarum networks are constantly changing (at least in their foraging state), looking for new sources of food, and their dynamics is nontrivial [19]. The network of tubes is of course coupled to the network of flows, which also has interesting dynamics, related to the rhythmic contraction of its cytoskeleton [20, 21]. Some of that dynamics (shuttle streaming) is incorporated in our model in the simplest form, by randomly selecting source and sink FS. Another interesting spatio-temporal behavior is the formation of the initial macroplasmodium network

from microplasmodia, which shows a percolation transition, that has been analyzed using the configuration model [22, 23].

Several measures were taken for the core network, at different times in its evolution, and for different placement of FSs (independent and with uniform distribution). These are shown in Table 1, all the quantities are calculated for the largest connected component, and are averaged over 10 samples of FS placements. Lengths refer to Euclidean lengths.

A general trend can be seen in Table 1, for the network to reach more of the food sources, as time increases. However, there appear to be fluctuations, with the network loosing connection to a FS. Furthermore, in the experiments with more FSs (50), these fluctuations appeared to be larger. This may be due the way we are simulating shuttle streaming, as, by only having a single source and a sink at every time step, the flow needed to reinforce a particular tube may occur very infrequently. At worst, if that particular flow only occurs for a particular pair of FSs, it will only occur a fraction $\frac{1}{FS(FS-1)} \approx 1/2500 \approx 4 \times 10^{-4}$ of the time for $FS = 50$ food sources. In this time, the tube will likely have decayed, and will only regrow once the right flow happens again. This is a limitation of the model, that will likely be fixed by allowing several concurrent sink and sources.

The measure of cost, TL_{MST} does seem to be improving as time increases, while the transport efficiency (MD_{MST}) improves for the first few hundred time steps, and then plateaus (or even worsens a little). By time step 2000, the network is 85% longer than the MST, but has a mean shortest path length 0.76 times that of the MST. The network is also evidently more fault tolerant than the MST (which has $FT = 0$). α is a measure of the trade-off between fault tolerance and cost, and does appear to increase with time, showing that the network is becoming more efficient (using less "material" for same fault tolerance). These values seem roughly consistent with those reported in [2]. They obtain $TL_{MST} = 1.68$, $MD_{MST} = 0.83$, for the steady state network using the same values of γ and I_0 as here. These are for their arrangement of FSs imitating the cities visited by Tokyo rail network.

One important difference is that their network is constrained not to cross regions corresponding to sea in the real geography. This may explain their larger value of $MD_{MST} = 0.83$ (even though it falls within the standard deviation). Also, their slightly smaller value for TL_{MST} may be due to the way they measure lengths. Although they do not say it explicitly, it seems they measure lengths in straight lines even when the physarum graph is crooked, while I measured lengths following the actual physarum network, giving larger results. Finally, they obtain a value $FT = 0.96$, but this corresponds to tolerance against removing an edge, while our values here are against removing a node, a more severe fault, which should produce a lower tolerance. Calculating FT against edge removal for our networks, gives a value of essentially 1, which is closer to their value.

Regarding the average degree, our values are consistent with values measured from actual *P. polycephalum* networks in [24]. However, if one ignores degree two nodes (as they are morphologically indistinguishable from just an edge), observed networks are essentially 3-regular graphs [25], which also agree with our simulations if degree 2 are ignored.

Overall, the model appears to find a network that offers good transport efficiency (short mean path), and fault toler-

Table 1. Evolution of several measures at different time steps for the configuration of FSs in Fig. 1

t	$\overline{CC}$	$\overline{TL_{MST}}$	$\overline{MD_{MST}}$	$\overline{FT}$	$\overline{\alpha}$	$\overline{\langle k \rangle}$
50	18.3 (5)	4.07 (0.6)	0.98 (0.1)	0.62 (0.13)	0.15 (0.07)	3.49 (0.07)
100	24.6 (5)	3.72 (0.3)	0.81 (0.1)	0.70 (0.09)	0.19 (0.07)	3.16 (0.1)
300	28.8 (1)	2.31 (0.2)	0.75 (0.1)	0.74 (0.04)	0.32 (0.07)	2.65 (0.09)
500	28.7 (1)	2.00 (0.2)	0.75 (0.1)	0.73 (0.04)	0.37 (0.09)	2.56 (0.1)
1000	28.3 (2)	1.89 (0.2)	0.76 (0.1)	0.73 (0.05)	0.39 (0.1)	2.51 (0.09)
2000	29.1 (1)	1.85 (0.1)	0.76 (0.1)	0.73 (0.04)	0.40 (0.1)	2.48 (0.07)

t = time step
$\overline{CC}$ = average number of FSs in largest connected component.
$\overline{TL_{MST}}$ = average total length over total length for MST.
$\overline{MD_{MST}}$ = average mean shortest path length over that of MST.
$\overline{FT}$ = average fault tolerance (probability of not disconnecting part of the network by removing a single node).
$\overline{\alpha} = FT/TL_{MST}$ (efficiency)
$\overline{\langle k \rangle}$ = average mean degree.
MST = minimum spanning tree.
Values in parenthesis are standard deviations.

ance, without too much added cost (65% − 85% longer than MST depending on how one measures it), and these are all similar to what the real *P. polycephalum* finds. Nevertheless, the values of $\gamma = 2$ and $I_0 = 1.8$ have been found to give more optimal networks ($\alpha \approx 0.7$ $MD_{MST} \approx 0.85$) than both the slime mold network, and the real Tokyo rail network [2].

Applications of the model

In this section we look at some of the ways this model has been applied: as a null model for transportation networks, and as the basis for a new class of optimization algorithms.

Comparison with real transportation networks. Some amount of research has been done on comparing *P. polycephalum* networks with road networks [24, 26, 27]. The main problem with these experiments is that, while obtaining good statistical data on the physarum networks isn't hard (it is easier than obtaining ant route data, for instance), obtaining statistical data from road networks is much more challenging. In [24], the authors briefly recount the long history that lead to modern motorways, which spans up to prehistoric times. The problem is that we only have access to one realization of the complicated and stochastic process that led to our current road networks, and thus there is no obvious way in which to extract statistics from the empirical data. One approach is to consider different regions as samples from some underlying stochastic process; but this still doesn't allow for sampling the distribution, for a given arrangement of largest cities, for example.

Another possible approach is to compare the physarum network statistics with statistics from models that define random graph ensembles of realistic road networks. There appears to be more models available for urban road networks, than for interurban road networks. However, Levison and Xie have developed a model that includes interurban highways in its scope [28]. Interestingly, one of the principles on which the model is based appears very similar to that of the physarum network model discussed here. In their words, "we develop a network growth model that incorporates decentralized investment processes on individual links, by which much used links continuously get reinforced while less used ones shrink". However, their model is otherwise rather different, and in fact produces network with mean degree about 2, and very few loops. They propose other models too, and it would be interesting to compare them more thoroughly.

Applications in optimization algorithms. Another application of the model is not to the modeling of transportation networks, or even of *P. polycephalum* itself, but to the development of new algorithms. In this case, the issues are not model validation with empirical data, but correctness proofs, and convergence bounds. As was found in [2], for the growth function $f(x)$ we used here, $\gamma = 1.8$, $I_0 = 2$ gave the optimal results for their particular problem. However, most of the literature on the analytical properties of the model focuses on the linear function $f(x) = x$, which is more tractable. For this case, the model has been shown to converge to the shortest path between two nodes, independently of the network structure, and initial condition [29, 30]. The convergence properties and complexity bounds were then proven for this problem [31]. The model has also been shown to give solutions to the linear transshipment problem [32], and the convergence properties for this have also been given very recently [33]. Following on these results, the physarum model (suitably interpreted) has been shown to solve linear programs (perhaps the most complex in *P*) [11].
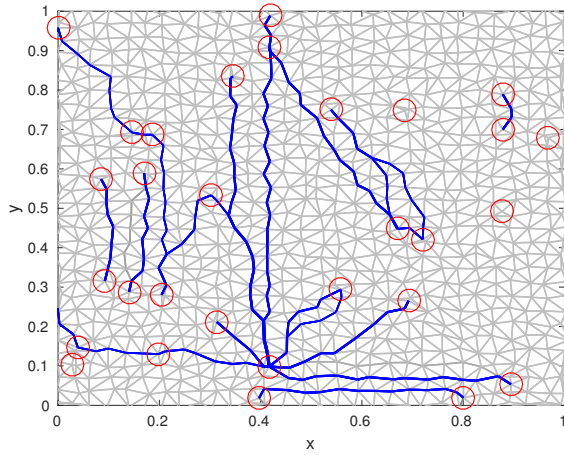
Some analysis using the sigmoid growth function (Eq. 4) shows that, for a very simple case, the system doesn't converge to a unique network (so that it'll depend on initial conditions) [16]. Using the homogeneous initial conditions for D_{ij}, I found that the network converged to a certain value of the *cost*, as defined for the linear transshipment problem [32]:

$$c(Q) = \sum_{ij} L_{ij} Q_{ij} \qquad [5]$$

An example of a resulting network is shown in Fig. 3. However, using initial conditions with random fluctuations, the network did not appear to converge, and even appeared chaotic. Furthermore, the sigmoid function appears to give marginally lower values of the cost than the linear function, for a given time step (see Fig. 5). This indicates that the sigmoid function may not only cause the model to converge to the optimal answer, but that it may do so slightly faster (at least in terms of time steps).

Another indication that this is true is given by the actual solution computed using the linear function. At time step

Fig. 3. Resulting network, at time step $t = 400$, when the sinks and sources are fixed at certain FSs, computed using the sigmoid growth function Eq. 4. The coloring scheme is slightly modified so that the underlying network is visible.
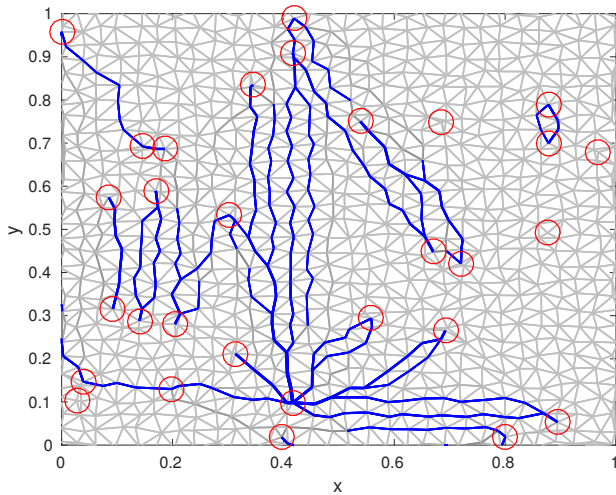

Fig. 4. Resulting network, at time step $t = 400$, computed using the linear growth function

$t = 300$ (Fig. 4), the topology is similar, but different than the one in Fig. 3. However, by time step $t = 900$, the topology is virtually the same as in Fig. 3.

The model is also being applied to other problems. In [10] it is used to give approximate solutions to the Steiner tree problem. For an overview of many more current applications we point the reader to [34] (although the book focuses on the unconventional computing aspects, new algorithms naturally arise in that area).

Conclusion

In this report, we looked at the spatial network optimization properties of the *physarum polycephalum* slime mold, from the perspective of the model introduced by Tero [14]. After defining and discussing the model, we looked at some basic metrics of the networks that this model produces. We looked at the degree distribution and betweenness centrality-degree correlations, because these are often able to indicate if spatial
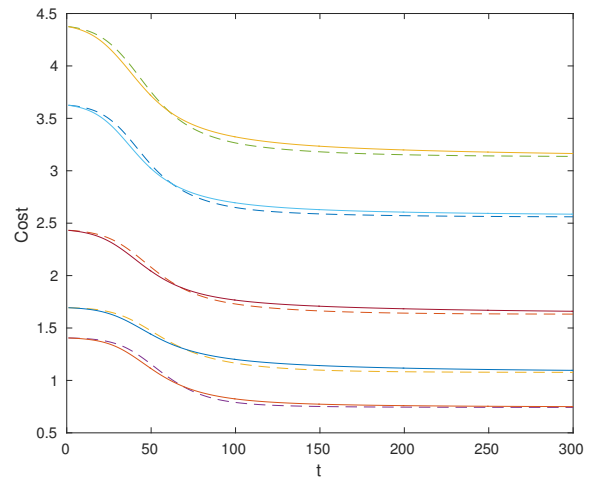
Fig. 5. Value of the cost, defined as in Eq. 5, vs time step t, for different FS configurations. Dashed lines correspond to the linear growth function; solid lines to the sigmoid growth function

constraints are at play, which they are for these networks.

We also looked at measures of efficiency, cost, and robustness following [2], and found results consistent with theirs, although with some differences, which we discussed. Finally, we reviewed some applications of the model that have been proposed in the literature. These include applications as a null model for road networks, that can give clues regarding their current optimality, and how their design may be improved. Difficulties with these empirical studies were discussed.

The model is also being fruitfully applied as an optimization algorithm for several problems, mostly in linear programming. This area seems particularly promising for the future, and there is a lot of research still to be done on it. For example, most of the literature has looked at the linear form of the growth function, as it is more analytically tractable. However, alternative forms may give new insights. As a first step, we compared numerically the convergence of the cost function for the sigmoid function versus the linear function, and found that they both appear to convergence to the same answer, and furthermore the sigmoid function seems to do so slightly faster.

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