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Are motorways rational from slime mould's point of view?

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We analyse the results of our experimental laboratory approximation of motorway networks with slime mould *Physarum polycephalum*. Motorway networks of 14 geographical areas are considered: Australia, Africa, Belgium, Brazil, Canada, China, Germany, Iberia, Italy, Malaysia, Mexico, the Netherlands, UK and USA. For each geographical entity, we represented major urban areas by oat flakes and inoculated the slime mould in a capital. After slime mould spanned all urban areas with a network of its protoplasmic tubes, we extracted a generalised Physarum graph from the network and compared the graphs with an abstract motorway graph using most common measures. The measures employed are the number of independent cycles, cohesion, shortest paths lengths, diameter, the Harary index and the Randić index. We obtained a series of intriguing results, and found that the slime mould approximates best of all the motorway graphs of Belgium, Canada and China, and that for all entities studied the best match between Physarum and motorway graphs is detected by the Randić index (molecular branching index).

Keywords: transport networks; motorways; slime mould; unconventional computing

1. Introduction

The increase of long-distance travel and subsequent reconfiguration of vehicular and social networks [32] requires novel and unconventional approaches towards analysis of dynamical processes in complex transport networks [15], routing and localisation of vehicular networks [39], optimisation of interactions between different parts of a transport network during scheduling of the road expansion and maintenance [49] and shaping of transport network structure [17]. 'The concept of a network is useful, but it may be misleading, because it gives the impression that it arises from a coherent planning process, whereas in practice almost all road networks have evolved gradually, being added to and altered over time to meet the ever-changing needs and demands of travellers. ⟨...⟩ even

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our more recently built network of roads, the motorways designated for exclusive use of motor vehicles, has been result of nearly a century of thinking and rethinking about what should be built' [21].

Modern motorway networks are based on the millennium-long emergence of roads. First, there were prehistoric trackways – mesolithic footways established by early men 'seeking most direct and convenient alternatives by process of trial and error' [16,21] or based on the routes selected by the animals [50], timber trackways and droveways (used primarily by cattle). Further development of roads was country specific. Talking about England we can speculate that Romans were building roads along pre-existing trackways and possibly along Ridgeways. In the 1700s, turnpikes were established. They were based on pre-existing roads with few local diversions [18]. The turnpikes were then substituted by single carriageways, dual carriageways and, finally, motorways [21]. Thus, backtracking the history of motorways we arrive to pathways developed by living creatures. How were the pathways developed? Were they efficient? More or less accurate answers could be found by imitating the road network development with living substrates.

While choosing a biological object to imitate the growth of road networks we want it to be experimental laboratory friendly, easy to cultivate and handle, and convenient to analyse. Ants would indeed be the first candidate. They do develop trails very similarly to prehistoric people. The great deal of impressive results has been published on ant-colony-inspired computing [22,45]. However, ant colonies require substantial laboratory resources, experience and time in handling them. Actually very few, if any, papers were published on experimental laboratory implementation of ant-based optimisation (also there is the issue of what happens if ant collide on the paths, or fight), the prevalent majority of publications being theoretical. There is however an object which is extremely easy to cultivate and handle, and which exhibits remarkably good foraging behaviour and development of intracellular transport networks. This is the plasmodium of *Physarum polycephalum*. Plasmodium is a vegetative stage of acellular slime mould *P. polycephalum*, a single cell with many nuclei, which feeds on microscopic particles [45]. When foraging for its food the plasmodium propagates towards sources of food particles and microbes, surrounds them, secretes enzymes and digests the food. Typically, the plasmodium forms a congregation of protoplasm covering the food source. When several sources of nutrients are scattered in the plasmodium's range, the plasmodium forms a network of protoplasmic tubes connecting the masses of protoplasm at the food sources. A structure of the protoplasmic networks is apparently optimal, in a sense that it covers all sources of nutrients and provides a robust and speedy transportation of nutrients and metabolites in the plasmodium's body [35–37].

Motorway networks are designed for efficient vehicular transportation of goods and passengers, protoplasmic networks are developed for efficient intracellular transportation of nutrients and metabolites. Is there a similarity between these two networks?

To uncover analogies between biological and human-made transport networks and to project behavioural traits of biological networks onto development of vehicular transport networks, we conducted a series of experimental laboratory studies on evaluation and approximation of motorway networks by *P. polycephalum* in 14 geographical regions: Africa, Australia, Belgium, Brazil, Canada, China, Germany, Iberia, Italy, Malaysia, Mexico, the Netherlands, UK and USA [2–14,47]. We represented each region with an agar plate, imitated major urban areas with oat flakes, inoculated plasmodium of *P. polycephalum* in a capital and analysed structures of protoplasmic networks developed. For all regions studied in laboratory experiments [2–14,47], we found that the network of protoplasmic tubes grown by plasmodium matches, at least partly, the network of human-made transport arteries. The shape of a country and the exact spatial distribution of urban areas, represented by sources of nutrients, may play a key role in determining the exact structure of the plasmodium network. In this study, we aim to answer two principal questions. What measures, apart from straightforward comparison of edges between motorway and plasmodium networks, are reliable indicators of matching? Which regions have the most 'Physarum friendly' motorway networks, i.e. show highest degree of matching between motorways and protoplasmic networks along several measures? In the course of investigation, we got the answers to these questions and also obtained a few quite intriguing results on hierarchies of motorway and protoplasmic networks based on measures and topological indices.

2. Experimental

In laboratory experiments [2–14,47], we considered 14 regions: Australia, Africa, Belgium, Brazil, Canada, China, Germany, Iberia, Italy, Malaysia, Mexico, the Netherlands, UK and USA. Agar plates, 2% agar gel (Select agar, Sigma Aldrich, http://www.sigmaaldrich.com/united-kingdom.html), were cut in a shape of any particular region and placed in polystyrene square Petri dishes 120 mm × 120 mm or 220 mm × 220 mm. For each region we chose the most populated urban areas **U** scaled down locations of which were projected onto agar gel. Numbers of the areas selected for each country are as follows: Africa $n = 35$, Australia $n = 25$, Belgium $n = 21$, Brazil $n = 21$, Canada $n = 16$, China $n = 31$, Germany $n = 21$, Iberia $n = 23$, Italy $n = 11$, Malaysia $n = 20$, Mexico $n = 19$, the Netherlands $n = 21$, UK $n = 10$ and USA $n = 20$, see detailed configurations in Refs [2–14,47].

At the beginning of each experiment a piece of plasmodium, usually already attached to an oat flake, is placed in the capital city. The Petri dishes with plasmodium were kept in darkness, at temperature 22–25°C, except for observation and image recording (Figure 1). Periodically (usually in 12 or 24 h intervals), the dishes were scanned in Epson Perfection 4490. Examples of typical protoplasmic networks recorded in laboratory experiments are

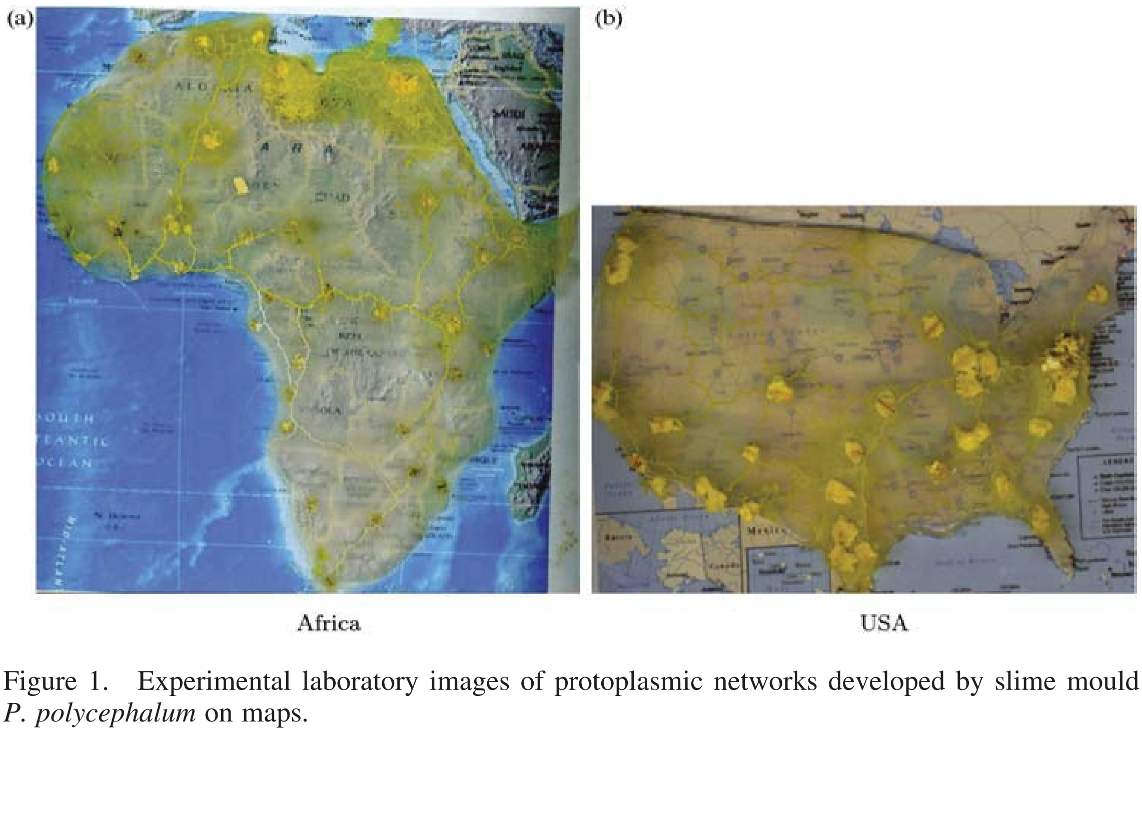

Figure 1. Experimental laboratory images of protoplasmic networks developed by slime mould *P. polycephalum* on maps.

shown in Figure 2. Detailed examples and scenarios of colonisation of various regions by the slime mould are provided in original papers [2–14,47].

In our experiments, we always inoculated plasmodium of *P. polycephalum* in a capital of any particular country. This is because in the majority of cases – but not in all cases indeed – capitals are the most populated and industrially developed urban areas, and the road 'diffusion' in ancient times was usually originated from the capital city. For example, see a rough scheme of turnpikes in England (Figure 3(a)), which demonstrates a classical growth pattern, typical for fungi, myxomycetes and bacterial colonies. Moreover, we can even see evidence of secondary growth from other cities, e.g. in Figure 3(b) we see the main turnpike network growing from London and several sub-networks growing from Bristol, Ross, Leominster, Worcester and Manchester.

Unlike bacterial colonies and fungal mycelia, the Physarum plasmodium is able to shift the mass of its body plan by the adaptive assembly and disassembly of its protoplasmic tube network and utilise the transport of structural components within the network to the leading edge of growth. The morphology of the plasmodium is thus less dependent on the initial inoculation site and the active zone of growth can move throughout the environment as the plasmodium forages for food.

Also, from our previous experimental studies we know that when plasmodium is inoculated in every point of a given planar set, the protoplasmic network formed approximates the Delaunay triangulation of the set [1,44]. Neither of the motorway networks considered match the Delaunay triangulation of major urban areas, thus simultaneous inoculation in all urban areas would not bring any additional benefits.

As with every living creature, the plasmodium of *P. polycephalum* does not always repeat its foraging pattern. To generalise our experimental results, we constructed a Physarum graph with weighted edges. A Physarum graph is a tuple $\mathbf{P} = \langle \mathbf{U}, \mathbf{E}, w \rangle$, where $\mathbf{U}$ is the set of urban areas, $\mathbf{E}$ is the set edges and $w : \mathbf{E} \rightarrow [0, 1]$ associates each edge of $\mathbf{E}$ with a frequency (or weight) of the edge occurrence in laboratory experiments. 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 weight calculated as a ratio of experiments where protoplasmic link (a, b) occurred in the total number of experiments k. We do not take into account the exact configuration of the protoplasmic tubes but merely their existence. In original papers [2–14,47], we dealt with threshold Physarum graphs $\mathbf{P}(\theta) = \langle \mathbf{U}, T(\mathbf{E}), w, \theta \rangle$. The threshold Physarum graph is obtained from the Physarum graph by the transformation: $T(\mathbf{E}) = \{e \in \mathbf{E} : w(e) > \theta\}$. That is, all edges with weights $\leq \theta$ are removed. With the increase of θ in a family of threshold Physarum graphs $\{\mathbf{P}(\theta), \theta = 0, 1, 2, \ldots, k-1\}$, the graphs undergo the following transitions (see country-specific details in Refs [2–14,47]): non-planar connected $\rightarrow$ planar connected $\rightarrow$ disconnected $\rightarrow$ all nodes are isolated.

In this study, we consider only 'stressed' Physarum graphs $\mathbf{P}(\theta')$, which have maximum possible values θ' and yet remain connected: $\theta' = \max\{\theta : \mathbf{P}(\theta) = \text{connected}\}$. These Physarum graphs are shown in Figure 4. Values of θ' for studied regions are illustrated in Figure 6(a).

To compare the Physarum graphs with motorway graphs, we construct a motorway graph $\mathbf{H}$ as follows. Let $\mathbf{U}$ be a set of urban regions, for any two regions a and b from $\mathbf{U}$, the nodes a and b are connected by an edge (a, b) if there is a motorway starting in a and passing in the vicinity of b and not passing in the vicinity of any other urban area $c \in \mathbf{U}$. Motorway graphs extracted from maps of motorway/highway/expressway/autobahn networks are shown in Figure 5.

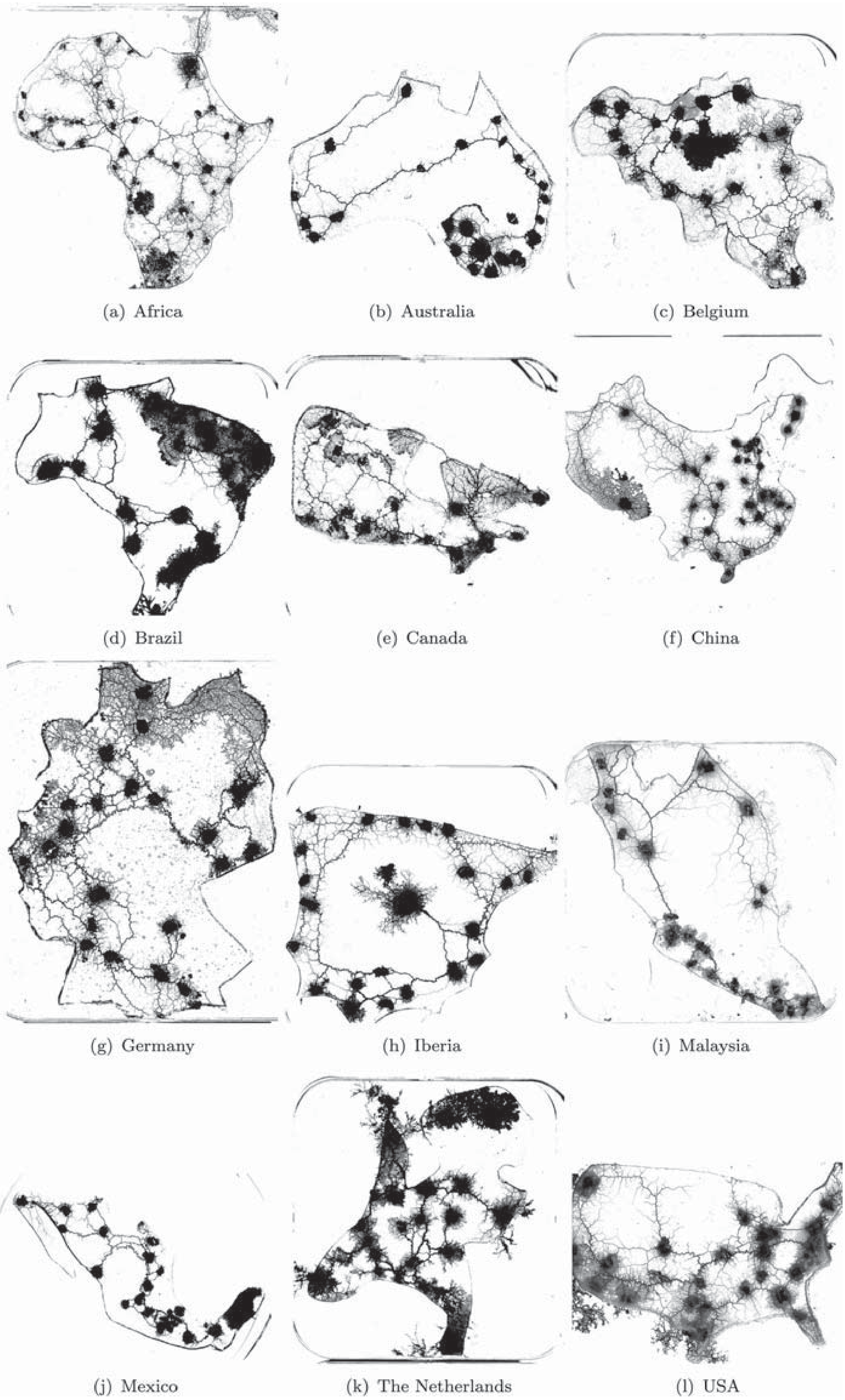

Figure 2. Exemplar configurations of protoplasmic networks developed by slime mould *P. polycephalum* on major urban areas **U** obtained in experimental laboratory studies.

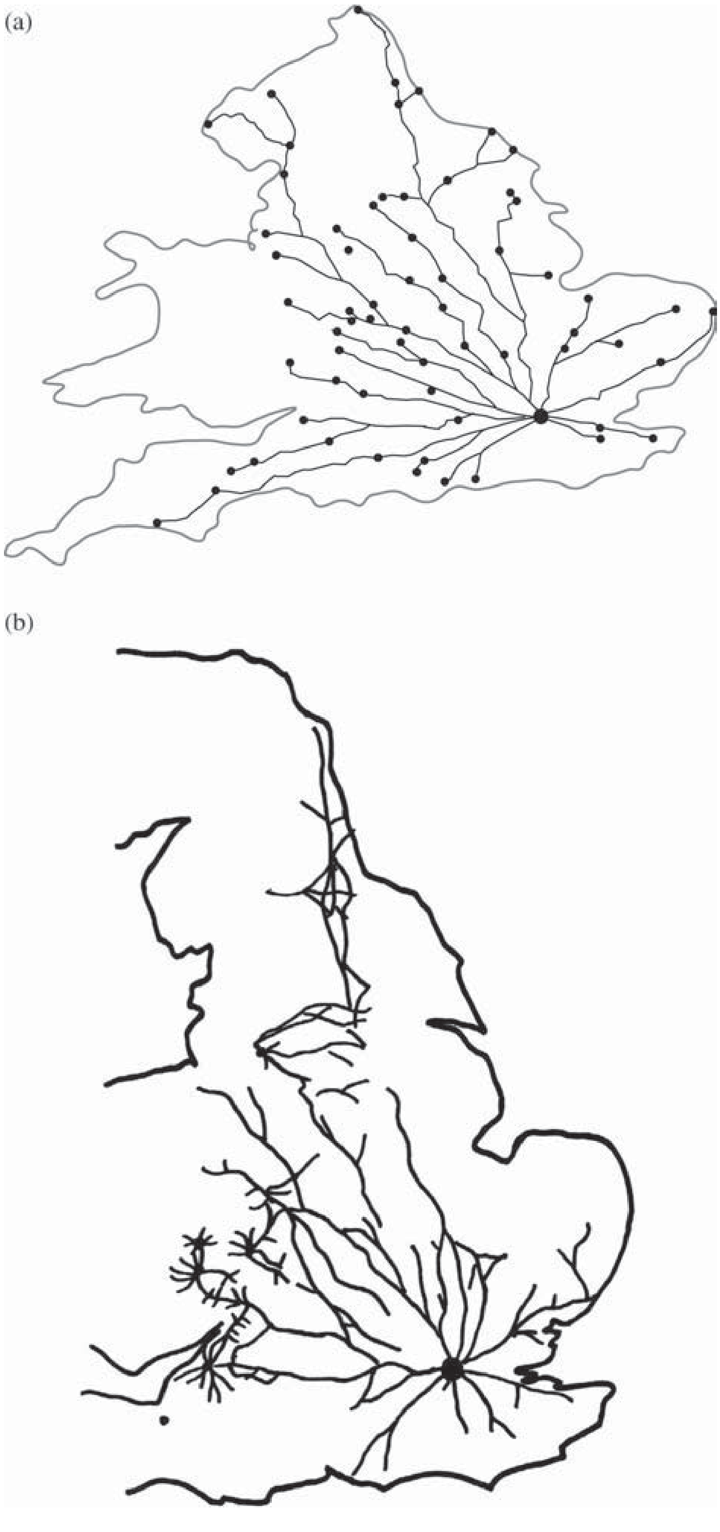

Figure 3. Turnpike road network. (a) A scheme of London turnpike network in England, c. 1720. Modified from Ref. [18]. (b) A scheme of the England turnpike network in 1750. Modified from Ref. [21].

Motorway and Physarum graphs were compared directly and using integral measures and indices. Let m be a number of edges in motorway graph $\mathbf{H}$, and f be the number of edges in Physarum graph $\mathbf{P}$, i and j be nodes and M and F be the adjacency matrices. Direct matching between motorway and Physarum graphs is calculated as

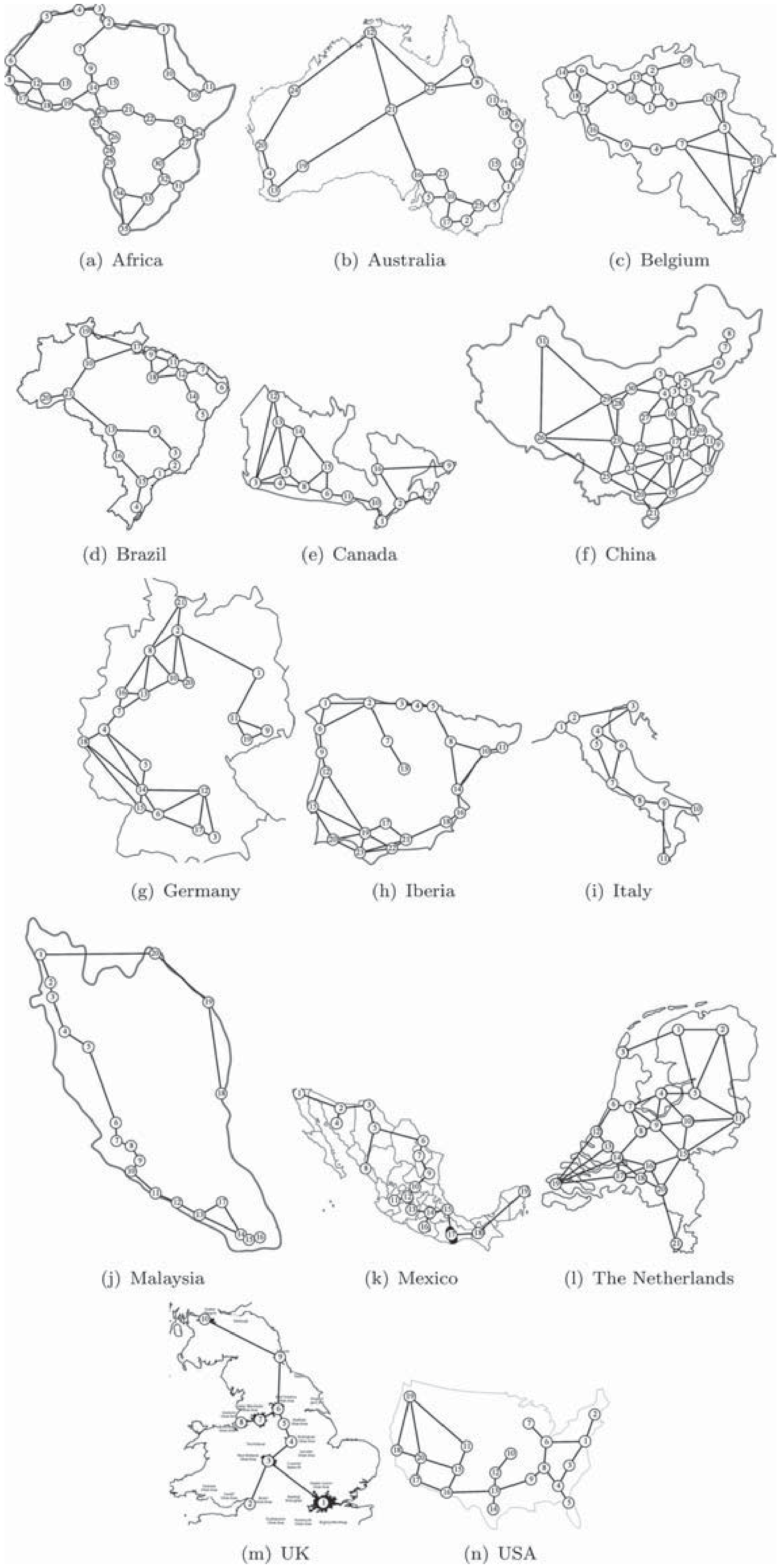

Figure 4. Physarum graphs $\mathbf{P}(\theta')$ for highest values of θ which do not make the graphs disconnected.

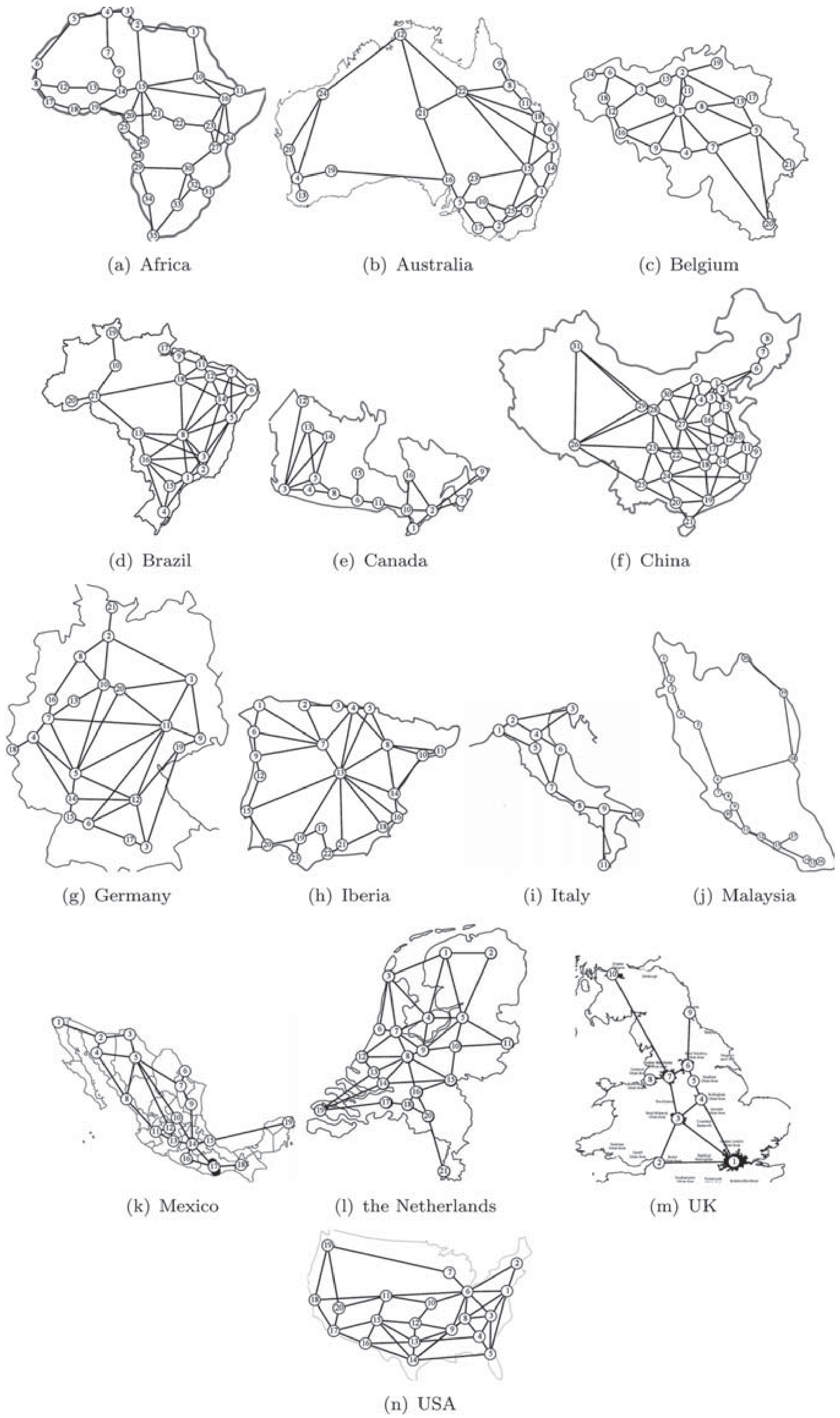

Figure 5. Motorway graphs **H**.

$\mu = 1/m\sum_{ij}\xi(M_{ij}, F_{ij})$, where $\xi(M_{ij}, F_{ij}) = 1$ if $M_{ij} = F_{ij}$, and 0, otherwise. An economy of matching is calculated as $\epsilon = \mu/f$. Also, we compared the graphs by their average shortest path measured in nodes, average shortest path measured in normalised edge lengths [for each edge $e \in \mathbf{E}$, we normalised its Euclidean length $l(e)$ as $l(e) \leftarrow l(e)/\max\{l(e') : e' \in \mathbf{E}\}$, average degrees (sum of degrees of nodes divided by a number of nodes), average edge length (of normalised edges), diameters (longest shortest path) in nodes and normalised edge lengths and maximum number of vertex-independent cycles (two cycles are independent of each other if they do not share nodes or edges).

To measure 'compactness' of graphs, we calculated average cohesion: let ν_{ij} be a number of common neighbours of nodes i and j, and d_i is the degree of node i, then cohesion κ_{ij} between nodes i and j is calculated as $\kappa_{ij} = \nu_{ij}/(d_i + d_j)$. Three topological indices were calculated: Harary index [38], Π-index [23] and Randić index [40].

The Harary index is calculated as follows: $H = 1/2\sum_{ij}\chi(D_{ij})$, where D is the graph distance matrix, D_{ij} is the length of a shortest path (in normalised edge lengths) between i and j and $\chi(D_{ij}) = D_{ij}^{-1}$ if $i \neq j$ and 0, otherwise. The Π-index shows a relationship between the total length of the graph $L(\mathbf{G})$ and the distance along its diameter $D(d)$ [23]: $\Pi = L(G)/D(d)$. The Randić index [40] is calculated as $R = \sum_{ij} C_{ij} \times (1/\sqrt{(d_i \times d_j)})$, where C_{ij} is an adjacency matrix, $C = M$ or $C = F$.

3. Results

3.1 Matching and economy

Top three regions in the best matches μ between motorway and Physarum graphs are Malaysia, Italy and Canada and top three most economically ϵ matched are Italy, Brazil and UK (Figure 6(b)).

Finding 1. Let $C_1 \lhd C_2$ if $\mu(C_1) < \mu(C_2)$, then regions can be arranged in the following hierarchy of absolute Physarum matching: USA ◁ Brazil ◁ {Mexico, Iberia} ◁ Australia ◁ {Germany, UK} ◁ {Africa, the Netherlands } ◁ {China, Belgium } ◁ Canada ◁ Italy ◁ Malaysia.

We can consider a product of matching to economy $\omega = \mu \cdot \epsilon$ as a rough parameter for estimating 'slime-optimality' of motorways approximation. By values of ω regions can be arranged in the descending slime-optimality as follows (exact values of ω are in brackets):

(1) Italy (0.85),
(2) Malaysia (0.76),
(3) Canada (0.67), China (0.65), Belgium (0.6), Africa (0.6) and UK (0.59),
(4) the Netherlands (0.49), Germany (0.48), Australia (0.47), Brazil (0.44), Mexico (0.42) and USA (0.4),
(5) Iberia (0.34).

3.2 Average degrees

Averages degrees of motorway graphs are usually lower than degrees of the corresponding Physarum graphs (Figure 7(a)). This is particularly visible with USA and Brazil motorway graphs, which average degrees are nearly 4.5 while Physarum graphs approximating the motorways have twice less average degree. Belgium, Canada and Malaysia show almost perfect match between Physarum and motorway graphs in average degrees (Figure 7(a)).

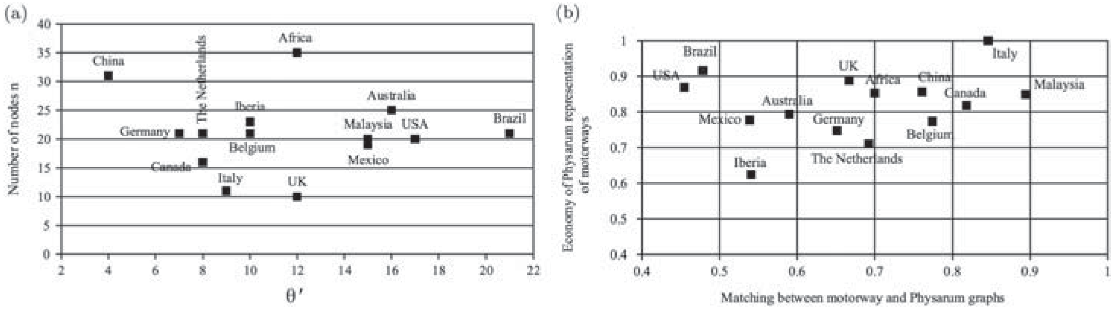

Figure 6. (a) θ' versus number of nodes and (b) matching μ versus economy ϵ.

3.3 *Maximum number of independent cycles*

Motorway and Physarum graphs of China, the Netherlands, Canada and Italy have the maximum number of independent cycles (Figure 7(b)) and show a good match. Other regions can be subdivided into two groups:

- The number of independent cycles is higher in motorway graphs: Africa, Australia, Brazil, Mexico, UK and USA.
- The number of independent cycles is higher in Physarum graphs: Belgium, Berlin, Canada, Germany, Iberia and Malaysia.

The maximum number of independent cycles may characterise the two properties of transport networks: fault-tolerance (more cycles indicate more chances for a transported objects to avoid faulty impassable links, sites of accidents and jams) and locality (distant links increase chances of two cycles of sharing a node). Thus, we can propose that China motorway network is most fault-tolerant and locally connected, while transport networks in Canada, Italy, Malaysia and UK could be sensitive to disasters and overloads.

3.4 *Average edge length*

The closest match between Physarum and motorway graphs in average edge length is observed for Italy, Iberia, Germany, Mexico, Canada and Malaysia (Figure 7(c)). The highest mismatch is shown by the Netherlands (edges of motorway graph are longer than edges of Physarum graph) and Brazil, Africa and USA (edges of Physarum are longer, in average, than of motorway graphs).

3.5 *Average shortest paths*

The average length of a shortest path between nodes shows little match between Physarum and motorway graphs (Figure 7(d),(e)). Usually Physarum graphs exhibit 1.5–2 times longer average shortest paths, this varies however between regions. Malaysia and Africa are the regions with longest average shortest paths, measured in nodes, in motorway and Physarum graphs (Figure 7(d)). When shortest paths are measured in normalised edge length, Africa and Brazil have longest average shortest paths in Physarum graphs, and Malaysia and Italy in motorways graphs. Countries which show closest match between Physarum and motorway graphs – in average shortest path, measured in nodes

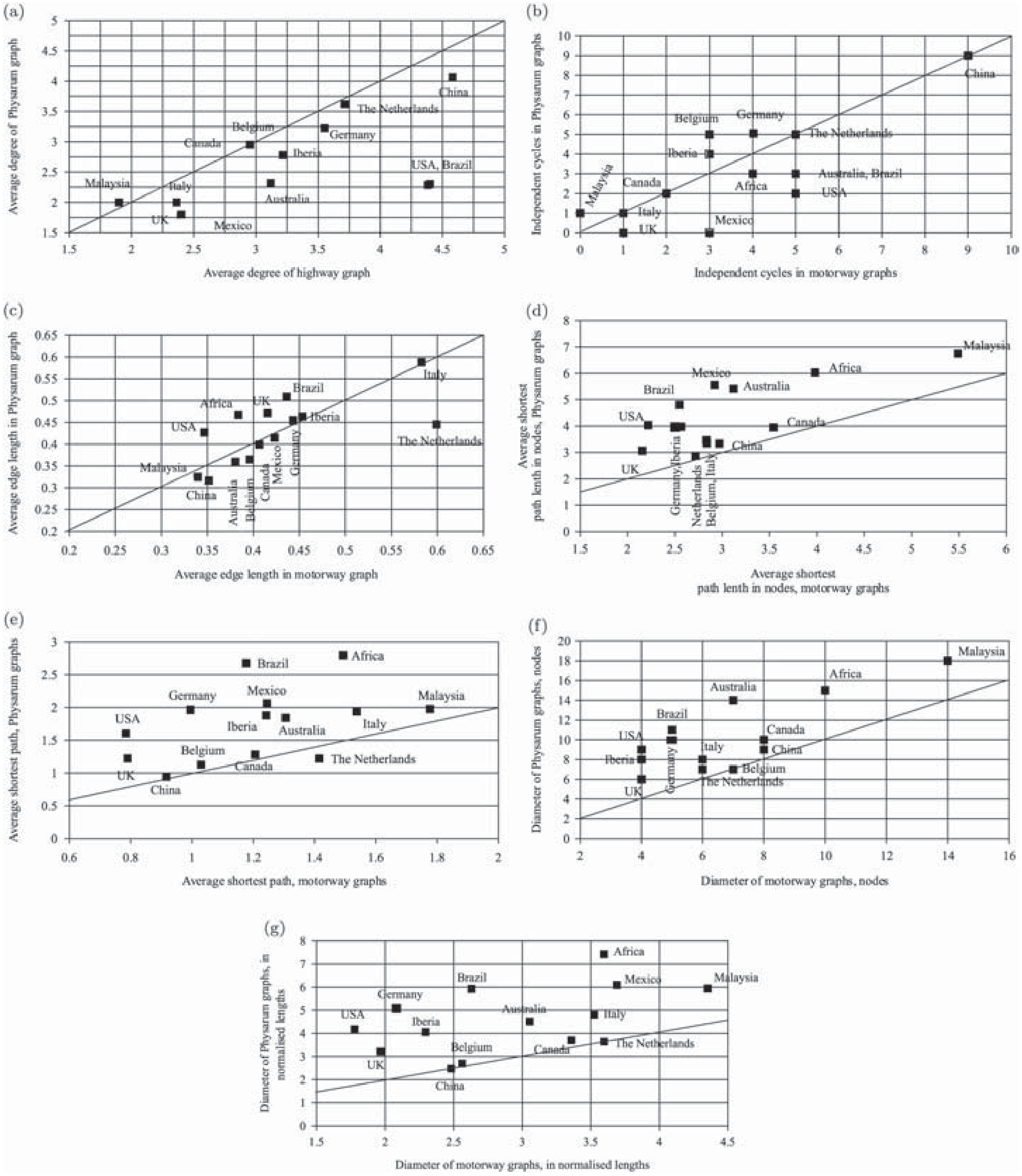

Figure 7. (a) Average degrees, (b) maximum number of vertex-independent cycles, (c) average edge link, (d) average length of a shortest path in nodes, (e) average length of a shortest path in real values, (f) diameter in nodes and (g) diameter in real values.

(Figure 7(d)) – are Canada, China and the Netherlands and – in average shortest path, measured in normalised lengths (Figure 7(e)) – are Belgium, Canada and China.

3.6 Diameters

Being the longest shortest path, the diameter shows even less matching between Physarum and motorway graphs (Figure 7(f),(g)) than average shortest path matching. Physarum graphs match motorways in diameter measured in nodes for Belgium, and in diameter measured in normalised lengths for Belgium, China and the Netherlands.

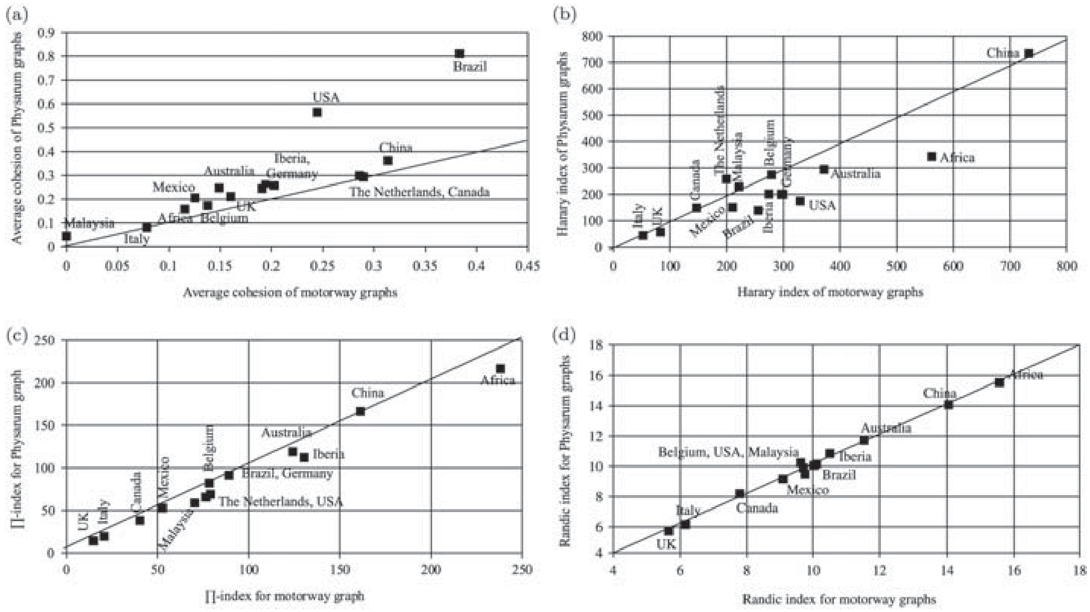

Figure 8. (a) Average cohesion, (b) the Harary index, (c) the π index and (d) the Randić index.

3.7 Cohesion

For most regions considered, average cohesion of Physarum graphs is typically higher than of motorway graphs (Figure 8(a)). The difference is particularly strong for Brazil and USA, e.g. average cohesion of Brazilian motorway network is 0.8 while of the corresponding Physarum graphs it is 0.4. There is a match between Physarum and motorway graphs of Canada, Italy and the Netherlands. The top three entries with highest cohesion of motorway graph are Brazil, Canada, China and the Netherlands, and the top three regions with highest cohesion of Physarum graphs are Brazil, China and USA. Cohesion of each edge in the complete graph is $n - 2/2(n-1) \sim 0.44$, this limit is nearly approached by **H** (Brazil; Figure 8(a)). Motorway and, especially, Physarum graphs of Malaysia and Italy show minimal cohesion, because cohesion is zero in chains and graphs with cycles over three nodes.

Finding 2. Physarum matches motorway network of Canada, Italy and the Netherlands in terms of compactness, local densities and fault-tolerance of transport networks.

Average cohesion is an indicator of compactness [28]. A sub-set of the graph with high cohesion remains connected even when some edges are removed, thus cohesion may characterise stability [43] or even fault-tolerance of graphs. The cohesion of a node is the minimum number of edges whose deletion makes the node a cut node of the resulting graph [41], thus the cohesion is used to characterise a local density of sub-graphs [51], and it is related to centrality [20] and statistical properties of connectivity of graphs [48].

3.8 The Harary index

The Harary index [38] is well known for its predictive properties in chemistry [26,27], and the index is based on the chemists intuitive expectation that distant sites in a structure should influence each other less than the near site' [34]. This is probably not the case with slime mould and man-made motorway networks. Only 4 out of 14 regions satisfy the relation $|1 - \eta(P)/\eta(H)| \leq 0.1$: China, Canada, Belgium and Malaysia, where η is the

Harary index. Physarum poorly approximates motorways, in terms of the Harary index, in Brazil and USA (Figure 8(b)).

3.9 The Π-index

Five regions show over 0.1 mismatch, $|1 - \Pi(P)/\Pi(H)| > 0.1$, between the Π-indices of Physarum and motorway graphs: Germany, Iberia, the Netherlands, Malaysia and USA (Figure 8(c)). This result is quite interesting. Recall, that the Π-index is a ratio of a total length of all normalised edges of a graph to a distance along the graph's diameter. Physarum graphs neither match motorways in diameters (Figure 7(f),(g)), nor do we witness a good match in average edge length, or shortest paths (Figure 7(c)–(e)). However, when these factors are considered in proportion the match between the graphs occurs.

3.10 The Randić index

Finding 3. Physarum perfectly approximates motorway networks in terms of the Randić index.

The Randić index R shows impeccable match between Physarum and motorway graphs (Figure 8(d) and Table 1). The largest value $1 - R(\mathbf{H})/R(\mathbf{P}) = 0.07$ is for Belgium motorway graph and the corresponding Physarum graph. Star graph has a minimum of the Randić index $\sqrt{n-1}$ [19]. For an arbitrary graph $\mathbf{G}$ the boundaries are $\sqrt{n-1} \leq R(\mathbf{G}) \leq n/2$. As we can see in Table 1, indices for all motorway and Physarum graphs are very close to upper boundary. The highest values for motorways are in Italy and USA, and for Physarum graphs are in Belgium, Malaysia and Canada.

The Randić index R (originally called by Milan Randić as molecular branching index) [40] characterises relationships between structure, property and activity of molecular components [25]. The index relates to diameter [24] and is actually the upper boundary of diameter [52]. It also relates to chromatic numbers of graphs and eigenvalues of adjacency matrices [33]. There are proven linear relationships between the Randić index and molecular polarisability, cavity surface areas calculated for water solubility of alcohols and hydrocarbons, biological potencies of anaesthetics [31], water solubility and boiling

Table 1. Values of the Randić index.

Country	$R(\mathbf{H})$	$R(\mathbf{P})$	$1 - R(\mathbf{H})/R(\mathbf{P})$	$n/2$
Africa	16.98	16.88	−0.006	17.5
Australia	11.9	12.17	0.022	12.5
Belgium	9.53	10.27	0.071	10.5
Brazil	10.04	10.14	0.01	10.5
Canada	7.25	7.76	0.066	8
China	15.08	15.1	0.002	15.5
Germany	9.94	10.15	0.02	10.5
Iberia	10.62	11.11	0.045	11.5
Italy	5.22	5.22	0	5.5
Malaysia	9.63	9.88	0.025	10
Mexico	8.87	8.95	0.009	9.5
The Netherlands	10.09	10.17	0.008	10.5
UK	4.61	4.7	0.021	5
USA	9.71	9.41	−0.031	10

point [30] and even bioconcentration factor of hazardous chemicals [42]. Estrada suggested the following structural interpretation: the Randić index is proportional to an area of molecular accessibility, i.e. area 'exposed' to outside environment. Or we can say that the index is inversely proportional to areas of overlapping between spheres of specified radius enclosing the nodes. The more the overlapping, the less is the Randić index. In terms of transport networks, we can interpret external accessibility as transport inaccessibility, proportional to areas of country not served by existing motorway links.

Finding 4. Physarum well approximates motorway graphs in terms of transport accessibility.

Along the above discourse, we can speculate that UK, Italy and Canada (first three regions with the smallest Randić indices) have better transport coverage of their territories than Africa, China and Australia (top three regions with the highest Randić indices).

3.11 Extremal regions

We call a region extremal if it displays minimum or maximum values of at least one measure over its motorway or Physarum graphs. The extremal regions are listed in Table 2:

- Africa shows maximum Π-index and Randić index on both **H** and **P**, and maximum average shortest path and diameter on **P**. This might indicate on critical dependencies between geographically close urban areas, large territorial spread of transport networks and relatively higher density of urban area along coasts (Figure 5(a)).
- Brazil shows maximum average cohesion on **H** and **P**. This is because Brazil has highest (amongst regions studied) number of locally connected sub-graphs with largest number of dependent cycles (Figure 5(d)).
- China shows maximum average degree, number of independent cycles and Harary index on **H** and **P**; minimum average edge length, average shortest path and diameter on **P**. These indicate on high accessibility of major urban area in China, and fault-tolerance of Chinese motorways at a large scale (Figure 5(f)). The expressway network in China has been developed much recently, known as the national trunk highway system, and it is a high-standard transport system planned by the central government. The system is designed to be optimal and many factors were properly taken into account including terrains and landscapes.

Table 2. Geographical regions with extremal values of measures over motorway graphs **H** and Physarum graphs.

Measure μ	Max $\mu(\mathbf{H})$	Min $\mu(\mathbf{H})$	Max $\mu(\mathbf{P})$	Min $\mu(\mathbf{P})$
Average degree	China	Malaysia	China	UK
Number of independent cycles	China	Malaysia	China	UK, Mexico
Average cohesion	Brazil	Malaysia	Brazil	Malaysia
Average edge length	The Netherlands	Malaysia	Italy	China
Shortest path, nodes	Malaysia	UK	Malaysia	The Netherlands
Shortest path	Malaysia	UK, USA	Africa	China
Harary index	China	Italy	China	Italy
Π-Index	Africa	UK	Africa	UK
Randić index	Africa	UK	Africa	UK
Diameter, nodes	Malaysia	Iberia, UK, USA	Malaysia	UK
Diameter	Malaysia	USA	Africa	China

- Iberia has minimum diameter in nodes on **H**. The man-made transport network structure resembles a wheel with an 'axle' at Madrid, most major urban areas around coast forming a 'rim' linked to Madrid by 'spokes' (Figure 5(h)).
- Italy shows minimum Harary index on **H** and **P**, and maximum average edge length on **P**. These are due to tree-like structure of the transport networks and constraining of the urban areas in the prolonged shape of the country (Figure 5(i)).
- Malaysia shows maximum shortest path in nodes and diameter in nodes on **H** and **P**; minimum average cohesion on **H** and **P**; maximum average shortest path and diameter on **H**; and minimum average degree, number of independent cycles and average edge length on **H**. This is because Malaysian transport network does not have cycles and consists of a chain connecting urban areas along western coast (Figure 5(j)).
- Mexico shows minimum number of independent cycles on **P** because the slime mould approximation is a tree, almost a chain with few branches (Figure 4(k)).
- The Netherlands shows maximum average edge length on **H** and minimum average shortest path in nodes on **P**, due to relatively compact location of urban areas with high density of local transport links (Figures 5(l) and 4(l)).
- UK shows minimum Π-index and Randić index and diameter in nodes on **H** and **P**; minimum average shortest path in nodes, shortest path on **H** and minimum average degree and number of independent cycles on **P** (Figures 5(m) and 4(m)).
- USA shows minimum average shortest path, diameter in nodes and diameter on **H**. These are because the motorway system in USA was built with optimality yet efficiency in mind.

3.12 Bio-rationality of measures

In Table 3, we provide binary evaluation $M(C, \mu)$ of matching between Physarum **P** and motorway **H** graphs calculated for each country C and measure μ as follows: $M(C, \mu) = 1$ if $|1 - \mu(\mathbf{H}(C))/\mu(\mathbf{P}(C))| \leq 0.1$ and 0, otherwise. A bio-rationality β of a measure μ is a number of regions C for which $\mu(\mathbf{H}(C)) = \mu(\mathbf{P}(C))$ (Table 3, bottom row).

Finding 5. Hierarchy of bio-rationality of measures: Randić index $>_\beta$ Π $>_\beta$ average edge length, Harary index $>_\beta$ average degree, number of independent cycles $>_\beta$ shortest path, diameter $>_\beta$ average cohesion $>_\beta$ diameter in nodes $>_\beta$ shortest path in nodes.

Matching between motorway graphs and Physarum graphs is most strongly expressed in the Randić index; further measures amongst the top ones are Π-index, Harary index and edge length. Thus, we can enhance Finding 3 as follows.

Finding 6. The Randić index is the most biocompatible measure of transport networks.

The Randić index is used to characterise relationships between structure, property and activity of chemical molecules [25]; thus, we can speculate that in terms of structure/property/activity, Physarum almost perfectly approximates motorway networks in all regions!

3.13 Bio-rationality of motorways

We calculate a bio-rationality of a motorway graph as follows $\rho(C) = \sum_\mu |\xi(|1 - \mu(\mathbf{H}(C))/\mu(\mathbf{P}(C))| \leq \varepsilon)$, $\xi(p) = 1$ if predicate p is true, and 0 otherwise. We chose $\epsilon = 0.1$. Values of bio-rationality of motorways are shown in last column in Table 3.

Table 3. Matching between Physarum and motorway graphs for each country and each measure.

	Av degree	Cycles	Cohesion	Edge length	SP in nodes	SP	Harary index	Π index	The Randic index	Diameter, nodes	Diameter	Bio-rationality of motorways
Africa									1			1
Australia								1	1			2
Belgium	1					1	1	1	1	1	1	7
Brazil			1					1	1			3
Canada	1	1		1		1	1	1	1			7
China		1				1	1	1	1		1	6
Germany				1				1	1			3
Iberia				1					1			2
Italy		1		1			1	1	1			5
Malaysia	1		1	1			1		1			5
Mexico				1				1	1			3
The Netherlands	1	1							1		1	4
UK							1	1	1			3
USA									1			1
Bio-rationality of measures	4	4	2	6	0	3	6	9	14	1	3	

Finding 7. Hierarchy of bio-rationality of regions is as follows:

{Belgium, Canada} $>_\rho$ China $>_\rho$ {Italy, Malaysia} $>_\rho$ the Netherlands $>_\rho$ {Brazil, Germany, Mexico, UK} $>_\rho$ {Africa, USA}.

Comparing hierarchies of absolute matching, see Finding 1, with the above hierarchy of bio-rationality we find Belgium, Canada, China and Italy are at the intersection of first three levels of the hierarchies. We omit Italy because its shape is intrinsically restrictive and invokes rather trivial architectures of protoplasmic networks.

Finding 8. Motorway networks in Belgium, Canada and China are most affine to protoplasmic networks of slime mould *P. polycephalum*.

4. Discussion

Based on the results of our previous laboratory experiments with slime mould imitating the development of transport networks in 14 regions [2–14,47], we undertook a comparative analysis of the motorway and protoplasmic networks. We found that in terms of absolute matching between slime mould networks and motorway networks, the regions studied can be arranged in the following order of decreasing matching: Malaysia, Italy, Canada, Belgium, China, Africa, the Netherlands, Germany, UK, Australia, Iberia, Mexico, Brazil and USA. We compared the Physarum and the motorway graphs using such measures as average and longest shortest paths, average degrees, number of independent cycles, the Harary index, the Π-index and the Randić index. We found that in terms of these measures, motorway networks in Belgium, Canada and China are most affine to protoplasmic networks of slime mould *P. polycephalum*. With regard to measures and topological indices, we demonstrated that the Randić index could be considered as most biocompatible measure of transport networks, because it matches incredibly well with the slime mould and man-made transport networks, yet efficiently discriminates between transport networks of different regions.

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