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Slime mould evaluation of Australian motorways

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Slime mould *Physarum polycephalum* is renowned for spanning spatially distributed sources of nutrients with a transport-wise optimal network of protoplasmic tubes. We explore analogy between slime mould transport of nutrients in its protoplasmic network and vehicular transport in a motorway network and evaluate how well the slime mould approximates major road network of Australia. We represent major urban area by oat flakes, inoculate plasmodium of *P. polycephalum* in Sydney and analyse protoplasmic network developed. We compare the slime mould networks with well-known proximity graphs and man-made motorway network, and speculate on how a transport network in Australia might re-structure, from 'slime mould's point of view', in a response to major disasters.

Keywords: biological transport networks; Australian motorways; slime mould; biocomputing

1. Introduction

Plasmodium is a vegetative stage of acellular slime mould *Physarum polycephalum*, a syncytium, a single cell with many nuclei, which feeds on microscopic particles [18]. The plasmodium is a unique user-friendly biological substrate from which experimental prototypes of massive-parallel amorphous biological computers are designed [3]. During its foraging behaviour, the plasmodium spans scattered sources of nutrients with a network of protoplasmic tubes. The protoplasmic network is optimised to cover all sources of food and to provide a robust and speedy transportation of nutrients and metabolites in the plasmodium body. The plasmodium's foraging behaviour is interpreted as computation: data are represented by spatial configurations of attractants and repellents, and results of computation by the structures of protoplasmic network formed by the plasmodium on the data sets [3,13,14]. The problems solved by plasmodium of *P. polycephalum* include shortest path [13,14], implementation of storage modification machines [2], Voronoi diagram [17], Delaunay triangulation [3], logical computing [4,20] and process algebra [16]; see overview in [3].

Previously [1], we have evaluated a road-modelling potential of *P. polycephalum*; however, no conclusive results were presented back in 2007. A step forward biological approximation, or evaluation, of man-made road networks was done in our previous papers on approximation of motorways/highways in the UK [5], Mexico [6] and the Netherlands [7] by plasmodium of *P. polycephalum*. For all the three countries we found

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that, in principle, a network of protoplasmic tubes developed by plasmodium matches, at least partly, a network of man-made transport arteries. Shape of a county and exact spatial distribution of urban areas (represented by source of nutrients) may play a key role in determining the exact structure of a plasmodium network. Also we suspect that a degree of matching between Physarum networks and motorway networks is determined by the original government designs of motorways in any particular country. This is why it is so important to collect data on the development of plasmodium networks in all major countries, and then undertake a comparative analysis.

In the present paper, we have chosen Australia due to many unique features of the Australian motorways network.

First, one may note a clear dominance of coastal routes that form a network of highways along the entire coast of the Australian continent (i.e. it is a cycle graph or a circuit). This network, called *Australia's Highway 1*, joins all mainland state capitals being the longest national highway in the world. The total length of Australia's Highway 1 is approximately 14,500 km, exceeding the length of the Trans-Siberian Highway ($\approx$ 11,000 km) and the Trans-Canada Highway ($\approx$ 8000 km). The Australia's Highway 1 contains specific highways, such as Pacific Highway – a major transport route along part of the east coast of Australia, between Sydney and Brisbane. The dominance of coastal routes is due to a range of historic, geographic, economic and geopolitical factors, including the history of early European settlements along the coast (these settlements initially used boats as a primary mode of transport); specifics of Australia's main industries and services such as mining and tourism; the harsh continental climate (with arid conditions and significant lack of water) that does not favour sustainable agriculture in regions located further from the coast than 1000 km on average and often just a few hundreds of kilometres.

Second, the Australian motorways network shows a relative abundance of tributaries of Highway 1: a set of smaller networks interconnecting cities and towns in a vicinity of major cities such as Sydney, Melbourne, Brisbane and so on. Each of these smaller networks reaches a sufficient density around their respective centres, typically attaining the complete sub-graph topology. Australia's Highway 1 passes through some of Australia's fastest growing regions, and in turn stimulates regional development making the tributaries necessary.

Third, Highway 1 includes the principal north–south route through the central (mostly desert) interior of mainland Australia, connecting Darwin, Northern Territory, with Port Augusta, South Australia – the Stuart Highway (or simply 'The Track'), as well as the north–east route including highways that connect Darwin in the north with Brisbane on the east coast. These two routes provide main 'short-cuts' through the interior of mainland Australia and also attract tributaries.

In summary, Australia presents a unique case combining the dominant coastal highway circuit, dense tributary routes around the main coastal cities and a small number of 'short-cut' routes through the interior of mainland Australia.

This paper is structured as follows. List of chosen urban areas and experimental set-up are discussed in Section 2. In Section 3, we describe foraging behaviour of plasmodium on a configuration of urban area and extract transport links built by the plasmodium. Physarum graphs are considered in a framework of planar proximity graphs in Section 4. We compare Physarum transport networks with existing Australian motorway network in Section 5. A response of plasmodium transport networks to major disasters is studied in Section 6.

2. Methods

Plasmodium of *P. polycephalum* is cultivated in plastic containers, on paper kitchen towels sprinkled with still drinking water and fed with oat flakes (Asda's Smart Price Porridge Oats). For experiments, we used 12×12 cm polystyrene square Petri dishes. Agar plates, 2% agar gel (Select agar, Sigma Aldrich), are cut in a shape of Australia. We consider the 25 most populated urban areas **U** of Australia (Figure 1(a)):

(1) Sydney, Newcastle, Central Coast, Wollongong, Maitland, Nowra–Bomaderry, Richmond-Windsor (New South Wales);
(2) Melbourne, Geelong, Ballarat, Melton, Bendigo, Sunbury, Shepparton-Mooroopna (Victoria);
(3) Brisbane, Sunshine Coast, Toowoomba, Gold Coast-Tweed Heads (Queensland/ New South Wales);
(4) Perth, Rockingham, Mandurah (Western Australia);
(5) Adelaide (South Australia);
(6) Bundaberg, Hervey Bay (Queensland);
(7) Canberra–Queanbeyan (Australian Capital Territory);

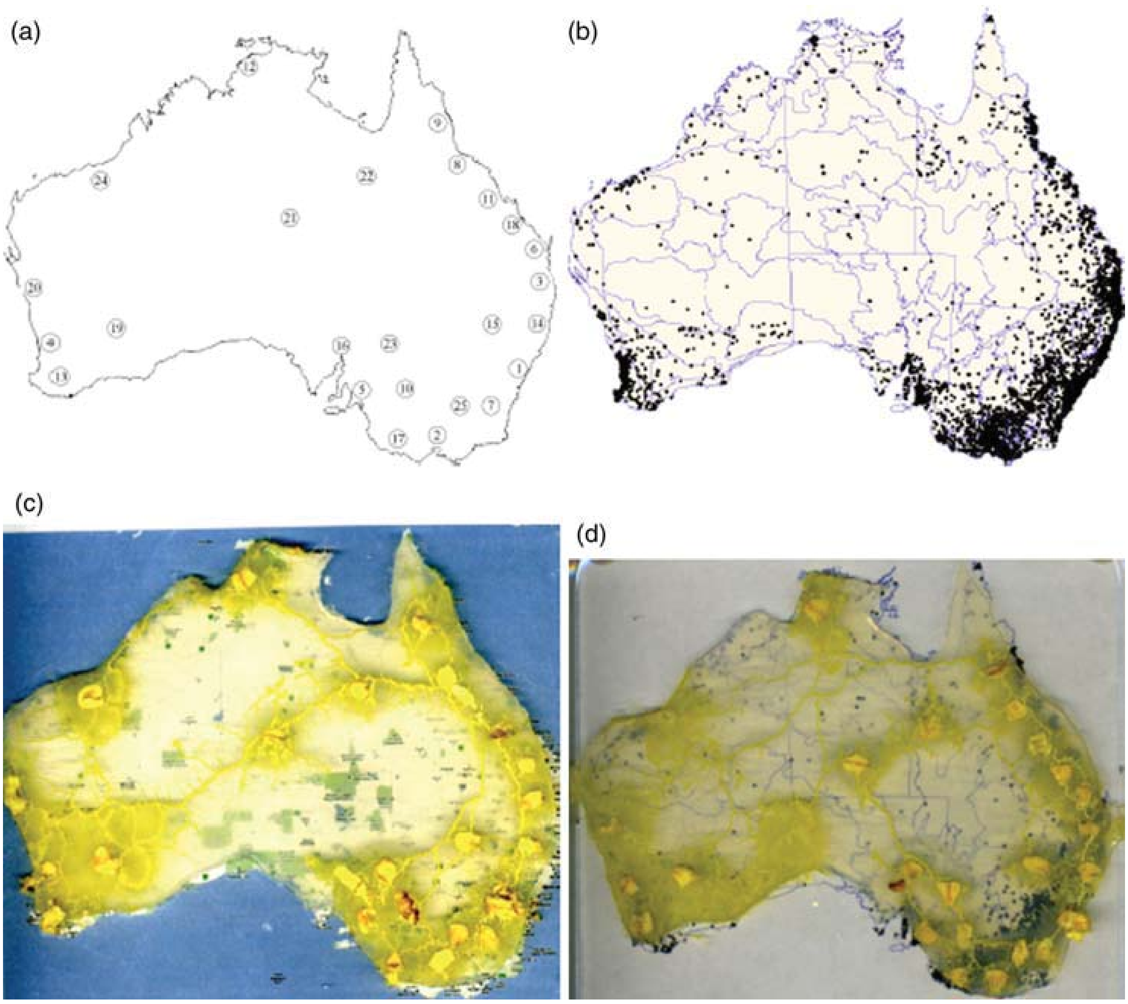

Figure 1. Experimental basics. (a) Contour map of Australia with 25 urban areas indicated. (b) Population density in 1997, from [21]. (c, d) Snapshot of a typical set-up: urban areas are represented by oat flakes, plasmodium is inoculated in Sydney, the plasmodium spans oat flakes by protoplasmic transport: (c) on map of Australia, (d) on population density map, from [21].

(8) Townsville–Thuringowa (Queensland);
(9) Cairns (Queensland);
(10) Mildura (Victoria);
(11) Mackay (Queensland);
(12) Darwin, Palmerston (Northern Territory);
(13) Bunbury, Albany (Western Australia);
(14) Port Macquarie, Lismore, Coffs Harbour (New South Wales);
(15) Dubbo, Tamworth (New South Wales);
(16) Port Augusta (South Australia);[2]
(17) Warrnambool (Victoria) and Mount Gambier (South Australia);
(18) Gladstone, Rockhampton (Queensland);
(19) Kalgoorlie–Boulder (Western Australia);
(20) Geraldton (Western Australia);
(21) Alice Springs;[2]
(22) Mount Isa, Cloncurry (Queensland);[2]
(23) Broken Hill (New South Wales);[2]
(24) South Hedland (Western Australia);[2]
(25) Albury–Wodonga (New South Wales/Victoria) and Wagga Wagga (New South Wales).

Our choice of urban areas provides an adequate sampling of population density distribution (Figure 1(b)). To project regions of **U** onto agar gel we place oat flakes in the positions of the regions of **U** (Figure 1(c),(d)). At the beginning of each experiment a piece of plasmodium, usually already attached to an oat flake, is placed in Sydney (region 1 in Figure 1(a)). The Petri dishes with plasmodium are kept in darkness at a temperature of 22–25°C, except for observation and image recording. We undertook 31 experiments. Periodically (usually in 12 or 24 h intervals) we scanned the dishes in Epson Perfection 4490.

3. Physarum transport networks

At the beginning of each experiment a piece of plasmodium, usually attached to an oat flake, is placed in the position of Sydney urban area. The plasmodium develops branching pseudo-podia, propagates on the agar gel towards neighbouring oat flakes, occupies them and connects them with protoplasmic networks. The exact way of the plasmodium exploration of its growth substrate and colonisation of urban area may differ from experiment to experiment. In some experiments, the plasmodium forms several active zones that propagate simultaneously and colonise urban areas in a concurrent manner, frequently even competing with each other. In example of concurrent colonisation as shown in Figure 2, in 8 h after inoculation in Sydney, the plasmodium propagates from Sydney to Port Macquarie area in the north and to Canberra–Queanbeyan in the south. By 31st hour since inoculation, the plasmodium forms branches from Canberra–Queanbeyan to South Hedland to Mildura and from Canberra–Queanbeyan to Melbourne to Warrnambool area. Plasmodium also connects Port Macquarie area with Dubbo–Tamworth area, and develops a transport chain from Port Macquarie area to Brisbane area to Bundaberg area to Townsville–Thuringowa area. In 50 h of experiment, the plasmodium connects Mildura and Adelaide, Adelaide and Port Augusta, Port Augusta and Broken Hill and Port Augusta to Alice Springs and Kalgoorlie–Boulder, and also establishes transport routes between Alice Springs and Kalgoorlie–Boulder on one side and Albury–Wodonga, South Hedland, Geraldton, Perth and Bunbury–Albany areas on the another side (see scheme of propagation in Figure 4(a)).

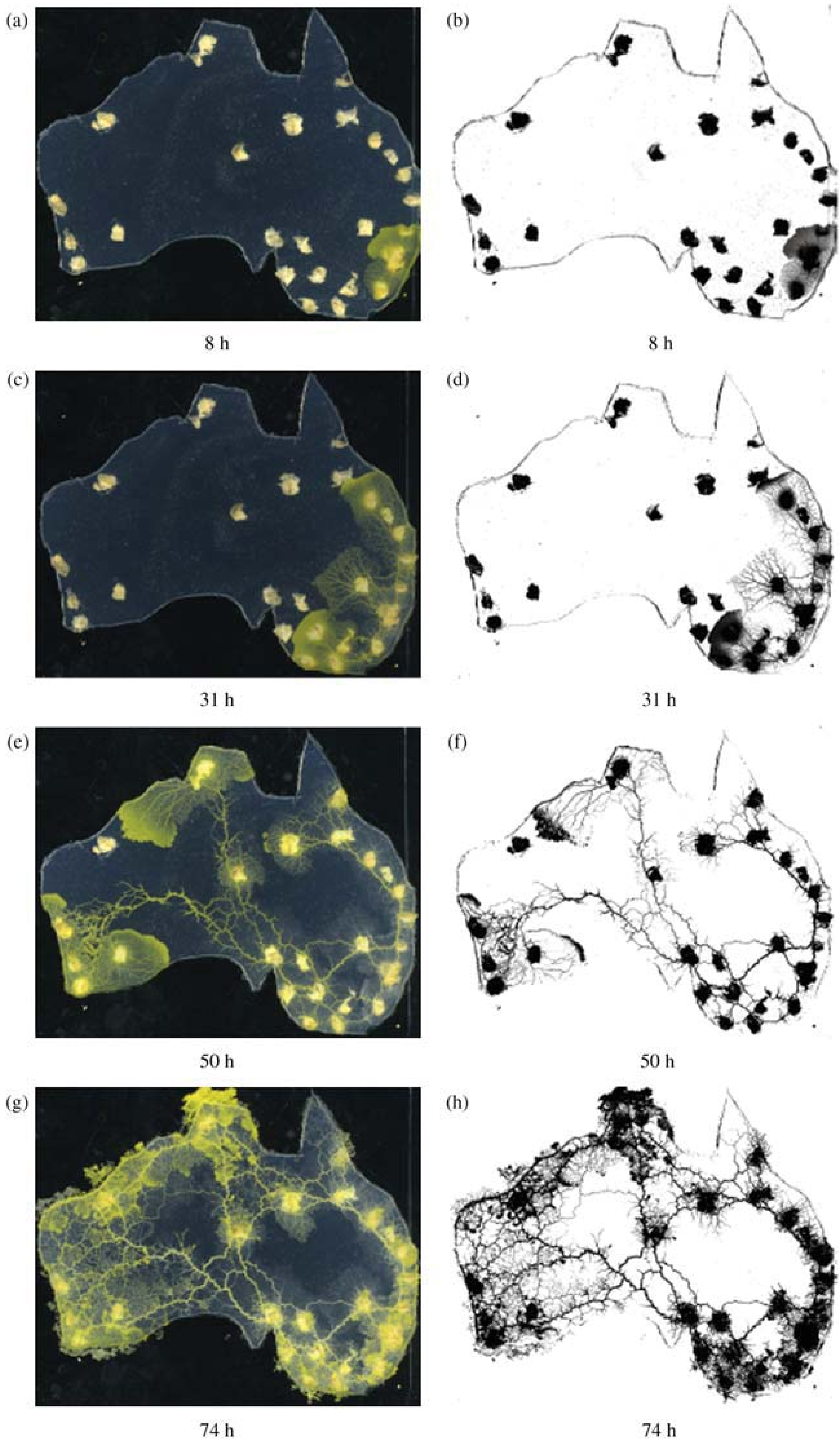

Figure 2. Images of plasmodium spanning urban areas **U** with its protoplasmic tubes, scenario of concurrent foraging. (a, c, e, g) colour images, (b, d, f, h) grey-scale-enhanced images.

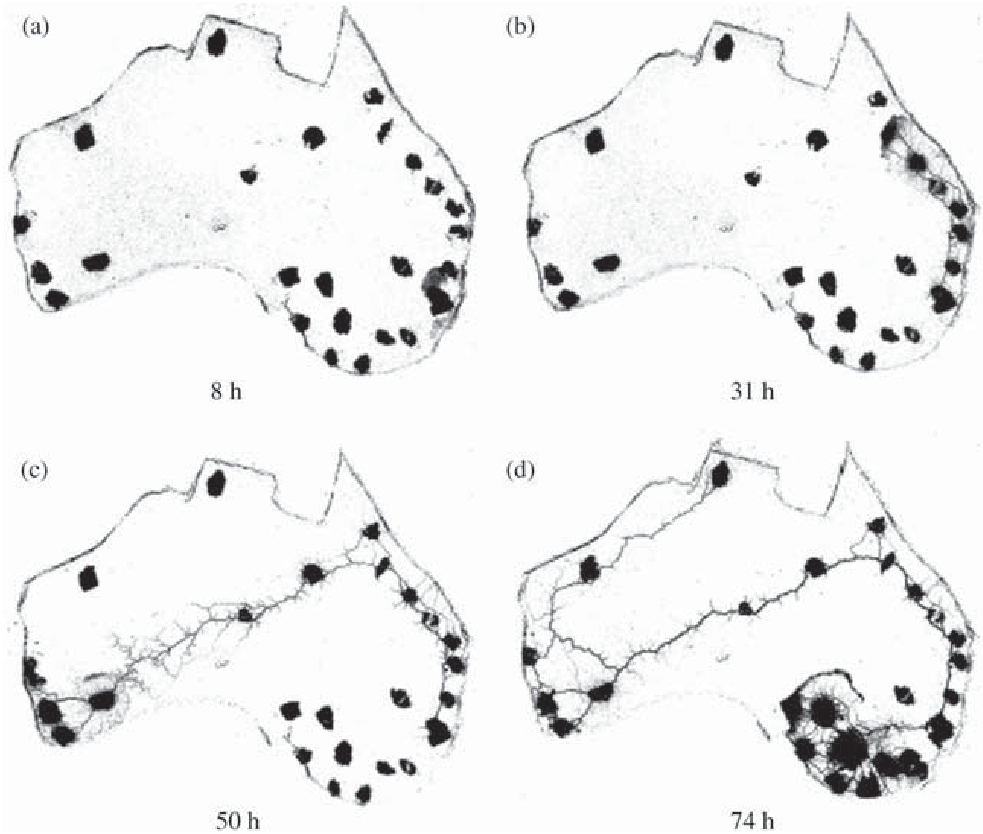

Figure 3. Images of plasmodium spanning urban areas **U** with its protoplasmic tubes, scenario of serial foraging; grey-scale-enhanced images.

Experiment shown in Figure 3 illustrates a rather sequential colonisation of urban zones by plasmodium. In first 8 h since inoculation in Sydney plasmodium builds a connection between Sydney and Perth areas. In next 23 h, plasmodium colonises urban areas along the West Coast from Perth–Rockingham–Mandurah to Townsville–Thuringowa (Figures 3(b) and 4(b)). Then plasmodium links Townsville–Thuringowa with Cairns and develops a chain: Mount Isa to Alice Springs to Kalgoorlie–Boulder. It then branches from Kalgoorlie–Boulder to Bunbury–Albany area and to Port Macquarie – Lismore – Coffs Harbour area (Figure 3(c)). At the last stages of colonisation, the plasmodium links Kalgoorlie–Boulder to Geraldton and Kalgoorlie–Boulder to South Hedland to Darwin–Palmerston area (Figures 3(d) and 4(b)).

To generalise our experimental results, we constructed a Physarum graph with weighted edges. Physarum graph is a tuple, $\mathbf{P} = \langle \mathbf{U}, \mathbf{E}, w \rangle$ where $\mathbf{U}$ is a set of urban areas, $\mathbf{E}$ is the set edges and $w : \mathbf{E} \to [0, 1]$ is the probability weights of edges from $\mathbf{E}$. For every two regions a and b from $\mathbf{U}$ there is an edge connecting a and b if a plasmodium's protoplasmic link is recorded at least in one of k experiments, and the edge (a, b) has a probability calculated as the ratio of experiments where protoplasmic link (a, b) occurred in the total number of experiments k. For example, if we observe protoplasmic tubes connecting cities a and b in 7 experiments, the weight of edge (a, b) will be $w(a, b) = \frac{7}{31}$. We do not take into account the exact configuration of the protoplasmic tubes but merely their existence. Furthermore, we will be dealing with threshold Physarum graphs $\mathbf{P}(\theta) = \langle \mathbf{U}, T(\mathbf{E}), w \rangle$. The threshold Physarum graph is modified from Physarum graph by the transformation: $T(\mathbf{E}) = \{e \in \mathbf{E} : w(e) > \theta\}$ that is all edges with weights less or equal to θ are removed. We call edge trimming the process of increasing θ.

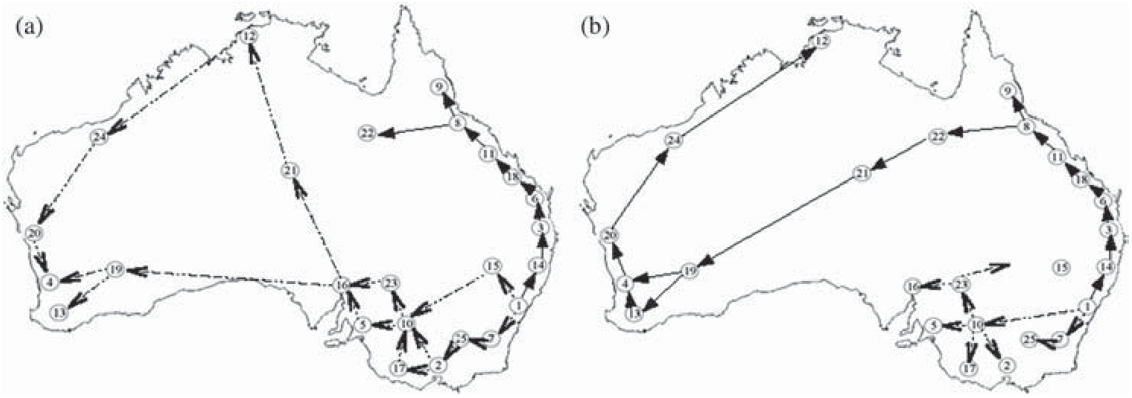

Figure 4. Schemes of plasmodium propagation extracted from (a) Figure 2 and (b) Figure 3.

Finding 1: Dubbo and Tamworth urban area is most sensitive to edge trimming node of a Physarum graph

When θ increases to $\frac{16}{30}$ the Dubbo–Tamworth urban area becomes isolated (Figure 5(b),(c)). In a raw Physarum graph $\mathbf{P}(0)$, this area has the highest degree of connectivity, yet a weight of each edge is small compared with the weights of edges connecting other nodes (Figure 5(a)). A possible explanation may be in Physarum strategy of foraging. Inoculated in Sydney urban area, the plasmodium more likely propagates along the East Coast towards Cairns. Oat flakes representing East Coast urban areas are so dense that slime mould often just spans this chain of areas without an attempt to branch towards Dubbo–Tamworth.

Finding 1 may be easily correlated with historical developments: when Sydney became the major centre, the transport routes were mostly developed along the East Coast. So it is not a surprise that oat flakes representing the dense East Coast urban areas attract the slime mould to span their chain without an attempt to branch towards Dubbo–Tamworth – Dubbo has developed into the cross-roads of New South Wales only as a result of the gold rush of the 1860s that brought an increase in north–south trade, becoming a city only in 1966; while Tamworth was reached by the railway only in 1878, becoming a city only in 1946.

Finding 2: Physarum graph is split into three components for $\theta = \frac{18}{31}$.

For $\theta = \frac{18}{31}$ three components are observed (Figure 5(e)). The first component is a tree T rooted at Alice Springs with three branches:

- Alice Springs – Mount Isa – Townsville–Thuringowa – Cairns,
- Alice Springs – Kalgoorlie–Boulder – Bunbury–Albany,
- Alice Springs – Darwin–Palmerston – South Hedland – Geraldton – Perth area.

The second component consists of a chain Mackay – Gladstone–Rockhampton – Bundaberg – Brisbane – Port Macquarie – Sydney – Canberra–Queanbeyan with two cycles attached: Albury–Wodonga – Melbourne – Warrnambool – Mildura and Mildura – Adelaide – Port Augusta – Broken Hill. The third component is an isolated node Dubbo–Tamworth. Here, we observe separation of Eastern Australia from the rest of the country.

When θ increases to $\frac{19}{31}$ the chain Darwin–Palmerston – South Hedland – Geraldton – Perth–Rockingham–Mandurah becomes disconnected from tree in the west (Figure 6(a)) but the eastern component remains unchanged.

Finding 2, we believe, is also well correlated with historical developments: the second component (the East coast) covers the area developed first of all (driven by

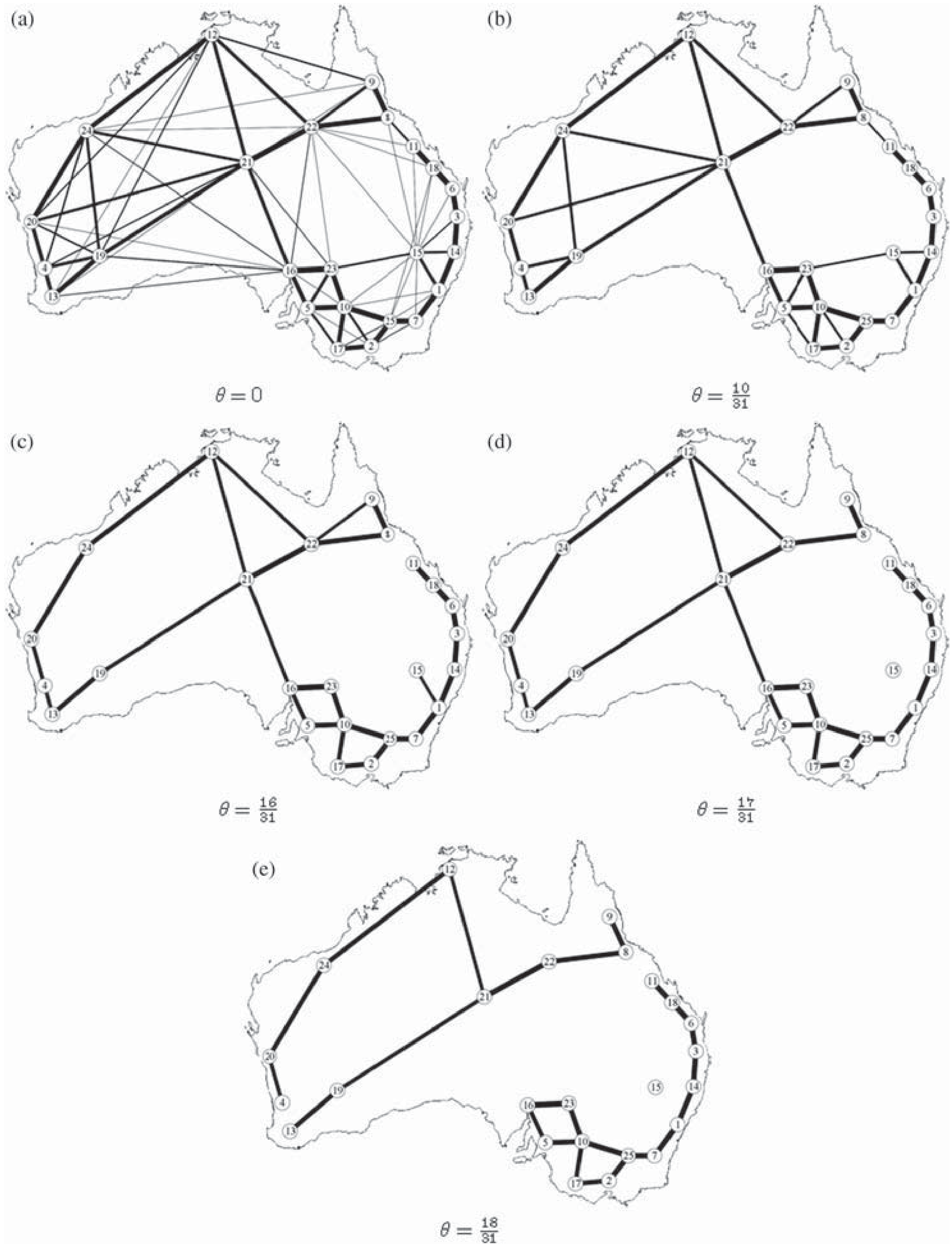

Figure 5. Configurations of Physarum graph $\mathbf{P}(\theta)$ for various cut off values of θ. Thickness of each edge is proportional to the edge's weight.

farming and mining in New South Wales, Victoria and South Australia), with the third component (Dubbo–Tamworth node) roughly corresponding to the gold rush networking, while the first component (the rest of the country) spans the area that has developed later in time, in response to mining booms during late nineteenth and twentieth centuries, utilising various mineral resources in Northern Territory and Western Australia.

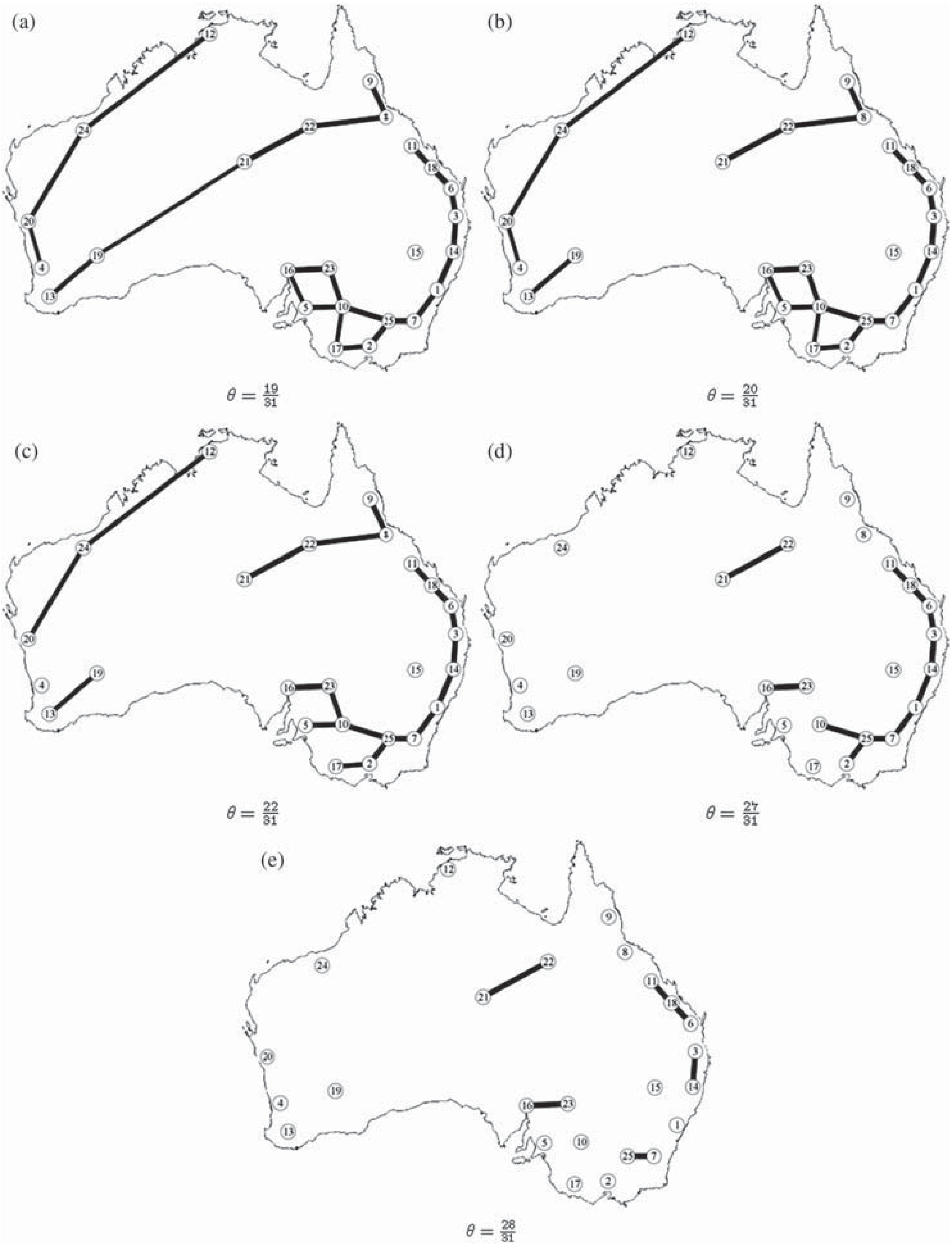

Figure 6. Configurations of Physarum graph $\mathbf{P}(\theta)$ for various cut off values of θ. Thickness of each edge is proportional to the edge's weight.

Finding 3: Physarum graph becomes acyclic only for $\theta = \frac{22}{31}$.

There are six components in the graph $\mathbf{P}(\frac{22}{31})$ (Figure 6(c)):

- Geraldton – South Hedland – Darwin–Palmerston;
- Bunbury–Albany – Kalgoorlie–Boulder;
- Cairns – Townsville–Thuringowa – Mount Isa – Alice Springs;

- Mackay – Gladstone–Rockhampton – Port Augusta – Brisbane – Port Macquarie — Sydney – Canberra–Queanbeyan – Albury–Wodonga with branches Albury–Wodonga – Melbourne – Warrnambool and a tree with branches Albury–Wodonga – Mildura – Adelaide and Albury–Wodonga – Mildura – Broken Hill – Port Augusta;
- two isolated nodes Perth–Rockingham–Mandurah and Dubbo–Tamworth.

At this stage, we point out that edge trimming may not only reveal historical parallels but also indicate somewhat weaker links in transport networks. Thus, Finding 3 may be interpreted as an indication that the features of the Australian city network make it fairly robust to disruptions. This is due to the dominance of coastal routes complemented by the tributaries and short-cuts; since these three features were reproduced by the slime mould, the resulting network becomes acyclic only when most of the tributaries and all the short-cuts are removed.

Finding 4: The most stable (often appearing) components of Physarum graph are two-node chains Alice Springs – Mount Isa and Port Augusta – Broken Hill and a chain Mackay –Gladstone-Rockhampton – Bundaberg – Brisbane – Port Macquarie – Sydney – Canberra–Queanbeyan – Albury–Wodonga with a fork (Mildura, Melbourne) attached to South Hedland.

These components are present in over 27 of 31 experiments (Figure 6(d)).

Again, Finding 4 indicates both the strongest and historically earlier component(s) – in this instance, Pacific Highway. The two-node chains (Alice Springs – Mount Isa, and Port Augusta – Broken Hill) are quite curious and point out that these links may be less dependent on the rest of the network than the first glance would suggest (also, Alice Springs and Broken Hill are the main interior-mainland centres).

4. Physarum graph vs. proximity graphs

A planar graph consists of nodes which are the points of Euclidean plane and edges which are the straight segments connecting the points. A planar proximity graph is a planar graph where the two points are connected by an edge if they are close in some sense. A pair of points is assigned certain neighbourhood, and points of the pair are connected by an edge if their neighbourhood is empty. Relative neighbourhood graph (RNG) [9], Gabriel graph (GG) [11], β-skeletons [10] and spanning tree (ST) are most known examples of proximity graphs. These graphs are defined as follows:

- RNG: Points a and b are connected by an edge in RNG if no other point c is closer to a and b than $\text{dist}(a,b)$ [19] (Figure 7(a)).
- GG: Points a and b are connected by an edge in GG if disc with diameter $\text{dist}(a,b)$ centred in middle of the segment ab is empty [8,11] (Figure 7(b)).
- BS(β): A β-skeleton, $\beta \geq 1$, is a planar proximity undirected graph of an Euclidean point set where the nodes are connected by an edge if their lune-based neighbourhood contains no other points of the given set; parameter β determines the size and shape of the nodes' neighbourhoods [10] (see examples in Figure 8).
- Minimal ST (MST): The Euclidean MST [12] is a connected acyclic graph which has minimal possible sum of edges' lengths (Figure 7(c)).

The graphs are related as MST $\subseteq$ RNG $\subseteq$ BS $\subseteq$ GG [9,11,19].

Finding 5: MST = RNG/{(Mount Isa – Alice Spring) + (Port Augusta – Broken Hill)}.

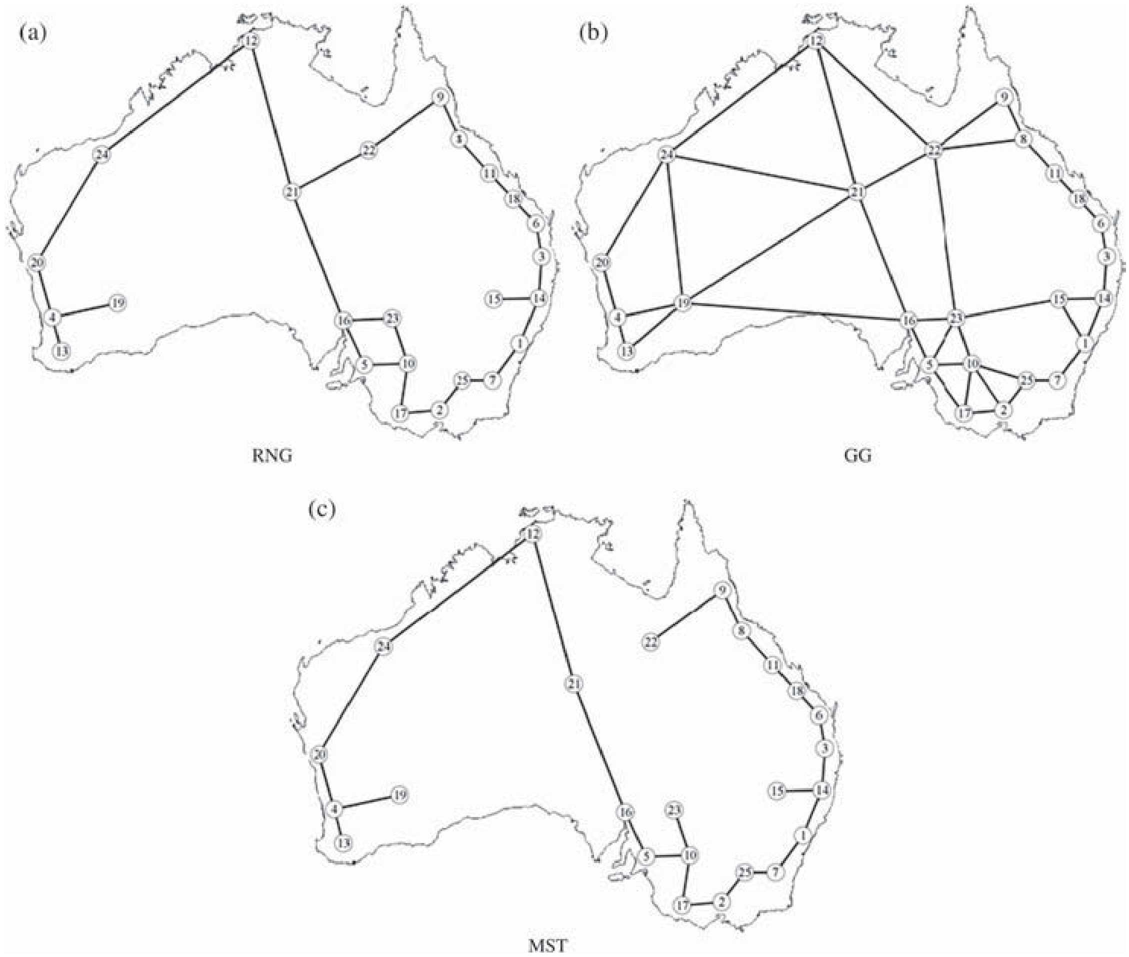

Figure 7. Proximity graphs constructed on urban areas **U**: (a) relative neighbourhood graph RNG, (b) Gabriel graph GG, (c) spanning tree ST rooted at Sydney.

Finding 5 indicates that configuration of urban areas allows for a very efficient spanning. Also, it is worth pointing out that the difference between MST and RNG is precisely the union of the two-node chains that were identified in Finding 4 as the most stable two-node chains. In other words, adding two stable routes to an efficient MST produces precisely the RNG where efficiency and stability are combined. These two-node

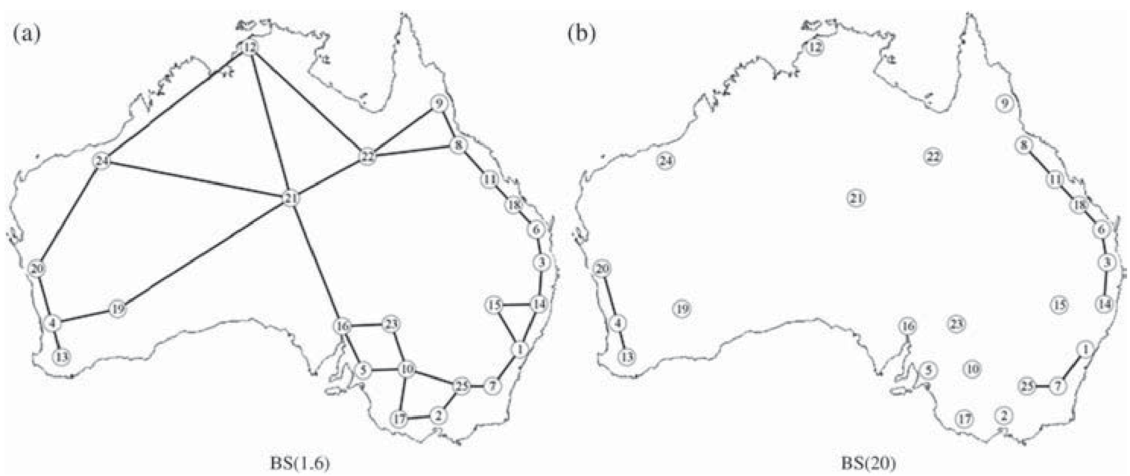

Figure 8. β-skeletons constructed on **U** for (a) $\beta = 1.6$ and (b) $\beta = 20$.

transport links may be seen as bridges between cyclicity and acyclicity of proximity graphs constructed on **U** (Figure 7(a),(c)).

Finding 6: $\mathbf{P}(\frac{10}{31}) = \mathrm{GG} +$ (Geraldton – Alice Spring).

See Figures 5(b) and 7(b).

Finding 6 presents a strong evidence that the graph constructed by the slime mould with limited edge trimming, $\mathbf{P}(\frac{10}{31})$, is almost identical to GG. To re-iterate, GG captures one notion of spatial proximity, connecting the points that are near to each other in a certain sense. That is, there are no links in GG which avoid a closer node. The fact that the limited edge trimming almost makes GG indicates that the slime mould is very parsimonious – the resulting graph has no unnecessary connections, with only close neighbours being connected.

Similar conclusions can be reached by analysing the following Finding 7.

Finding 7: BS(1.6) is closest to Physarum graphs β-skeleton.

To transform BS(1.6) to $\mathbf{P}(\frac{16}{31})$, we must do the following operations on $\mathbf{P}(\frac{16}{31})$ (Figures 5(c) and 8(a)):

- remove edges (Townsville–Thuringowa – Mackay), (Port Macquarie – Dubbo-Tamworth), (Perth – Kalgoorlie–Boulder);
- add edge (Bunbury–Albany – Kalgoorlie–Boulder)

There is no direct similarity between θ parameter of weighted Physarum graph and β parameter of β-skeletons apart from that both θ and β define 'continuous' family of graphs,where number of edges decreases with an increase in the parameter. Physarum graphs become a set of isolated nodes when β reaches 1. β-skeletons on **U** are never reduced to a set of isolated nodes because few edges survive for any high value of β. We call transport link $(a - b)$ stable if it survives for high values of θ and β.

Links (Alice Spring – Mount Isa), (Port Augusta – Broken Hill), (Canberra-Queanbeyan – Albury–Wodonga), (Brisbane – Bunbury–Albany), (Bundaberg – Gladstone–Rockhampton – Mackay) survive till $\theta = \frac{28}{31}$ (Figure 6). The link (Alice Spring – Mount Isa) also survives in β-skeleton till $\beta = 7.7$.

A comparison shows that the most stable links in β-skeletons are (Bunbury–Albany – Perth–Rockingham – Geraldton), (Sydney – Canberra–Queanbeyan – Albury–Wodonga), (Townsville–Thuringowa – Mackay – Gladstone–Rockhampton – Bundaberg – Brisbane – Port Macquarie). These links are presented in BS (Figure 8(b)).

5. Physarum vs. man-made network

We construct the motorway graph **H** as follows. Let **U** be a set of urban regions, for any two regions a and b from **U**, the nodes a and b are connected by an edge $(a - b)$ if there is a motorway starting in vicinity of a and passing in vicinity of b and not passing in vicinity of any other urban area $c \in \mathbf{U}$. A scheme of Australian motorway network is shown in Figure 9(a), and a graph **H** derived from the network is shown in Figure 9(b). Motorway graph **H** does not match the proximity graphs studied (Figure 9(c),(d),(e)): neither of the graphs is a sub-graph of **H**. This may give us the first indication that Australian motorway network is far from geometrical optimality.

Finding 8: Australian motorway graph **H** is most closed to Gabriel graph GG.

Namely, intersection of **H** and GG is with the following edges removed:

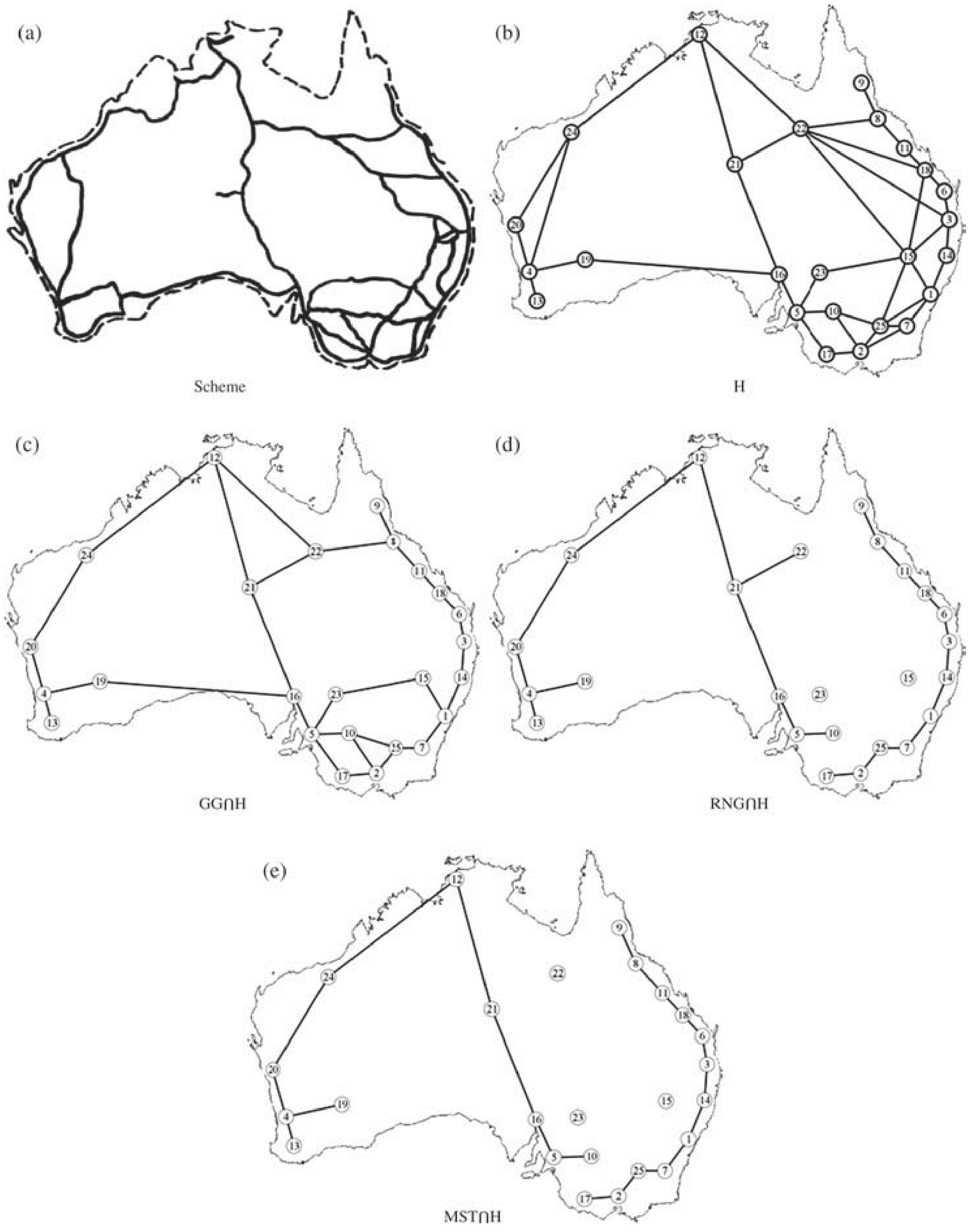

Figure 9. Structure of Australian motorways. (a) Scheme (adapted from [15]) and (b) graph **H** of man-made motorway network in Australia. (c, d, e) Intersection of **H** with GG (c), RNG (d) and ST rooted in Sydney (e).

- Perth–Rockingham – South Headland,
- Melbourne – Canberra–Queanbeyan,
- Albury–Wodonga – Bunbury–Albany,
- Dubbo–Tamworth – Mount Isa,
- Dubbo–Tamworth – Gladstone-Rockhampton,
- Dubbo–Tamworth – Brisbane,
- Gladstone–Rockhampton – Melbourne.

Dubbo–Tamworth urban area is linked to the highest number of ‘non-optimal’ edges.

The similarity between the motorway graph **H** and the Gabriel graph GG shows that the motorway connections are indeed very parsimonious, without unnecessary connections, and with only close neighbours connected. Hence, the Findings 6 and 7 do support the proposition that the graph built by the slime mould, with an appropriate limited edge trimming, is a good approximation for the motorway graph **H** (and Gabriel graph GG).

Finding 9: Intersection of **H** and MST consists of two connected components and three isolated nodes.

The connected components are eastern chain spanning urban area from Warrnambool and Mount Gambier in the south to Cairns in the north and a chain spanning Mildura in the south-east to Darwin-Palmerston in the north-west to Bunbury-Albany in the south-west. Three isolated urban areas: Dubbo-Tamworth, Mount Isa and Broken Hill (Figure 9(e)).

Finding 9 points to growing regional centres, Dubbo-Tamworth, Mount Isa and Broken Hill, as the areas around which transport links may have developed in a sub-optimal way. That is, locally optimal solutions may have been at odds with the global network optimum Australia-wide.

Finding 10: $\mathbf{P}(0) \cap \mathbf{H} = \mathbf{H}/(\text{Broken Hill} - \text{Brisbane})$.

That is, Australian motorway graph is almost a sub-graph of generalised Physarum graph. Intersection of motorway graph **H** with several Physarum graphs is shown in Figure 10. The offending link (Broken Hill – Brisbane) is actually the only edge contributing to non-planarity of **H**, so the link’s removal sounds reasonable. The graph $\mathbf{P}(0)$ includes all protoplasmic tubes ever occurred in experiments; thus, the fact that it almost includes **H** is encouraging but not exciting. Let us compare **H** with more trimmed Physarum graph $\mathbf{P}(\frac{10}{31})$, where only the edges recorded in over 30% of experiments are present.

Finding 11: $\mathbf{P}(\frac{10}{31}) \cap \mathbf{H} = \text{GG} \cap \mathbf{H}/(\text{Kalgoorlie–Boulder} - \text{Port Augusta})$.

Finding 12: The only parts of Australian motorway graph that is represented by Physarum protoplasmic tubes in almost all experiments are a transport link connecting Alice Springs and Mount Isa and Cloncurry, and an East Coast transport chain from Melbourne urban area in the south to Mackay area in the north.

This is illustrated in Figure 10(h). This finding infers that only the eastern part of Australian motorway network is substantiated by biological logic of *P. polycephalum*.

We believe that, analogous to Finding 2, these findings are mostly related to the historical developments of Australia: the East coast had been developed prior to an inception of the overall transport network coverage, while the rest of the country has developed later and in separate phases, in response to various events such as mining booms. One may argue that different levels of edge trimming correspond to the stages of the overall network development, with higher levels corresponding to earlier stages and lower levels corresponding to later stages.

6. Famine and large-scale contamination

Finding 13: In response to exhaustion of natural resources, or crop underproduction, the most active pattern of migration should be observed in north and north-west parts of the Western Australia.

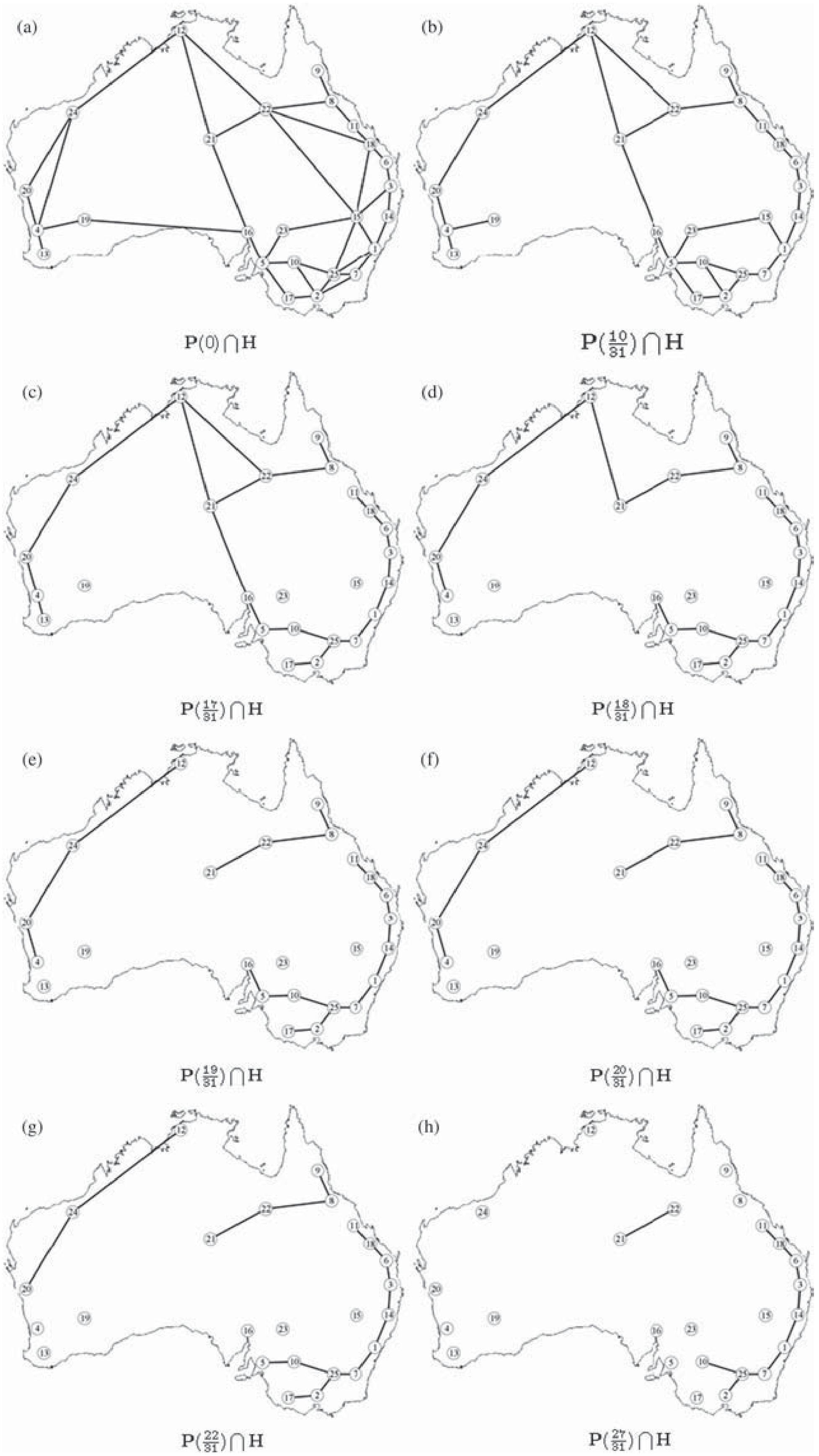

Figure 10. Intersection of Physarum graphs for various values of θ and motorway graph **H**.

To simulate a famine, we allow plasmodium to popular agar plate for over 5–6 days. By that time nutrients, or bacteria, in oat flakes are exhausted, humidity of substrate decreases and more likely concentration of metabolites excreted by the plasmodium significantly increases. Such living conditions become inappropriate for plasmodium and it starts abandoning its network of protoplasmic tubes (Figure 11) and attempts to explore new territories outside its agar plate. Typically, a plasmodium advances in north–north-west direction from South Hedland in the Western Australia. Other yet less frequent directions of emigration include Northward migration from Darwin area in Northern Territory and Rocky Point in Queensland, as well as south–west direction from Perth, Bunbury and Albany in Western Australia (Figure 11).

To imitate response of plasmodium protoplasmic network to a spatially extended contamination, we placed a crystal of sodium chloride site at the proposed Jervis Bay Nuclear Power Plant on the south coast of New South Wales (westward of urban area 7 in

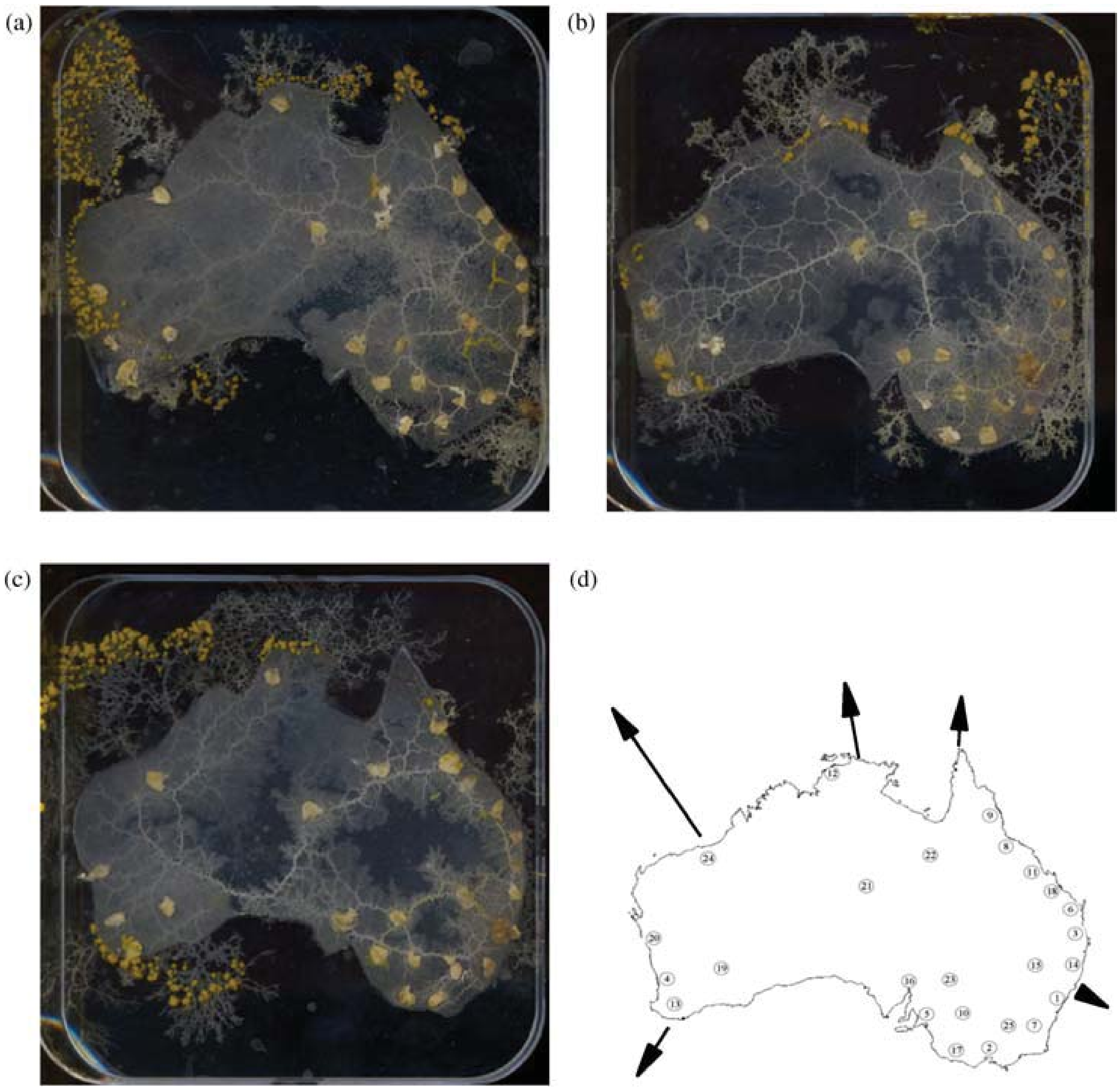

Figure 11. Plasmodium attempting to explore new territories outside its agar plate. (a–c) Images of three experiments recorded 5–6 days after inoculation of plasmodium. (d) A scheme of the plasmodium exodus, lengths of arrows are roughly proportional to the frequency of the directions used by the plasmodium. White/light-coloured protoplasmic network consists of abandoned protoplasmic tubes. Yellows/bright blobs on the Petri bare plastic bottom are parts of escaping plasmodium.

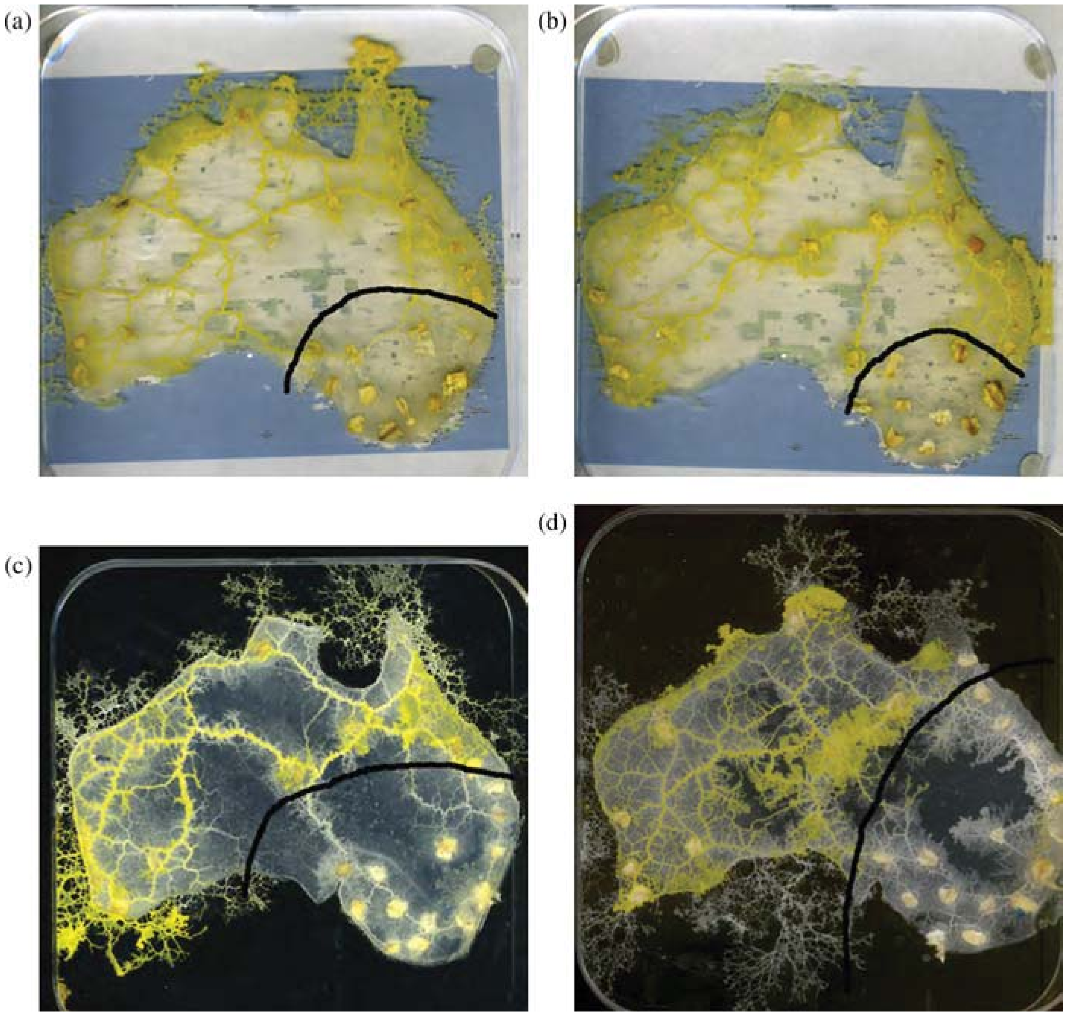

Figure 12. Images of plasmodium 20–26 h after a crystal of sodium chloride placed westward of Canberra. Extent of abandoned transport networks is marked by a line.

Figure 1). Sodium chloride diffusing in agar gel makes an unsuitable living condition for plasmodium. This causes plasmodium to migrate away (Figure 12), see scheme in Figure 13. Protoplasmic tubes residing in directly affected areas, where concentration of salt exceeds a level tolerable by plasmodium, become abandoned. They are visible as a white or discoloured network as shown in Figure 12. The area of abandoned transport links can be considered as an area of direct damage. In some of our experiments, the area of direct damage was as small as from the epicentre of contamination to Adelaide in South Australia, Broken Hill in New South Wales and Brisbane in Queensland. The largest area of direct damage observed propagated as far as Port Augusta in South Australia and Cairns in Queensland (Figure 12).

Finding 14: In response to a contamination propagating from a site of Jervis Bay Nuclear Power Plant, plasmodium.

- substantially increases capacity and traffic through transport links connecting Geraldton to Alice Springs to Mount Isa and Cloncurry;
- increases traffic in links (Geraldton, South Hedland), (Alice Springs, South Hedland), (Darwin – Palmerston, Mount Isa – Cloncurry);

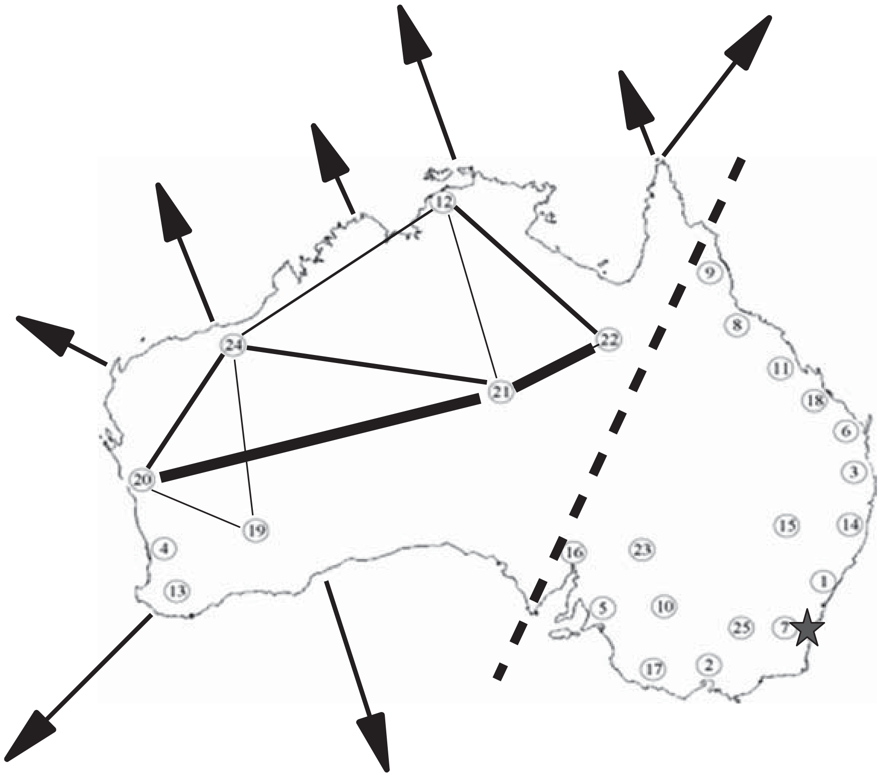

Figure 13. Scheme of plasmodium reaction on spreading contamination. Approximate location of contamination source is shown by star. Dotted line indicated maximum size of contaminated territory. Arrows show directions of attempted escape, length of arrow is proportional to intensity of escape efforts, visible as size of plasmodium sprouting. Transport links usually enhanced in response to contamination are shown by line segments, and thickness of segments is proportional to experimental observations.

- shows high level of attempted emigration south–south-west of Bunbury and Albany, south of Kalgoorlie–Boulder, north of Darwin and Palmerston, north–north-west of South Hedland and north–north-east of Bamaga and Lockhart River.

Transport links enhanced in the result of response to contamination and directions of emigration are shown in Figure 13. They summarise our analyses of 10 experiments on contamination.

It is important to realise that an increase in plasmodium's capacity corresponds to the need to increase transport capacity of the relevant transport links and to mitigate adverse ramifications of such unfortunate events. Some of the transport links may become completely overloaded, e.g. the west–northeast routes through the central interior of mainland Australia. This in turn can lead to further fragmentation of the overall network's connectivity, exacerbating the damage.

Indiscriminate sprouting of existing protoplasmic tubes is yet another interesting phenomenon observed in plasmodium networks dealing with a strain of contamination. In a normal condition, a protoplasmic tube usually connects few sources of nutrients, and branches only in few places, sometimes similar to the formation of Steiner points. When a substantial domain of a substrate becomes contaminated, major protoplasmic tubes form branches all over their bodies, as shown in Figure 14. Similar type of sprouting is recorded in plasmodium's response to physical damage, e.g. cutting, of its protoplasmic tubes [3].

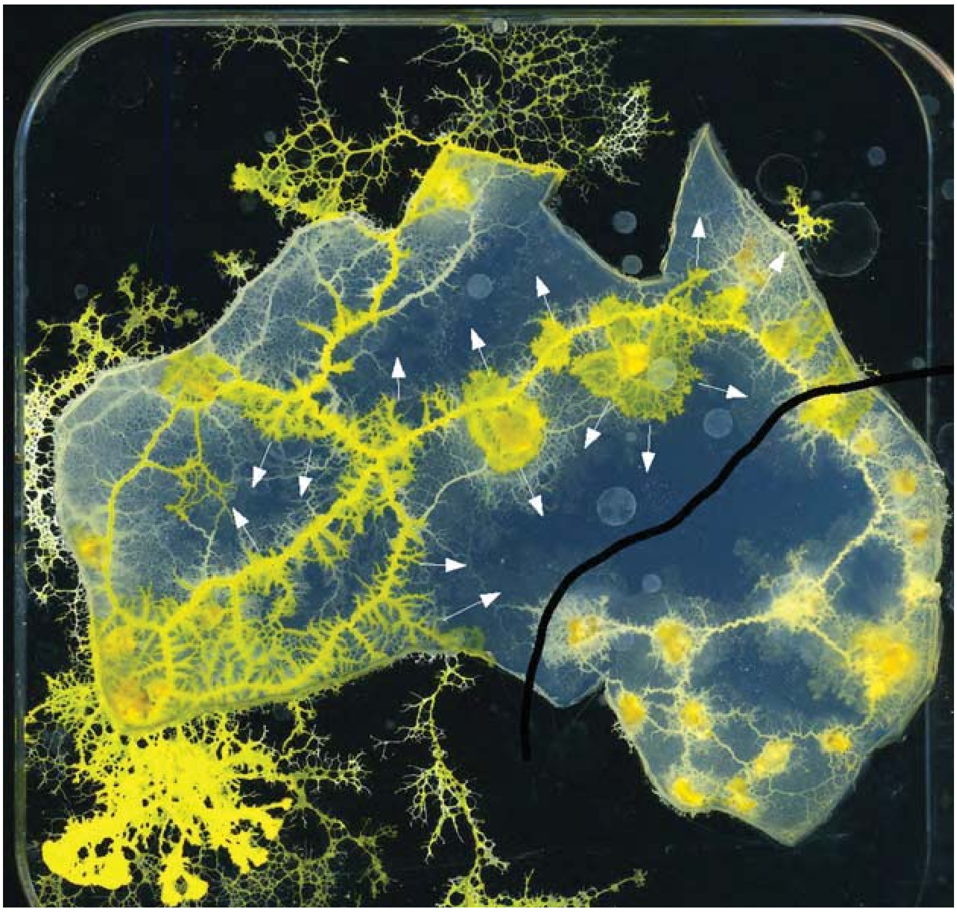

Figure 14. Example of sprouting in response to contamination. Region with abandoned transport networks is marked by thick black line. Directions of sprouting are shown by white arrows.

7. Discussion

We represented 25 major urban areas with oat flakes, positioned the flakes on an agar plate shaped in the form of Australia and inoculated plasmodium of *P. polycephalum* in Sydney. In a few days after inoculation, the plasmodium formed a network of protoplasmic tubes spanning the oat flakes. Structures of protoplasmic networks obtained in 31 experiments were converted to a weighted Physarum graph, where the weight of each edge was set to a frequency of corresponding protoplasmic tube's occurrence in laboratory experiment. We found that Physarum graph becomes planar when all edges with weight below $\frac{16}{31}$ are removed. Isolated urban areas, without transport links, appear in over 17 experiments. The Physarum graphs become disconnected when we remove all edges with weights less than $\frac{22}{31}$. Also, when comparing Physarum graphs with most common proximity graphs, we found that in over 70% of experiments slime mould's protoplasmic networks are almost identical to GG.

Physarum graph does not match existing motorway network of Australia. Only untrimmed Physarum graph $\mathbf{P}(0)$ is almost super-graph of Australian motorway graph $\mathbf{H}$. With regard to large-scale disasters, we found that in response to diminished resources increased migration is observed in north and north–west directions. In response to a contamination propagating from a site of Jervis Bay Nuclear Power Plant, plasmodium substantially increases capacity and traffic through transport links connecting Geraldton to Alice Springs to Mount Isa and Cloncurry and exhibits a high level of attempted emigration south–south-west of Bunbury and Albany, south of Kalgoorlie–Boulder, north of Darwin and Palmerston, north–north-west of South Hedland and north–north-east of Bamaga and Lockhart River.

Obviously, results presented in this paper are only indicative. By imitating Australia as a flat plate of agar, with geometrically approximated boundaries, we only discover very rough effects that spatial configurations of urban areas make on the formation of biological transport networks (possibly with some influence of boundary conditions). To make results more accurate, we must somehow imitate geo-physical gradients across the continent, by e.g. representing mountains and deserts with gradients of humidity and illumination. This could be a topic of our future studies.

Notes

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2. Included only for completeness.

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