Scaling and Power Laws with a Case Study in Biological Allometry

by
Van Savage
Harvard Medical School, Systems Biology Dept.

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Outline

I. General review of power laws
   1. Identifying power laws
   2. Some Examples
   3. Self Similarity
   4. Universality classes and critical points
II. Dimensional Analysis
III. Introduction to scaling in biology (aka Allometry)
   1. Examples of processes that vary systematically with body size and temperature over a large range.
   2. Theory for these patterns

IV. Conclusions

I. Types of Power Laws

$$y = Ax^b$$

1. Physical laws--planetary orbits, parabolic motion of thrown objects, classical forces, etc. (these are really idealized notions and do not exist in real world)
2. Scaling relations--relate two fundamental parameters in a system like lifespan to body mass in biology (Physical Laws are special/strong case)
3. Statistical distributions

1. Identifying Power Laws

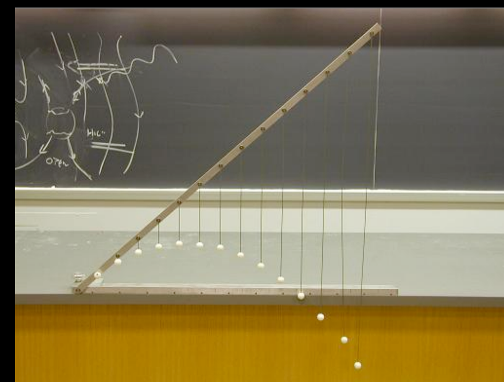
$$\ln y = b \ln x + \ln a$$

Linear plot: slope=b and intercept=ln a

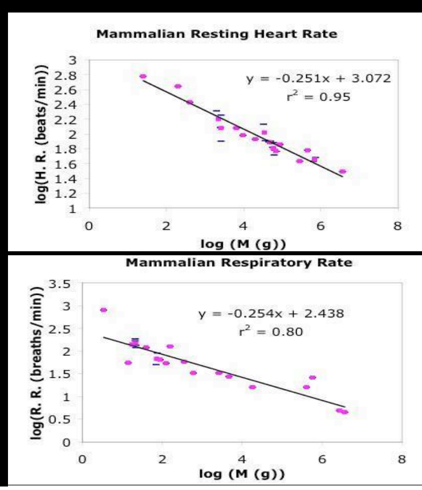
- Need big range on *x*- and *y*-axes to determine power laws because this minimizes effects of noise and errors
- Can give good measure of *b*, the exponent
- r^2 is property of data and measures how much variance in *y* is explained by variance in *x*. It is NOT really a measure of goodness of fit!

2. Examples of Power Laws

Parabolic Motion (Type 1)

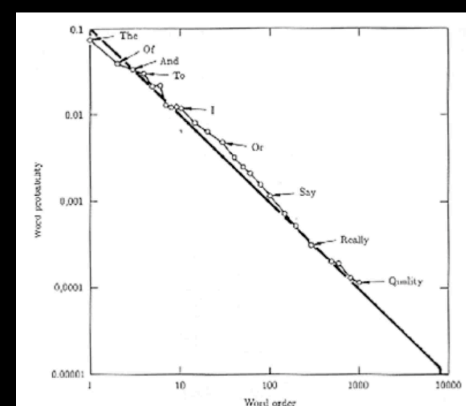


Typical Mass-Specific Rates (Type 2)

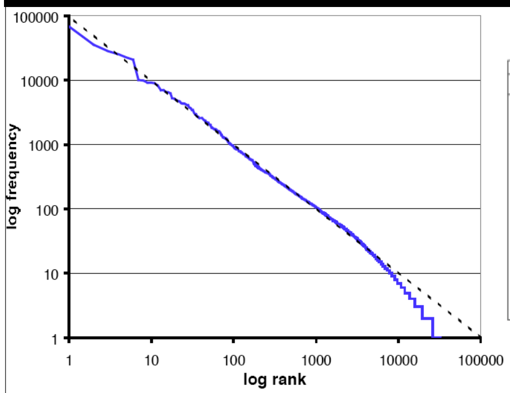


Savage, et al.,
Func. Eco., 2004

Word usage (Type 3)

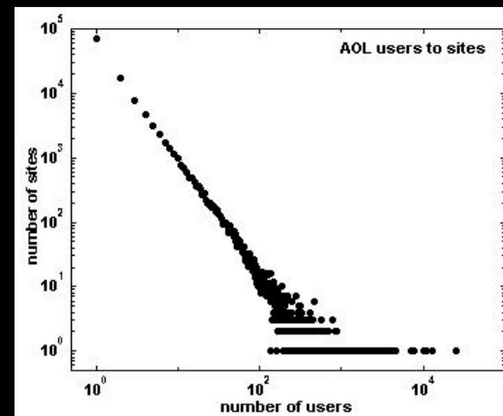


Word Usage (Type 3)



Unigrams		
Freq	Token	Meaning
620619	的	Of
308826	国	State
219543	一	One
209497	中	Centre / Middle
176905	在	In / At
159861	和	And
143359	人	Human
139713	了	Perfective marker
133696	会	Get together/Meeting/Association
128805	年	Year

Web Sites (Type 2)

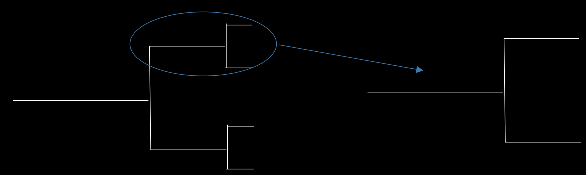


Identifying Power Laws

- Maximum likelihood methods are good for identifying power laws if used in correct way
- Whether to curve fit in linear or logarithmic space depends on distribution of errors because regressions make assumptions about these: homoscedascity->variance in *y* is independent of value of *x*
- Parabolic motion (error in distance measures is independent of *y* or *x*)--linear space
- Body size (for population, variance in body size or heart rate varies linearly with *x*)--logarithmic space

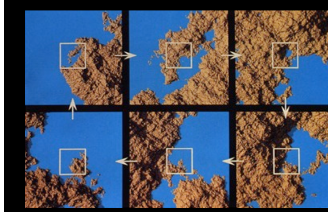
3. Self Similarity and Fractals

- Once a useful process is found in nature, it tends to be used over and over again--physics constrains possible processes and evolution tends maintains it because most mutations are harmful



Imagine taking a picture of smaller piece and magnifying it, and then it looks like original part.

Other examples of self similarity



Power Laws ⇔ Self Similarity

Equation form for self similarity: $f(\lambda x) = \lambda^k f(x)$

->

$$f(x) = ax^k$$
$$f(\lambda x) = a(\lambda x)^k = \lambda^k a x^k = \lambda^k f(x)$$

<-

Chain Rule

Equation above

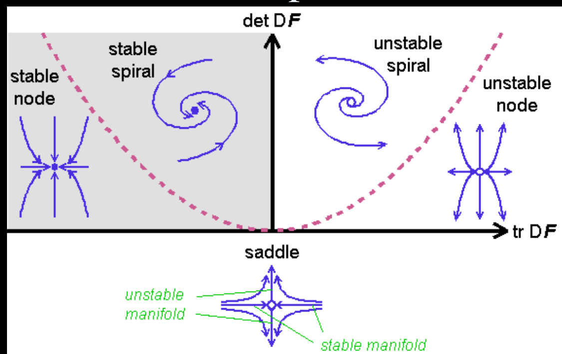
$$k\lambda^{k-1} f(x) = \frac{df(\lambda x)}{d\lambda} = \frac{d(\lambda x)}{d\lambda}\frac{df(\lambda x)}{d(\lambda x)} = x\frac{df(\lambda x)}{d(\lambda x)}$$

Free to choose λ=1

$$x\frac{df(x)}{dx} = kf(x) \Rightarrow \frac{df}{f} = k\frac{dx}{x}$$
$$\Rightarrow f(x) = Ax^k$$

4. Fixed Points and Universality

Dynamical systems flow relative to fixed points



What is functional form as fixed point is approached? This describes region and dynamics that are relevant for many scientific questions.

Non-power-law functions often behave as power laws near critical points

- Other functions commonly occur in nature: e^x, sin(x), cosh(x), $J_v(x)$, Ai(x)
- These functions can generally be expressed in Taylor or power series near critical points (phase transitions, etc.). When x is close to x*, difference is small, and first term dominates.

$$f(x) = \sum \frac{(x-x^*)^k}{k!} f^{(k)}(x-x^*) \sim C(x-x^*)^p$$

p-exponent of leading-order term

Any functions with the same first term in their series expansion behave the same near critical points, which is of great physical interest, even if they behave very differently elsewhere. Source of universality classes.

II. Dimensional Analysis and Power Laws

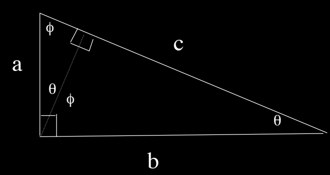
Dimensional Analysis

- Often used in physics
- For reasons given thus far, many processes should scale as a power law.
- Given some quantity, f, that we want to determine, we need to intuit what other variables on which it must depend, $\{x_1, x_2, \ldots, x_n\}$.
- Assume f depends on each of these variables as a power law.
- Use consistency of units to obtain set of equations that uniquely determine exponents.

$$f(x_1, x_2, \ldots, x_n) = x_1^{p_1} x_2^{p_2} \ldots x_n^{p_n}$$

Example 1: Pythagorean Theorem

- Hypotenuse, c, and smallest angle, θ, uniquely determine right triangles.
- Area=f(c, θ), DA implies Area=$c^2g(\theta)$.

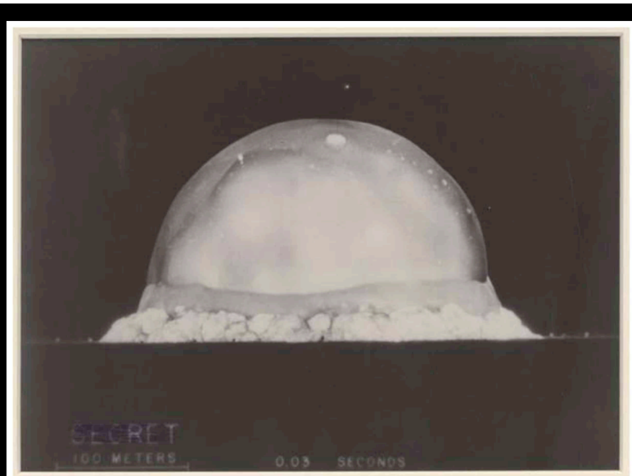


Area of whole triangle=sum of area of smaller triangles

$$a^2 g(\theta) + b^2 g(\theta) = c^2 g(\theta)$$
$$\Rightarrow a^2 + b^2 = c^2$$

Example 2: Nuclear Blast

- US government wanted to keep energy yield of nuclear blasts a secret.
- Pictures of nuclear blast were released in Life magazine
- Using DA, G. I. Taylor determined energy of blast and government was upset because they thought there had been a leak of information



- Radius, R, of blast depends on time since explosion, t, energy of explosion, E, and density of medium, ρ, that explosion expands into
- [R]=m, [t]=s,[E]=kg*m^2/s^2, ρ=kg/m^3
- R=$t^pE^q\rho^k$

$$1 = 2q - 3k$$
$$0 = p - 2q$$
$$0 = q + k$$

q=1/5, k=-1/5, p=2/5

$$R = (E/\rho)^{1/5} t^{2/5} \Rightarrow E = \frac{R^5\rho}{t^2}$$

Pitfalls of Dimensional Analysis

- Miss constant factors
- Miss dimensionless ratios
- But, can get far with a good bit of ignorance!!!

Summary

- Self-similarity and fractals$\Leftrightarrow$Power Laws
- Behavior near critical point $\Rightarrow$Power Laws
- But, Power Laws$\not\Rightarrow$near critical points
- Dimensional Analysis assumes power law form and this is partially justified by necessity of matching units

The essence of mathematics is not to make simple things complicated, but to make complicated things simple.--S. Gudder

If people do not believe that mathematics is simple, it is only because they do not realize how complicated life is. -John von Neumann

A little philosophy of science

- Many major, “universal” patterns in different fields are power laws
- Can often explain these without knowledge of all the details of the system
- Art of science is knowing system well enough to have intuition about which details are important

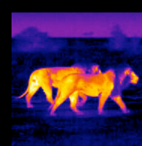
Explaining existence of single power law is not enough

- Need lots of data over large range of values to be statistically sure you have a power law!!! Don't be fooled.
- Much better to predict value of exponent and not just that it is a power law
- To really believe a theory we need multiple pieces of evidence (possibly multiple power laws) and need to be able to predict many of these.
- Understanding dynamics and some further details allows one to predict deviations from power law, and that is a very strong test and leads to very precise results

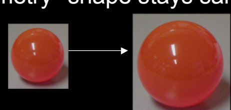
III. Biological Allometry

Metabolic Rate--"Fire of life"--Power for Maintenance, Growth, and Reproduction

Heat loss:
metabolic rate=heat loss rate $\propto$ surface area
↑ Stefan-Boltzmann law



Isometry--shape stays same

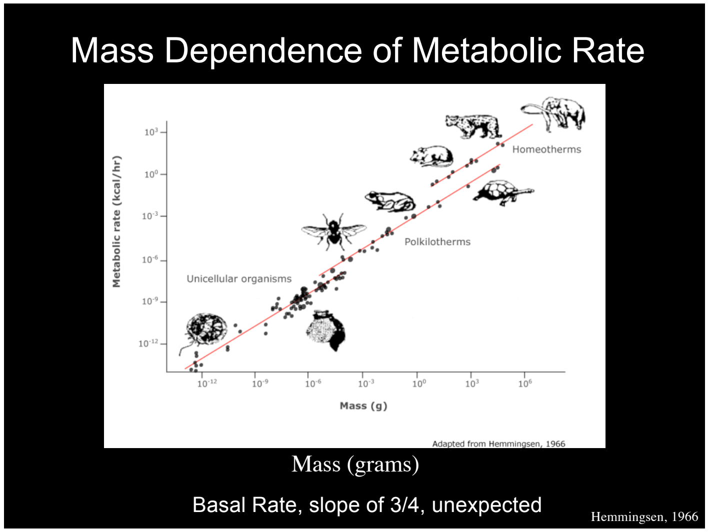


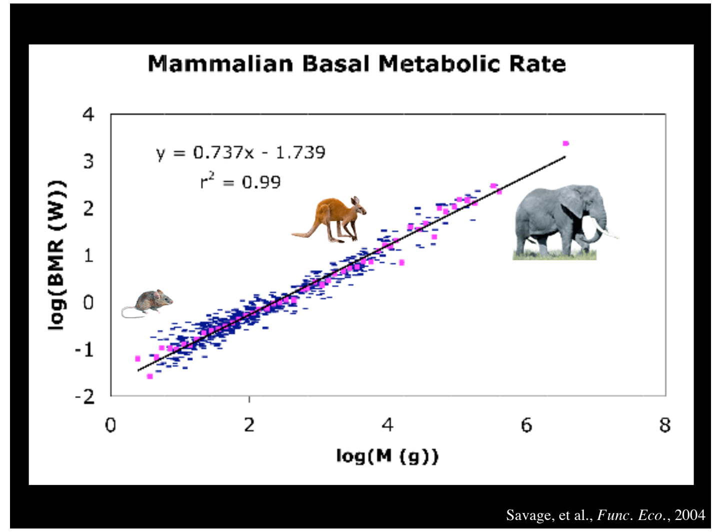
Allometry--shape changes

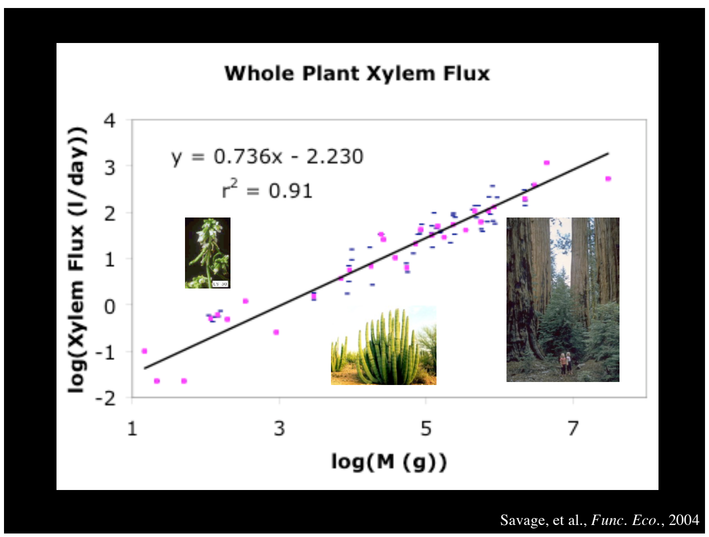
isometry $\Rightarrow$ metabolic rate=heat loss rate $\propto$ surface area $\propto$ (volume)$^{2/3}$

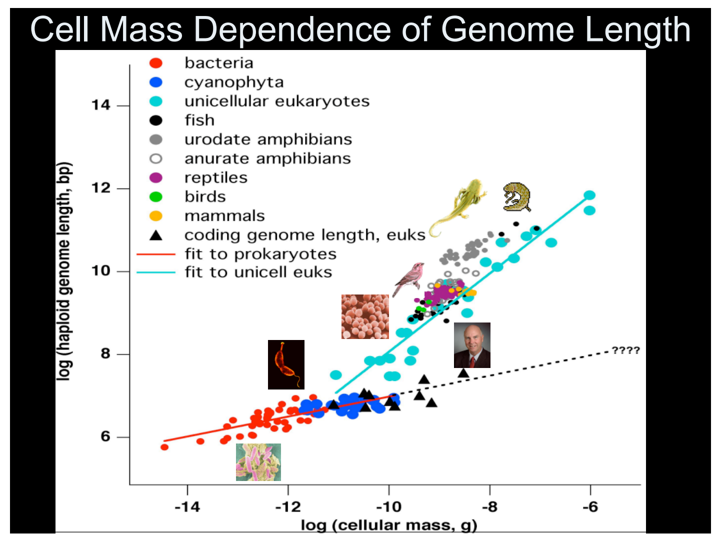
Animals are not isometric, so 2/3 is not a good guess!

Large Scale Patterns


Mass Dependence of Metabolic Rate
Metabolic rate (kcal/hr)
Homeotherms
Polkilotherms
Unicellular organisms
Mass (g)
Adapted from Hemmingsen, 1966
Mass (grams)
Basal Rate, slope of 3/4, unexpected
Hemmingsen, 1966

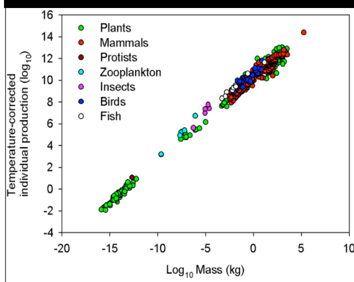

Mammalian Basal Metabolic Rate
y = 0.737x - 1.739
r² = 0.99
log(BMR (W))
log(M (g))
Savage, et al., Func. Eco., 2004

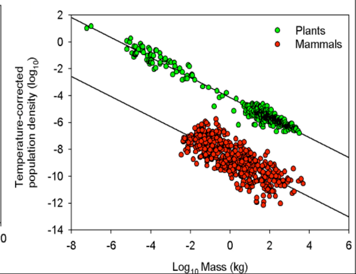

Whole Plant Xylem Flux
y = 0.736x - 2.230
r² = 0.91
log(Xylem Flux (l/day))
log(M (g))
Savage, et al., Func. Eco., 2004


Cell Mass Dependence of Genome Length
bacteria
cyanophyta
unicellular eukaryotes
fish
urodate amphibians
anurate amphibians
reptiles
birds
mammals
coding genome length, euks
fit to prokaryotes
fit to unicell euks
????
log (haploid genome length, bp)
log (cellular mass, g)

Annual Biomass Production

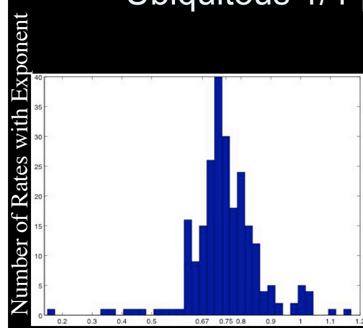
Population Density

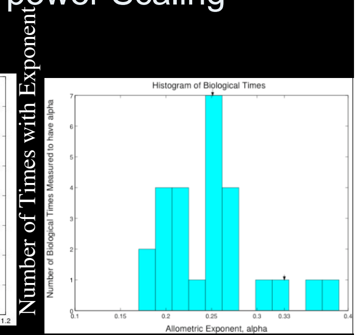




Ernest, et al., *Ecol. Lett.*, 2003

Ubiquitous 1/4-power Scaling





Scaling Exponent

Rates at the cellular, individual, and population level for many different taxa scale in this way. Many times and lengths also scale.

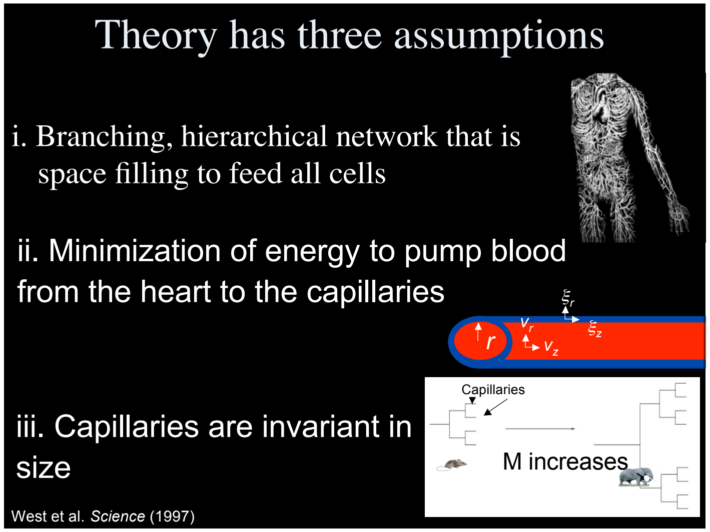
Compiled from Peters, *Ecological Implications of Body Size*, (1983);Savage *et al*., Func. Eco. 2004

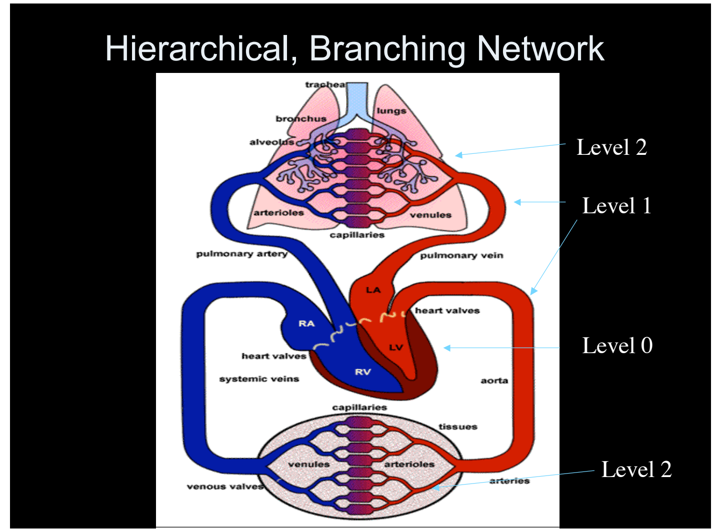
Theory for body mass scaling

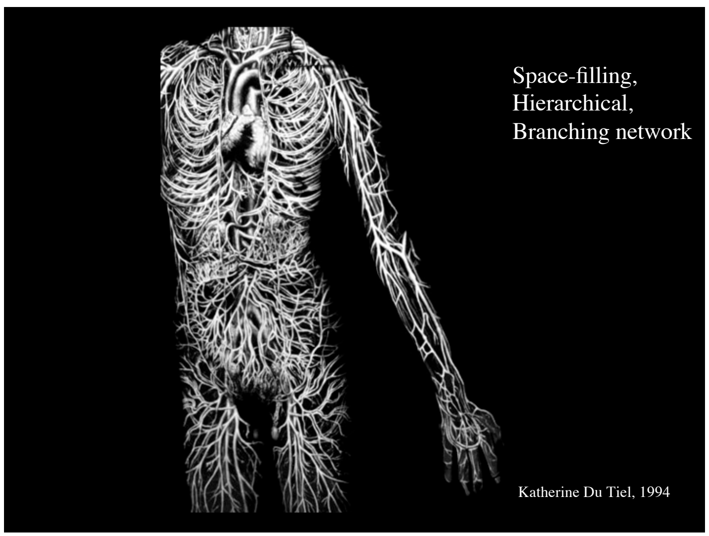
Theories are approximations that hope to impart deeper understanding

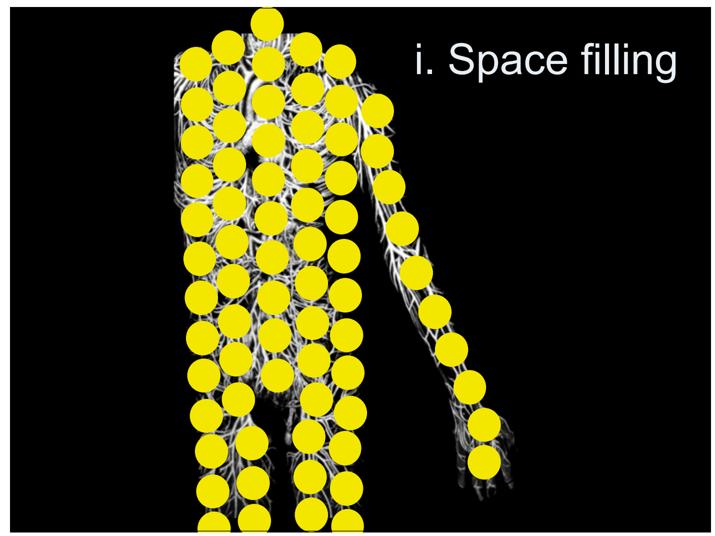
We all know that art [theory] is not truth. Art [theory] is a lie that makes us realize truth, at least the truth that is given us to understand. The artist [theorist] must know the manner whereby to convince others of the truthfulness of his lies.

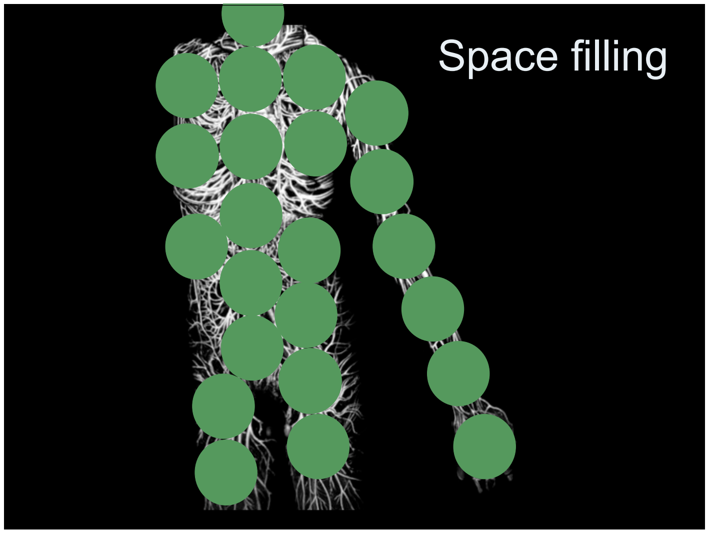
--Pablo Picasso

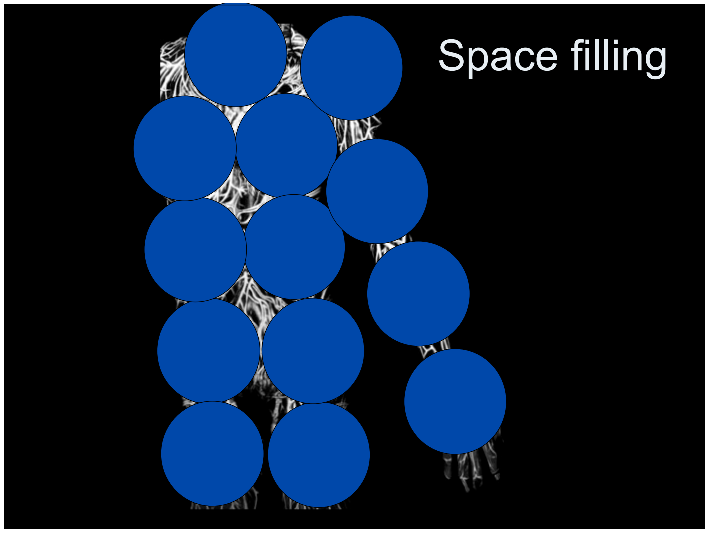

Theory has three assumptions
i. Branching, hierarchical network that is space filling to feed all cells
ii. Minimization of energy to pump blood from the heart to the capillaries
iii. Capillaries are invariant in size
Capillaries
M increases
West et al. Science (1997)

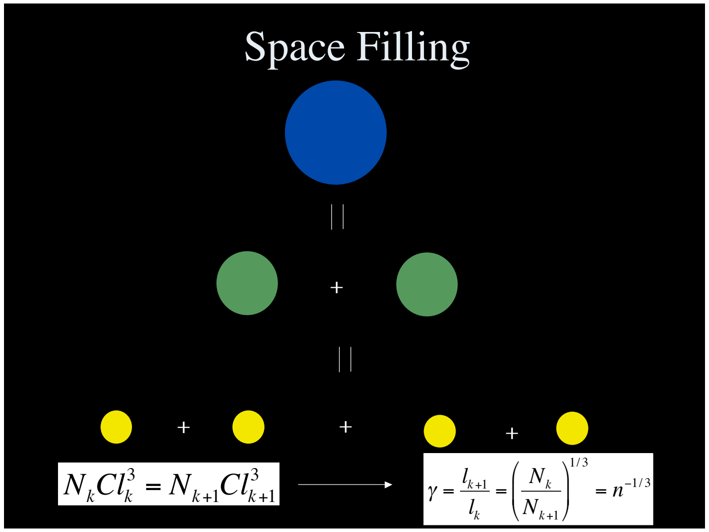

Hierarchical, Branching Network
trachea
lungs
bronchus
alveolus
arterioles
venules
capillaries
pulmonary artery
pulmonary vein
LA
RA
heart valves
LV
RV
heart valves
systemic veins
aorta
capillaries
tissues
venules
arterioles
venous valves
arteries
Level 2
Level 1
Level 0
Level 2

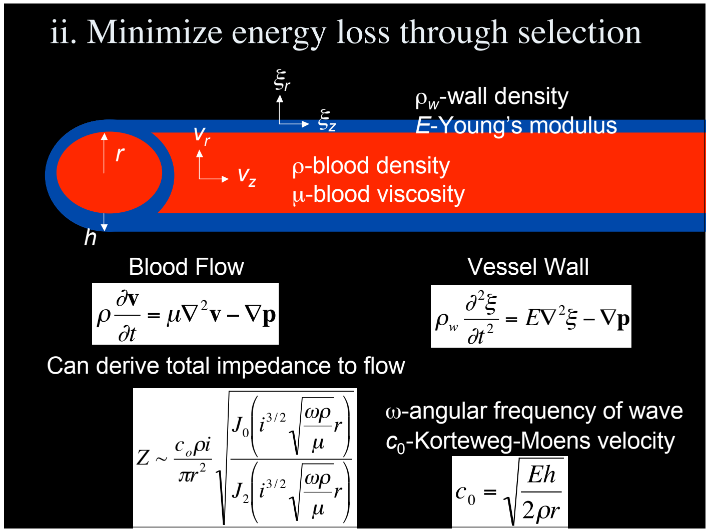

Space-filling,
Hierarchical,
Branching network
Katherine Du Tiel, 1994


i. Space filling


Space filling

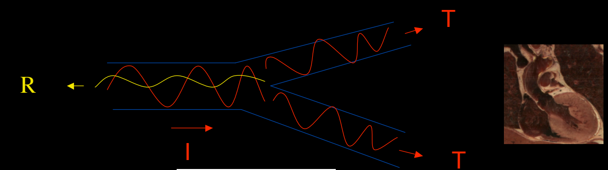

Space filling


Space Filling
=
+
=
+ + +
$N_k C l_k^3 = N_{k+1} C l_{k+1}^3$
$\gamma = \frac{l_{k+1}}{l_k} = \left(\frac{N_k}{N_{k+1}}\right)^{1/3} = n^{-1/3}$


ii. Minimize energy loss through selection
ξ_r
ξ_z
ρ_w-wall density
E-Young's modulus
v_r
v_z
r
h
ρ-blood density
μ-blood viscosity
Blood Flow
$\rho \frac{\partial \mathbf{v}}{\partial t} = \mu \nabla^2 \mathbf{v} - \nabla \mathbf{p}$
Vessel Wall
$\rho_w \frac{\partial^2 \xi}{\partial t^2} = E \nabla^2 \xi - \nabla \mathbf{p}$
Can derive total impedance to flow
$Z \sim \frac{c_o \rho i}{\pi r^2} \sqrt{\frac{J_0\left(i^{3/2}\sqrt{\frac{\omega\rho}{\mu}}r\right)}{J_2\left(i^{3/2}\sqrt{\frac{\omega\rho}{\mu}}r\right)}}$
ω-angular frequency of wave
c_0-Korteweg-Moens velocity
$c_0 = \sqrt{\frac{Eh}{2\rho r}}$

ii. Minimize energy loss (selection)

Reflection at junctions (Important for larger vessels, pulsatile flow)

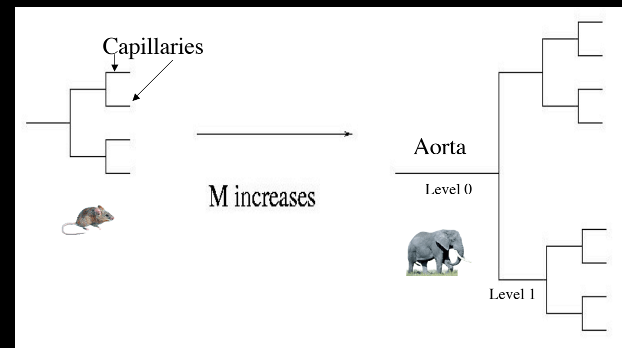


$$\beta = \frac{r_{k+1}}{r_k} = n^{-1/2}$$ Area Preserving

Dissipation (Important for small vessels, Poiseuille flow)

$$\beta = \frac{r_{k+1}}{r_k} = n^{-1/3}$$ Area Increasing

Body Size Changes Network Size



Terminal units are invariant.

Metabolic Rate, *B*, and Body Mass, *M*

$$M \propto V_b = \sum_{levels} n_k \pi r_k^2 l_k \propto N_T^{4/3} V_T \propto B^{4/3}$$

- Mass → M
- Blood volume → V_b — Follows from Energy Min.
- Number of Terminal units → N_T
- Volume of Terminal units → V_T
- Met Rate → B
- Use scale factors to relate each level to terminal units.
- Invariance of terminal units $B=N_T B_T$

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

West et al. *Science* (1997)

Theory has three assumptions

- Branching, hierarchical network that is space filling to feed all cells->relates vessel lengths across levels of cardiovascular system
- Minimization of energy to send vital resources to the terminal units (pump blood from the heart to the capillaries)->relates vessel radii across levels of cardiovascular system and connects blood volume to body size
- Capillaries are invariant in size->sets overall scale for cardiovascular system

Together these determine the scaling for the network.

IV. Conclusions

1. Power laws are common in nature due to self similarity and behavior near critical points.

2. Be careful to make sure you have a power law.

3. Can often explain and predict a lot without knowing *details* of the problem

4. Power laws are common in biology (and elsewhere)

5. Dynamical model based on distribution of resources makes many predictions that match data.