Network permeability changes according to a quadratic power law upon removal of a single edge

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Abstract – We report a phenomenological power law for the reduction of network permeability in statistically homogeneous spatial networks upon removal of a single edge. We characterize this power law for plexus-like microvascular sinusoidal networks from liver tissue, as well as perturbed two- and three-dimensional regular lattices. We provide a heuristic argument for the observed power law by mapping arbitrary spatial networks that satisfy Darcy’s law on a small-scale resistor network.

Introduction. – Spatial transport networks are found in biology, e.g., leaf venation networks [1], fungal mycelium [2,3], and microvasculature [4–8], as well as in technical systems, e.g., power grids [9,10]. Transport in porous media such as rock and soil can be described in terms of flow networks, where clogging of individual pores corresponds to blocking of edges [11,12]. The resilience of these networks against failure of individual edges is thus both of practical and theoretical interest.

Previous research addressed the trade-off between network resilience and the building and repair costs of networks [13,14], as well as self-organized networks that optimize resilience and adaptation to fluctuations in load [1,15]. Different measures were proposed to quantify network resilience, e.g., permeability at risk, i.e., the reduction of permeability as a function of the fraction of removed edges [8], or the probability of becoming non-conductive upon removal of a single edge [1]. The latter provides a link to the bond percolation problem in the theory of random resistor networks [16,17].

Both DC electrical resistor networks and biological flow networks are well described by Kirchhoff equations of current conservation and an effective Ohm’s law [18]. For flow networks, this follows from Poiseuille’s law for the Stokes flow in pipes at low Reynolds numbers, which states a linear relation between the pressure difference at the end points of an edge and the current through that edge [19].

Resilience of networks against local damage has been studied for both biological and technical transport networks [1,13–15,20]. Previous work addressed in particular re-routing of flow and the change of flow through individual edges upon removal of another edge [21,22]. To the best of our knowledge, it is not known how the permeability of the entire network changes upon removal of a single edge.

Here, we report a phenomenological power law for the reduction of network permeability, which we observe in sinusoidal microvasculature networks from liver tissue, as well as perturbed regular networks. We find that upon removal of a random edge, the permeability of these networks is reduced by a relative amount that scales quadratically with the current through that edge in the unperturbed network. We provide a heuristic explanation for this power law in non-hierarchical networks: we map a spatial network with a distinguished central edge to an effective small-scale resistor network. This allows us to relate the change in permeability upon removal of the central edge and the current through this central edge in the unperturbed network.

Permeability of spatial networks. – We consider special cases of spatial, non-hierarchical networks with a characteristic mesh size \( a \), inside a cuboid region of interest of dimensions \( L_x \times L_y \times L_z \), see fig. 1(A).

We impose the pressure \( p_0 + \Delta p \) at all network nodes at \( x = 0 \) (source nodes), and the pressure \( p_0 \) at all network nodes at \( x = L_x \) (sink nodes). An analogous problem
We define the normalized permeability $K_0$ of the network as [8, 24]

$$K_0 = \frac{\kappa L_z I_{tot}}{A \Delta p}$$

with units of an area density, where $I_{tot}$ denotes the total current through the unperturbed network and $A = L_y L_z$ its cross-sectional area. Note that $K_0$ is independent of $\Delta p$. The normalization factor $\kappa L_z/A$ turns $K_0$ into a “material constant” of the network that depends on the statistics of its local geometry, but is independent of its size. This is essentially Darcy’s law [24]. Darcy’s law was originally formulated for a flow through porous media, yet it applies also to statistically homogeneous spatial networks as a special case. Note that for a network consisting of $n$ straight lines parallel to the $x$-axis that connect $x = 0$ and $x = L$, we would have $K_0 = n/A$.

We investigated the change in network permeability upon removal of a single edge in sinusoidal networks in liver tissue, which provides an example of a three-dimensional biological transport network. Let $K'$ denote the permeability of the perturbed network and $I_{edge}$ the current that flowed through this edge before its removal. We observed an approximate power law with exponent two,

$$1 - \frac{K'}{K_0} = \gamma \left( \frac{I_{edge}}{I_{tot}} \right)^2,$$

with dimensionless factor of proportionality $\gamma$, see fig. 1. Here, a nematic axis of network alignment of the sinusoidal network [7, 8, 25] is oriented parallel to the $x$-axis. Analogous results hold for flow along the $y$-axis, i.e., perpendicular to the nematic axis of network alignment, see fig. S1 in the Supplemental Material.

We hypothesized that the phenomenological power law equation (2) requires only the statistical homogeneity of the network, i.e., an effective Darcy’s law. Below, we provide a heuristic argument for the quadratic law by mapping the entire network on an effective resistor diagram, where sub-networks are characterized in terms of effective resistances that can be expressed in terms of the homogeneous permeability $K_0$ of the network and the spatial dimensions of the sub-networks.

**Origin of the power law.** – We consider an edge connecting nodes labeled 1 and 2, carrying a directed current $I_{edge}$ in the unperturbed network. We will replace this edge by an equivalent source-sink dipole and map the flow problem on the small-scale resistor network shown in fig. 2.

Specifically, we can replace the link $(1, 2)$ by a sink of strength $-I_{edge}$ placed at node 1, and a source of strength
we introduce virtual boundaries at a distance small-scale resistor diagram, see text for details. In particular, effective resistances (blue, corresponding to, central edge (red), central motif region (rosé) around the central to the corresponding resistor diagram, while produced in panel (A) obtained by mapping the sinusoidal network $R$ from eq. (B.1), and identity.

To estimate the relative change in the network permeability as effective resistances $R_{\text{edge}}$, the right outer boundary to these virtual boundaries, as well placed at node 2. Inserting a source of strength $I$ at the left boundary $x = 0$ by an amount $\alpha I$, and increase the outflow $I_{\text{out}}$ at the right boundary $x = L$ by an amount $(1 - \alpha)I$, which defines a splitting ratio $\alpha$. If a sink is placed at node 1 and a source at node 2, the two nodes might have different splitting ratios $\alpha_1$ and $\alpha_2$, respectively. This results in a net change of the total current through the network upon insertion of the source-sink dipole (or equivalently insertion of the edge (1, 2))

$$I_{\text{tot}} = I'_{\text{tot}} + (\alpha_1 - \alpha_2)I_{\text{edge}}.$$  

Here, $I_{\text{tot}}$ is the current through the network with edge (1, 2) still present (or, equivalently, source-sink dipole added as described above), and $I'_{\text{tot}}$ is the current through the network without edge (1, 2). According to Darcy’s law, the effective resistances from a node to the left or right boundary of the network, respectively, should approximately have a ratio of $x : L - x$, where $x$ is the coordinate of the node along the direction of the pressure gradient. Thus, we expect for the splitting ratio $\alpha$ of this node, $\alpha/(1 - \alpha) \approx (L - x)/x$; hence, $\alpha \approx (L - x)/L$. In particular, node 1 and 2 will have similar splitting ratios, $\alpha_1 \approx \alpha_2$, such that the effect of a sink at node 1 and a source at node 2 partially cancel (in fact, their contributions cancel to linear order in $I_{\text{edge}}$, see also section “Continuum theory” in the SM text). The quadratic power law, eq. (2), follows from the fact that the difference $\alpha_1 - \alpha_2$ is not exactly zero, but approximately proportional to the current $I_{\text{edge}}$ in the unperturbed network, as we show next.

**Equivalent small-scale resistor network.** To proceed, we replace the large network by a simple effective resistor network, see fig. 2. Specifically, let $x_1$ and $x_2$ be the $x$ coordinates of node 1 and 2, and $x' = (x_1 + x_2)/2$ their mean. We expect that different splitting ratios $\alpha_1$ and $\alpha_2$ for nodes 1 and 2 reflect the local geometry of the network. In contrast, we anticipate that on larger spatial scales $\delta$ with $a \ll \delta \ll L_x$, flow can be considered homogeneous and described by effective resistances, thus corroborating Darcy’s law [24]. Specifically, we consider a plane normal to the $x$-axis placed at $x = x' - \delta$, and introduce an effective resistance $R_1$ for flow from node 1 to this virtual plane. Likewise, we introduce an effective resistance $R_L$ for the flow from this virtual plane to the left boundary at $x = 0$. Analogous to $R_1$ and $R_L$, we introduce a local resistance $R_3$ for the flow from node 1 to a second virtual plane at $x' + \delta$, as well as a resistance $R_R$ for the flow from this plane to the right boundary at $x = L_x$. For node 2, we introduce resistances $R_2$ and $R_4$ analogous to $R_1$ and $R_3$, respectively, see fig. 2. Finally, we introduce a resistance $R_M$ to account for the flow between the two virtual boundaries far from the edge (1, 2).

The length of edge (1, 2) is on the order of the mesh size $a$ of the network, and thus much smaller than the coarse-graining length scale $\delta$. We thus expect that the resistance $R_{12}$ of edge (1, 2) is much smaller than the resistances $R_1$, $R_2$, $R_3$, $R_4$ of the central network motif. For the following calculation, we make the simplifying assumption that $R_{12} = 0$. The current $I_{\text{edge}}$ through the edge (1, 2) is found to be proportional to an imbalance of resistances,

\[ I_{\text{edge}} = I_{\text{edge}}^{\text{predicted}} = \frac{I_{\text{edge}}}{I_{\text{tot}}} = \frac{1}{1 + \frac{\alpha_1 - \alpha_2}{\alpha},} \]

Fig. 2: Re-routing in non-hierarchical spatial networks upon removal of a single edge: mapping on small-scale resistor network. (A) We consider a single edge of a homogeneous network that connects nodes 1 and 2 with directed current $I_{\text{edge}}$. To estimate the relative change in the network permeability upon removal of edge (1, 2), and map the full network on a small-scale resistor diagram, see text for details. In particular, we introduce virtual boundaries at a distance $\delta$ from the central edge parallel to the boundaries of the network. We consider effective resistances $R_L$ and $R_R$ for the flow from the left and the right outer boundary to these virtual boundaries, as well as effective resistances $R_1$, $R_2$, $R_3$, $R_4$ for flow node 1 and 2 to the two virtual boundaries, respectively. (B) Illustration of resistor diagram for the sinusoidal network from fig. 1(A): central edge (red), central motif region (rosé) around the central edge using $\delta = 50 \mu m$, network regions left of the left boundary (blue, corresponding to $R_1$), and right of the right boundary (teal, corresponding to $R_R$). (B’ For all possible choices of a central edge as in panel (B), we compare the current $I_{\text{edge}}$ through that edge in the unperturbed network and a predicted current using eq. (B.10) in appendix B, which refines eq. (4), with effective resistances $R_1$, $R_2$, $R_3$, $R_4$, $R_L$, $R_R$, $R_0$ as introduced in panel (A) obtained by mapping the sinusoidal network to the corresponding resistor diagram, while $S_0$ was computed from eq. (B.1), and $R_{SM}$ implicitly from eq. (B.4), see methods supplement in SM text for details. Red diagonal indicates identity.
as expected

\[ I_{\text{edge}} = \frac{R_0R_3 - R_1R_4}{(R_1 + R_2)(R_3 + R_4)}(I_1 + I_2), \]

(4)

which implies that \( I_{\text{edge}} \) vanishes if \( R_1 : R_3 = R_2 : R_4 \).

The splitting ratios introduced above approximately satisfy

\[
\begin{align*}
\alpha_1 : 1 - \alpha_1 &= R_1 + R_L : R_3 + R_R \quad \text{and} \\
\alpha_2 : 1 - \alpha_2 &= R_2 + R_L : R_4 + R_R. 
\end{align*}
\]

(5)

(6)

In the limit \( R_1, R_2, R_3, R_4 \gg R_L, R_R, \) this implies for their difference

\[
\alpha_1 - \alpha_2 = \frac{R_2R_3 - R_1R_4}{(R_1 + R_2)(R_3 + R_4)} \sim I_{\text{edge}}.
\]

(7)

Together with eq. (3), eq. (2) follows.

A direct calculation provides an estimate for the proportionality factor \( \gamma \) in eq. (2) (up to a network-type specific factor of order unity), see appendix B,

\[
\gamma \sim \gamma_{\text{theory}} = \frac{a}{L_x} I_0 = A\frac{a}{L_x} K_0 = \frac{\kappa a}{R_0},
\]

(8)

where \( I_0 = \Delta p/(\kappa L_x) = I_{\text{tot}}/(K_0A) \). In short, we can use Kirchhoff’s laws to first compute the relative change in permeability upon removal of edge \((1, 2)\) of the central network motif shown in fig. 3. The hierarchy of length scales between the mesh size \( a \) of the network, the coarse-graining length scale \( \delta \), and the total size \( L_x \) of the network, \( a \ll \delta \ll L_x \), implies a hierarchy of resistances according to Darcy’s law with \( R_1, R_2, R_3, R_4 \sim (\delta/\delta^2) \kappa/K_0, R_M \sim (2\delta/A) \kappa/K_0, R_L + R_R \sim (L_x/A) \kappa/K_0 \); hence, \( R_M \ll R_1, R_2, R_3, R_4 \) and \( R_M \leq R_L + R_R \). Exploiting this hierarchy of resistances allows us to relate the relative change in the permeability of the central network motif to that of the full network. According to eq. (8), the prefactor \( \gamma \) equals the dimensionless ratio of the average resistance \( \kappa a \) of a single edge divided by the resistance \( R_0 \) of the full network. Simulation results for perturbed regular lattices are consistent with this result, eq. (8), see fig. 3(C). An approximate formula for the current \( I_{\text{edge}} \) through a central edge in the unperturbed network in terms of the effective resistances introduced above, eq. (B.10), compares reasonably to the actual currents, which supports the approximations made, see fig. 2. For the sinusoidal network shown in fig. 3, we can define a proxy for the mesh size as the median of edge lengths in the network \( a = 16.2 \mu m \) (mean \( + \text{s.e.} : 18.2 \pm 10.4 \mu m \)). Using this value for \( a \), we find for the ratio between the fitted factor of proportionality \( \gamma_{\text{fit}} \) from a fit of eq. (2) and the theoretical estimate \( \gamma_{\text{theory}} \) in eq. (8) \( \gamma_{\text{fit}}/\gamma_{\text{theory}} \approx 3.1 \) (similarly, we find 3.0 and 3.5 for two additional data sets from [8]).

Finally, we observed the power law equation (2) also in perturbed regular lattices, using honeycomb, square, and cubic lattices as prototypical examples, see fig. 3. For these regular networks, we added isotropic Gaussian noise to node positions. (Using log-normally distributed random edge resistances gave analogous results, not shown.) Interestingly, \( \gamma_{\text{fit}}/\gamma_{\text{theory}} \) approximately scales as \( 1/d \) in these examples, where \( d \) is the degree of the network (honeycomb lattice: \( d = 3 \), square lattice \( d = 4 \), cubic lattice...
d = 6, sinusoidal networks \( d \approx 3.39 \pm 0.07 \), mean \( \pm \) s.e.m., \( n = 3 \), see fig. 3(C). Furthermore, for these regular networks, any deviations from the power law equation (2) always occurred only for special edges: these edges were either close to the boundary of the region of interest, or carried an unusual high current. In one-dimensional networks, the quadratic power law does not hold, because a linear chain of edges becomes non-conductive upon removal of a single edge. Instead, in quasi-one-dimensional networks consisting of \( N_y \) parallel chains each with \( N_x \) identical edges in series (without any transverse connections), we have \( 1 - K' / K_0 = L_{\text{edge}} / L_{\text{tot}} \). However, simulations of perturbed ladder networks, i.e., perturbed square lattices of dimensions \( N_x \times 2 \), approximately satisfy the quadratic power law already, see fig. S2 in the SM text.

Discussion. – We reported a phenomenological scaling law for the relative change in network permeability of homogeneous spatial transport networks with characteristic mesh size, eq. (2), testing both sinusoidal blood networks in liver tissue as an example of a biological network, see fig. 1, as well as perturbed regular lattices, see fig. 3. We rationalize this phenomenological observation by mapping a generic homogeneous spatial network on an effective small-scale resistor network, see fig. 2. The change in network permeability upon removal of a single edge equals the product of the previous current through that edge and a prefactor given by a difference of flow splitting ratios. This prefactor turns out to likewise scale with the previous current; hence, the quadratic law.

Notably, the quadratic power law is consistent with symmetry: the sign of the directed current \( I_{\text{edge}} \) of the edge to be removed depends on the arbitrary ordering of its two vertices, but the change in the network permeability should not.

Previous authors considered the related, but different problem of computing the change of current through a single edge upon removal of another edge [21, 22]. In particular, a continuum theory was proposed, which predicts the local change in the flow upon removal of a single edge in terms of a dipole field, whose strength scales linearly with the current \( I_{\text{edge}} \) through the removed edge in the unperturbed network. Applied to our problem, this continuum theory predicts that network permeability does not change upon removal of a single edge, see SM text for details on the argument. By the phenomenological quadratic power law equation (20) reported here, this is expected for a linear theory. The factor of proportionality \( \gamma \) in the quadratic power law scales with the mesh size \( a \) of the network by eq. (8); this implies \( \gamma \rightarrow 0 \) for a continuum limit with \( a \rightarrow 0 \), in agreement with the prediction of the continuum theory.

The quadratic power law highlights the importance of high-current edges for the resilience of non-hierarchical transport networks against perturbations [8].

Future work may directly derive the quadratic power law from linear theories of local flow redistribution [21, 22, 26], yet such an approach will have to ensure the boundary condition for the pressure, as well as explicitly account for statistical properties of non-hierarchical, statistically homogeneous networks, possibly using random matrix theory, which is beyond the scope of this paper.

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Appendix A: methods. – Data acquisition for sinusoidal networks. As described previously [7, 23, 27], fixed tissue samples of murine liver were optically cleared and treated with fluorescent antibodies for fibronectin and laminin, thus staining the extracellular matrix surrounding the sinusoids. Subsequently, samples were imaged at high resolution using multiphoton laser-scanning microscopy (voxel size \( 0.3 \mu \text{m} \times 0.3 \mu \text{m} \times 0.3 \mu \text{m} \)). Three-dimensional image data was segmented and network skeletons computed using the MotionTracking image analysis software [27]. Raw network data was cleaned by discarding small disconnected network components, merging nodes less than 8 \( \mu \text{m} \) apart, and pruning dead ends [8]. The remaining node points are exactly the branch points of the sinusoidal network, whose positions are determined with high precision. This reduces ambiguity on small network details that were difficult to resolve with current imaging techniques. Note that the outer diameter of sinusoids is approximately 8 \( \mu \text{m} \), while their inner diameter measures approximately 6 \( \mu \text{m} \) [23]. The three sinusoidal networks analyzed here represent regions of interest of size \( 210 \mu \text{m} \times 215 \mu \text{m} \times 70 \mu \text{m} \), and are located centrally in a liver lobule between one portal and one central vein, with the x-axis aligned parallel to the PV-CV axis. These three networks contain 681, 823, 775 nodes, and 871, 1012, 1078 edges, respectively. Edge lengths follow a unimodal distribution with median and mean \( \pm \) standard deviation 16.2 \( \mu \text{m} \), 18.2 \( \pm \) 10.4 \( \mu \text{m} \), 14.8 \( \mu \text{m} \), and 15.9 \( \pm \) 8.5 \( \mu \text{m} \), 15.5 \( \mu \text{m} \), and 17.2 \( \pm \) 8.6 \( \mu \text{m} \), for the three networks, respectively. Likewise, the node degree distribution is unimodal with mean \( \pm \) standard deviation 3.3 \( \pm \) 0.6, 3.4 \( \pm \) 0.6, 3.5 \( \pm \) 0.7 (excluding nodes of degree 1 as found on the ROI boundary), respectively. Network data is available as supplementary open data accompanying [8].

Appendix B: details on origin of the quadratic power law. – Let \( S_0 \) and \( S' \) be the resistances of the central motif in fig. 2 with and without the central edge...
Here, the used notation $a \oplus b = (a^{-1} + b^{-1})^{-1}$ for the effective resistance of two parallel resistors $a$ and $b$. (Note that $\oplus$ is commutative and that the associate law holds, while the distributive law does not.)

Hence,\[1 - \frac{S_0}{S'} = \frac{(R_2R_3 - R_1R_4)^2}{(R_1 + R_2)(R_1 + R_3)(R_2 + R_4)(R_3 + R_4)}.\] (B.3)

For the resistances of the full resistor diagram, we have\[R_0 = R_L + (S_0 \oplus R_M) + R_R,\] (B.4)\[R' = R_L + (S \oplus R_M) + R_R.\] (B.5)

In the main text, we argue that the hierarchy of length scales, $a \ll \delta \ll L$, implies $R_M \ll R_1, R_2, R_3, R_4$ and $R_M \ll R_L + R_R$ as a consequence of Darcy’s law with $R_i \sim (\delta/\delta^2)^i K_0 / K_i$, $i = 1, \ldots, 4$, as well as $R_M \sim (2\lambda/\lambda^2) \kappa/K_0$, and $R_L, R_R \sim (L_x/\lambda) \kappa/K_0$. Thus, $S_0, S' \gg R_M$, as well as $R_L, R_R \gg R_M$. With this approximation, we find for the relative change in permeability upon removal of edge (1, 2) for the full network\[1 - \frac{K'}{K_0} = 1 - \frac{R_0}{R'} = 1 - \frac{R_L + (S_0 \oplus R_M) + R_R}{R_L + (S' \oplus R_M) + R_R} \approx \frac{1}{R_L + R_R} \left( (S' \oplus R_M) - (S \oplus R_M) \right).\] (B.6)

Hence,\[I_1 + I_2 \approx \frac{R_M}{R_M + S_0} I_{tot} \approx \frac{R_M}{S_0} I_{tot};\] (B.9)

hence eq. (4) yields\[I_{edge} = \frac{R_2R_3 - R_1R_4}{(R_1 + R_2)(R_3 + R_4)} \frac{R_M}{S_0} I_{tot}.\] (B.10)

We can thus rewrite eq. (B.3) as
\begin{equation}
1 - \frac{S_0}{S'} = \frac{(R_1 + R_2)(R_3 + R_4)}{(R_1 + R_2)(R_3 + R_4)} \left( \frac{S_0}{R_M} \right)^2 \left( \frac{I_{edge}}{I_{tot}} \right)^2.\end{equation} (B.11)

Here, we used in the last step that $R_1, R_2, R_3, R_4$ will be approximately of equal magnitude. Inserting the last result into eq. (B.8) yields
\[1 - \frac{K'}{K_0} \approx \frac{S_0}{R_L + R_R} \left( \frac{I_{edge}}{I_{tot}} \right)^2 + \frac{K\lambda}{R_0} \left( \frac{I_{edge}}{I_{tot}} \right)^2 = \frac{a}{R_x I_0} I_{tot}.\] (B.12)

Here, we used that the coarse-graining distance $\delta$ should be chosen larger, but proportional (and of the same order of magnitude) as the mesh size $a$ of the network; thus, we expect that $S_0$ scales proportional to $\kappa a$. Additionally, since $\delta \ll L_x$, we have $R_L + R_R \approx R_0$. From eq. (B.12), we conclude for the dimensionless factor of proportionality in eq. (2), $\gamma_{\text{theory}} = a I_{tot}/(L_x I_0)$, which provides a valid order-of-magnitude estimate for the examples in fig. 3.

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