The scaling of optimal supply networks: implications for biological and geophysical systems

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Optimal Supply Networks

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What's the best way to distribute stuff?

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What's the best way to distribute stuff?

► Stuff = medical services, energy, nutrients, people, ...

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What's the best way to distribute stuff?

- Stuff = medical services, energy, nutrients, people, ...
- Some fundamental network problems:
 - 1. Distribute stuff from single source to many sinks
 - Collect stuff coming from many sources at a single sink
 - 3. Distribute stuff from many sources to many sinks
 - 4. Redistribute stuff between many nodes

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- Focus on single source/sink problems.
- Q: How do optimal solutions scale with system size?

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Animal power

Fundamental biological and ecological constraint:

$$P = c M^{\alpha}$$

P = basal metabolic rate

M =organismal body mass





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Animal power

Fundamental biological and ecological constraint:

 $P = c M^{\alpha}$

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Prefactor *c* depends on body plan and body temperature:

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Prefactor *c* depends on body plan and body temperature:

Birds 39–41°*C*Eutherian Mammals 36–38°*C*Marsupials 34–36°*C*Monotremes 30–31°*C*





Frame 6/53



$$\alpha = 2/3$$

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History: Metabolism

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$$\alpha = 2/3$$
 because . . .

Dimensional analysis suggests an energy balance surface law:

$$P \propto S \propto V^{2/3} \propto M^{2/3}$$

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$$\alpha = 2/3$$
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▶ Dimensional analysis suggests an energy balance surface law:

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Lognormal fluctuations:
Gaussian fluctuations in $\log P$ around $\log cM^{\alpha}$.

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$\alpha = 2/3$ because . . .

Dimensional analysis suggests an energy balance surface law:

$$P \propto S \propto V^{2/3} \propto M^{2/3}$$

- Lognormal fluctuations:
 Gaussian fluctuations in $\log P$ around $\log cM^{\alpha}$.
- Stefan-Boltzmann relation for radiated energy:

$$\frac{\mathrm{d}E}{\mathrm{d}t} = \sigma\varepsilon ST^4$$

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The prevailing belief of the church of quarterology

$$\alpha = 3/4$$

$$P \propto M^{3/4}$$

Optimal Supply Networks

History: Metabolism

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The prevailing belief of the church of quarterology

$$\alpha = 3/4$$

 $P \propto M^{3/4}$

Huh?

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History: Metabolism

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Related putative scalings:

- ▶ number of capillaries $\propto M^{3/4}$
- ▶ time to reproductive maturity $\propto M^{1/4}$
- ▶ heart rate $\propto M^{-1/4}$
- ▶ cross-sectional area of aorta $\propto M^{3/4}$
- ▶ population density $\propto M^{-3/4}$

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1840's: Sarrus and Rameaux first suggested $\alpha = 2/3$.



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1883: Rubner found $\alpha \simeq 2/3$.



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History: Metabolism

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1930's: Brody, Benedict study mammals. Found $\alpha \simeq$ 0.73 (standard).



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History: Metabolism

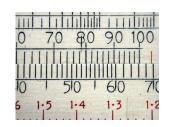
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1932: Kleiber analyzed 13 mammals. Found $\alpha = 0.76$ and suggested $\alpha = 3/4$.



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1950/1960: Hemmingsen Extension to unicellular organisms. $\alpha = 3/4$ assumed true.



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1964: Troon, Scotland: 3rd symposium on energy metabolism. $\alpha =$ 3/4 made official . . .



Optimal Supply Networks

History: Metabolism

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1964: Troon, Scotland: 3rd symposium on energy metabolism.

 $\alpha = 3/4$ made official 29 to zip.



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Today

Optimal Supply Networks

3/4 is held by many to be the one true exponent.

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In the Beat of a Heart: Life, Energy, and the Unity of Nature—by John Whitfield

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Today

Optimal Supply Networks

History: Metabolism

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3/4 is held by many to be the one true exponent.



In the Beat of a Heart: Life, Energy, and the Unity of Nature—by John Whitfield

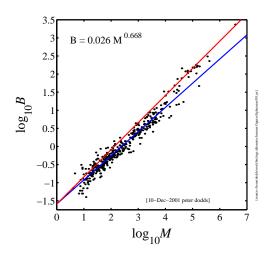
But—much controversy...

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Some data on metabolic rates



- ► Heusner's data (1991) [5]
- ▶ 391 Mammals
- ▶ blue line: 2/3
- ► red line: 3/4.
- ► (*B* = *P*)

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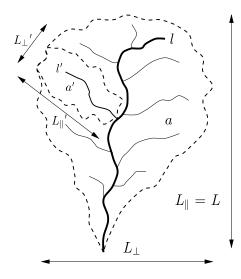
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Basic basin quantities: a, l, L_{\parallel} , L_{\perp} :



- a = drainage basin area
- ▶ ℓ = length of longest (main) stream
- L = L_{||} = longitudinal length of basin

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1957: J. T. Hack [4] "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

$$\ell \sim a^h$$

$$h \sim 0.6$$

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1957: J. T. Hack [4] "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

$$\ell \sim a^h$$

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▶ Anomalous scaling: we would expect h = 1/2...

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- ▶ Anomalous scaling: we would expect h = 1/2...
- ▶ Subsequent studies: $0.5 \lesssim h \lesssim 0.6$

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1957: J. T. Hack [4] "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

$$\ell \sim a^h$$

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- ▶ Anomalous scaling: we would expect h = 1/2...
- ▶ Subsequent studies: $0.5 \lesssim h \lesssim 0.6$
- ► Another quest to find universality/god...

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1957: J. T. Hack [4] "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

$$\ell \sim a^h$$

$$h \sim 0.6$$

- ▶ Anomalous scaling: we would expect h = 1/2...
- ▶ Subsequent studies: $0.5 \lesssim h \lesssim 0.6$
- Another quest to find universality/god...
- A catch: studies done on small scales.

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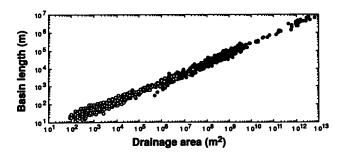
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Large-scale networks

(1992) Montgomery and Dietrich [7]:



- Composite data set: includes everything from unchanneled valleys up to world's largest rivers.
- Estimated fit:

$$L \simeq 1.78a^{0.49}$$

Mixture of basin and main stream lengths.

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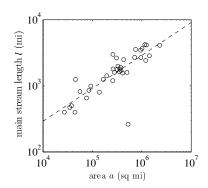
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World's largest rivers only:



- Data from Leopold (1994) [6, 2]
- ▶ Estimate of Hack exponent: $h = 0.50 \pm 0.06$

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Building on the surface area idea...

▶ Blum (1977) speculates on four-dimensional biology:

$$P \propto M^{(d-1)/d}$$

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Building on the surface area idea...

▶ Blum (1977) speculates on four-dimensional biology:

$$P \propto M^{(d-1)/d}$$

- ightharpoonup d = 3 gives $\alpha = 2/3$
- ▶ d = 4 gives $\alpha = 3/4$
- ▶ So we need another dimension...

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Building on the surface area idea...

▶ Blum (1977) speculates on four-dimensional biology:

$$P \propto M^{(d-1)/d}$$

- ightharpoonup d = 3 gives $\alpha = 2/3$
- d = 4 gives $\alpha = 3/4$
- So we need another dimension...
- Obviously, a bit silly.

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Building on the surface area idea:

- ► McMahon (70's, 80's): Elastic Similarity
- ► Idea is that organismal shapes scale allometrically with 1/4 powers (like nails and trees...)

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Building on the surface area idea:

- McMahon (70's, 80's): Elastic Similarity
- ▶ Idea is that organismal shapes scale allometrically with 1/4 powers (like nails and trees...)
- Appears to be true for ungulate legs.

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Building on the surface area idea:

- McMahon (70's, 80's): Elastic Similarity
- Idea is that organismal shapes scale allometrically with 1/4 powers (like nails and trees...)
- Appears to be true for ungulate legs.
- Metabolism and shape never properly connected.

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1960's: Rashevsky considers blood networks and finds a 2/3 scaling.

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Farlier theories

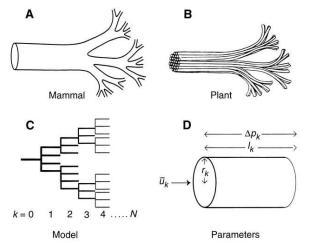
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- ▶ 1960's: Rashevsky considers blood networks and finds a 2/3 scaling.
- ▶ 1997: West et al. [11] use a network story to find 3/4 scaling.



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West et al.'s assumptions:

- hierarchical network
- capillaries (delivery units) invariant
- network impedance is minimized via evolution

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West et al.'s assumptions:

- hierarchical network
- capillaries (delivery units) invariant
- network impedance is minimized via evolution

Claims:

- $P \propto M^{3/4}$
- networks are fractal
- quarter powers everywhere

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Impedance measures:

Poiseuille flow (outer branches):

$$Z = \frac{8\mu}{\pi} \sum_{k=0}^{N} \frac{\ell_k}{r_k^4 N_k}$$

Pulsatile flow (main branches):

$$Z \propto \sum_{k=0}^{N} \frac{h_k^{1/2}}{r_k^{5/2} N_k}$$

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Not so fast ...

Actually, model shows:

- ▶ $P \propto M^{3/4}$ does not follow for pulsatile flow
- networks are not necessarily fractal.

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Actually, model shows:

- ▶ $P \propto M^{3/4}$ does not follow for pulsatile flow
- networks are not necessarily fractal.

Do find:

► Murray's cube law (1927) for outer branches:

$$r_0^3 = r_1^3 + r_2^3$$

- Impedance is distributed evenly.
- Can still assume networks are fractal.

Frame 29/53

1. Ratios of network parameters:

$$R_n = \frac{n_{k+1}}{n_k}, \ R_\ell = \frac{\ell_{k+1}}{\ell_k}, \ R_r = \frac{r_{k+1}}{r_k}$$

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2. Number of capillaries $\propto P \propto M^{\alpha}$.

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2. Number of capillaries $\propto P \propto M^{\alpha}$.

$$\Rightarrow \quad \boxed{\alpha = -\frac{\ln R_n}{\ln R_r^2 R_\ell}}$$

(also problematic due to prefactor issues)

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(also problematic due to prefactor issues)

Soldiering on, assert:

- area-preservingness: $R_r = R_n^{-1/2}$
- ▶ space-fillingness: $R_{\ell} = R_n^{-1/3}$

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•

$$\Rightarrow \alpha = 3/4$$

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Data from real networks

Network	R _n	R_r^{-1}	R_ℓ^{-1}	$-\frac{\ln R_r}{\ln R_n}$	$-\frac{\ln R_\ell}{\ln R_0}$	α
West et al.	_	_	_	1/2	1/3	3/4
rat (PAT)	2.76	1.58	1.60	0.45	0.46	0.73
cat (PAT) (Turcotte <i>et al.</i> ^[10])	3.67	1.71	1.78	0.41	0.44	0.79
dog (PAT)	3.69	1.67	1.52	0.39	0.32	0.90
pig (LCX) pig (RCA) pig (LAD)	3.57 3.50 3.51	1.89 1.81 1.84	2.20 2.12 2.02	0.50 0.47 0.49	0.62 0.60 0.56	0.62 0.65 0.65
human (PAT) human (PAT)	3.03 3.36	1.60 1.56	1.49 1.49	0.42 0.37	0.36 0.33	0.83 0.94

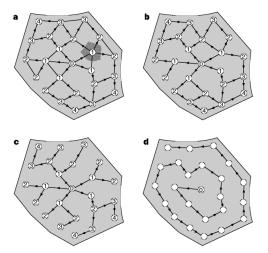
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Farlier theories

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- Banavar et al., Nature, $(1999)^{[1]}$
- Flow rate argument
- Ignore impedance
- Very general attempt to find most efficient transportation networks

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▶ Banavar et al. find 'most efficient' networks with

$$P \propto M^{d/(d+1)}$$

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Banavar et al. find 'most efficient' networks with

$$P \propto M^{d/(d+1)}$$

... but also find

$$V_{\rm network} \propto M^{(d+1)/d}$$

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▶ Banavar et al. find 'most efficient' networks with

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... but also find

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▶ d = 3:

$$V_{\rm blood} \propto M^{4/3}$$

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► *d* = 3:

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► Consider a 3 g shrew with $V_{\text{blood}} = 0.1 V_{\text{body}}$

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- ► Consider a 3 g shrew with $V_{blood} = 0.1 V_{body}$
- ▶ \Rightarrow 3000 kg elephant with $V_{blood} = 10 V_{body}$

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► *d* = 3:

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- ► Consider a 3 g shrew with $V_{blood} = 0.1 V_{body}$
- ▶ \Rightarrow 3000 kg elephant with $V_{blood} = 10 V_{body}$
- Such a pachyderm would be rather miserable.

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- Consider one source supplying many sinks in a d-dim. volume in a D-dim. ambient space.
- Assume sinks are invariant.
- Assume $\rho = \rho(V)$.
- Assume some cap on flow speed of material.

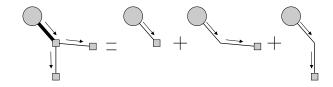
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- ► Consider one source supplying many sinks in a d-dim. volume in a D-dim. ambient space.
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- See network as a bundle of virtual vessels:



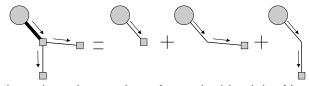
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Q: how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?

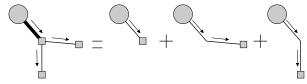
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- Assume some cap on flow speed of material.
- See network as a bundle of virtual vessels:



- Q: how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?
- ▶ Or: what is the highest α for $N_{\text{sinks}} \propto V^{\alpha}$?

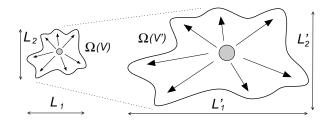
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Allometrically growing regions:



Have d length scales which scale as

$$L_i \propto V^{\gamma_i}$$
 where $\gamma_1 + \gamma_2 + \ldots + \gamma_d = 1$.

- For isometric growth, $\gamma_i = 1/d$.
- For allometric growth, we must have at least two of the $\{\gamma_i\}$ being different

Optimal Supply Networks

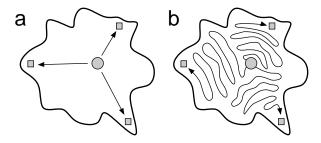
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Best and worst configurations (Banavar et al.)



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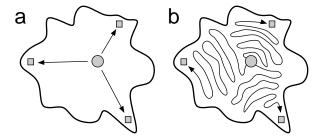
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Best and worst configurations (Banavar et al.)



► Rather obviously: min $V_{\text{net}} \propto \sum$ distances from source to sinks.

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Real supply networks are close to optimal:

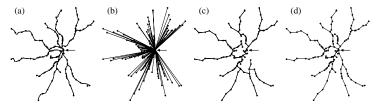


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

(2006) Gastner and Newman [3]: "Shape and efficiency in spatial distribution networks"

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Approximate network volume by integral over region:

$$\mathsf{min} \; V_{\mathsf{net}} \propto \mathsf{min} \; V_{\mathsf{net}} \propto \int_{\Omega_{d,D}(V)} \rho \, ||\vec{x}|| \, \mathrm{d}\vec{x}$$

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Approximate network volume by integral over region:

$$egin{aligned} \mathsf{min} \; V_{\mathsf{net}} &\propto \mathsf{min} \; V_{\mathsf{net}} &\propto \int_{\Omega_{d,D}(V)}
ho \, ||ec{x}|| \, \mathrm{d}ec{x} \end{aligned}$$

$$\rightarrow \rho V^{1+\gamma_{\max}} \int_{\Omega_{d,D}(\mathcal{C})} (c_1^2 u_1^2 + \ldots + c_k^2 u_k^2)^{1/2} \mathrm{d}\vec{u}$$

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Approximate network volume by integral over region:

$$\min \, \textit{\textbf{V}}_{\rm net} \propto \min \, \textit{\textbf{V}}_{\rm net} \propto \int_{\Omega_{d,D}(\textit{\textbf{V}})} \rho \, ||\vec{\textit{\textbf{x}}}|| \, \mathrm{d}\vec{\textit{\textbf{x}}}$$

$$\rightarrow \rho V^{1+\gamma_{\mathsf{max}}} \int_{\Omega_{d,D}(c)} (c_1^2 u_1^2 + \ldots + c_k^2 u_k^2)^{1/2} \mathrm{d}\vec{u}$$

$$\propto \rho V^{1+\gamma_{\text{max}}}$$

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General result:

$$\min \textit{V}_{\rm net} \propto \rho \textit{V}^{1+\gamma_{\rm max}}$$

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General result:

min
$$V_{\rm net} \propto \rho V^{1+\gamma_{\rm max}}$$

▶ If scaling is isometric, we have $\gamma_{max} = 1/d$:

$$\min V_{\text{net/iso}} \propto \rho V^{1+1/d} = \rho V^{(d+1)/d}$$

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General result:

$$\min \textit{V}_{\text{net}} \propto \rho \textit{V}^{1+\gamma_{\text{max}}}$$

▶ If scaling is isometric, we have $\gamma_{max} = 1/d$:

$$\min V_{\text{net/iso}} \propto \rho V^{1+1/d} = \rho V^{(d+1)/d}$$

If scaling is allometric, we have $\gamma_{\text{max}} = \gamma_{\text{allo}} > 1/d$: and

min
$$V_{\rm net/allo} \propto \rho V^{1+\gamma_{\rm allo}}$$

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$$\min V_{\rm net} \propto \rho V^{1+\gamma_{\rm max}}$$

▶ If scaling is isometric, we have $\gamma_{max} = 1/d$:

$$\min V_{\text{net/iso}} \propto \rho V^{1+1/d} = \rho V^{(d+1)/d}$$

If scaling is allometric, we have $\gamma_{\text{max}} = \gamma_{\text{allo}} > 1/d$: and

min
$$V_{\rm net/allo} \propto \rho V^{1+\gamma_{\rm allo}}$$

Isometrically growing volumes require less network volume than allometrically growing volumes:

$$rac{ ext{min } extit{V}_{ ext{net/iso}}}{ ext{min } extit{V}_{ ext{net/allo}}}
ightarrow 0 ext{ as } extit{V}
ightarrow \infty$$

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▶ Material costly ⇒ expect lower optimal bound of $V_{\rm net} \propto \rho V^{(d+1)/d}$ to be followed closely.

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- ▶ Material costly \Rightarrow expect lower optimal bound of $V_{\rm net} \propto \rho V^{(d+1)/d}$ to be followed closely.
- ▶ For cardiovascular networks, d = D = 3.

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- ▶ Material costly \Rightarrow expect lower optimal bound of $V_{\text{net}} \propto \rho V^{(d+1)/d}$ to be followed closely.
- For cardiovascular networks, d = D = 3.
- ▶ Know that volume of blood scales linearly with blood volume [9], $V_{\rm net} \propto V$.

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▶ Material costly \Rightarrow expect lower optimal bound of $V_{\text{net}} \propto \rho V^{(d+1)/d}$ to be followed closely.

- For cardiovascular networks, d = D = 3.
- ▶ Know that volume of blood scales linearly with blood volume [9], $V_{\text{net}} \propto V$.
- Sink density must ∴ decrease as volume increases:

$$ho \propto V^{-1/d}$$
.

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References

- ▶ Material costly \Rightarrow expect lower optimal bound of $V_{\text{net}} \propto \rho V^{(d+1)/d}$ to be followed closely.
- For cardiovascular networks, d = D = 3.
- ▶ Know that volume of blood scales linearly with blood volume [9], $V_{\text{net}} \propto V$.
- Sink density must ∴ decrease as volume increases:

$$ho \propto V^{-1/d}$$
.

Density of suppliable sinks decreases with organism size.

Then P, the rate of overall energy use in Ω, can at most scale with volume as

$$P \propto \rho V$$

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Then P, the rate of overall energy use in Ω, can at most scale with volume as

$$P \propto \rho V \propto \rho M$$

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Then P, the rate of overall energy use in Ω, can at most scale with volume as

$$P \propto \rho V \propto \rho M \propto M^{(d-1)/d}$$

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Then P, the rate of overall energy use in Ω, can at most scale with volume as

$$P \propto \rho V \propto \rho M \propto M^{(d-1)/d}$$

▶ For d = 3 dimensional organisms, we have

$$P \propto M^{2/3}$$

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River networks

- View river networks as collection networks.
- Many sources and one sink.
- Assume ρ is constant over time:

$$V_{\rm net} \propto \rho V^{(d+1)/d} = {\rm constant} \times V^{3/2}$$

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River networks

- View river networks as collection networks.
- Many sources and one sink.
- ▶ Assume ρ is constant over time:

$$V_{\rm net} \propto \rho V^{(d+1)/d} = {\rm constant} \times V^{3/2}$$

Network volume grows faster than basin 'volume' (really area).

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River networks

- View river networks as collection networks.
- Many sources and one sink.
- Assume ρ is constant over time:

$$V_{\rm net} \propto \rho V^{(d+1)/d} = {\rm constant} \times V^{3/2}$$

- Network volume grows faster than basin 'volume' (really area).
- ► It's all okay: Landscapes are d=2 surfaces living in D=3 dimension.
- Streams can grow not just in width but in depth...

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Hack's law

- Volume of water in river network can be calculated by adding up basin areas
- Flows sum in such a way that

$$V_{
m net} = \sum_{
m all\ pixels} a_{
m pixel}\, i$$

Hack's law again:

$$\ell \sim a^h$$

Can argue

$$V_{\rm net} \propto V_{\rm basin}^{1+h} = a_{\rm basin}^{1+h}$$

where *h* is Hack's exponent.

.: minimal volume calculations gives

$$h = 1/2$$

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 Banavar et al.'s approach [1] is okay because ρ really is constant.

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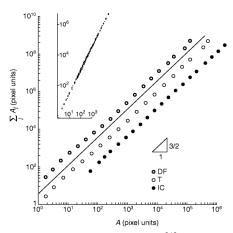
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 Banavar et al.'s approach [1] is okay because ρ really is constant.



From Banavar et al. (1999) [1]

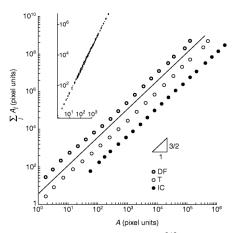
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- Banavar et al.'s approach [1] is okay because ρ really is constant.
- ► The irony: shows optimal basins are isometric



From Banavar et al. (1999) [1]

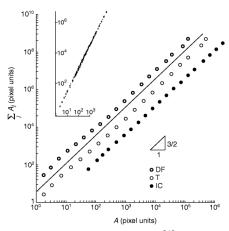
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- Banavar et al.'s approach [1] is okay because ρ really is constant.
- The irony: shows optimal basins are isometric
- ► Optimal Hack's law: $a \sim \ell^h$ with h = 1/2



From Banavar et al. (1999) [1]

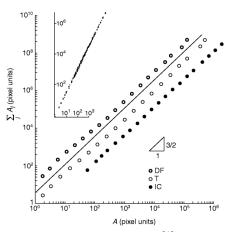
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- Banavar et al.'s approach [1] is okay because ρ really is constant.
- The irony: shows optimal basins are isometric
- ► Optimal Hack's law: $a \sim \ell^h$ with h = 1/2
- ► (Zzzzz)



From Banavar et al. (1999) [1]

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Supply network story consistent with dimensional analysis.

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- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.

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- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter (D = d versus D > d).

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- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter (D = d versus D > d).
- Deviations from optimal scaling suggest inefficiency (e.g., gravity for organisms, geological boundaries).

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- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter (D = d versus D > d).
- Deviations from optimal scaling suggest inefficiency (e.g., gravity for organisms, geological boundaries).
- Actual details of branching networks not that important.

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- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter (D = d versus D > d).
- Deviations from optimal scaling suggest inefficiency (e.g., gravity for organisms, geological boundaries).
- Actual details of branching networks not that important.
- Exact nature of self-similarity varies.

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References I

- J. R. Banavar, A. Maritan, and A. Rinaldo. Size and form in efficient transportation networks. *Nature*, 399:130–132, 1999. pdf (⊞)
- P. S. Dodds and D. H. Rothman. Scaling, universality, and geomorphology. Annu. Rev. Earth Planet. Sci., 28:571–610, 2000. pdf (⊞)
- M. T. Gastner and M. E. J. Newman. Shape and efficiency in spatial distribution networks. J. Stat. Mech.: Theor. & Exp., 1:01015−, 2006. pdf (⊞)

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References

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References II

J. T. Hack.

Studies of longitudinal stream profiles in Virginia and Maryland.

United States Geological Survey Professional Paper, 294-B:45–97, 1957.

A. A. Heusner. Size and power in mammals. Journal of Experimental Biology, 160:25–54, 1991.

L. B. Leopold.
 A View of the River.
 Harvard University Press, Cambridge, MA, 1994.

D. R. Montgomery and W. E. Dietrich. Channel initiation and the problem of landscape scale.

Science, 255:826–30, 1992. pdf (⊞)

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References III

N. Rashevsky.

General mathematical principles in biology.

In N. Rashevsky, editor, *Physicomathematical Aspects of Biology*, Proceedings of the International School of Physics "Enrico Fermi"; course 16, pages 493–524. New York, 1962, Academic Press.

W. R. Stahl. Scaling of respiratory variables in mammals. Journal of Applied Physiology, 22:453–460, 1967.

D. L. Turcotte, J. D. Pelletier, and W. I. Newman. Networks with side branching in biology. *Journal of Theoretical Biology*, 193:577–592, 1998. Optimal Supply Networks

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tory: Metabolism

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References

G. B. West, J. H. Brown, and B. J. Enquist.

A general model for the origin of allometric scaling laws in biology.

Science, 276:122-126, 1997. pdf (⊞)

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