ECOL586 Lecture 4 Allometry 3: Models and theory for the origin of allometric scaling

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Background

- Organism size is *the most important trait* in biology.
- Biological diversity is essentially just differences in size.
- The study of size (allometry) is perhaps the longest studied and most contentious areas of biology.
Talk Outline

- Metabolic Scaling Theory (MST) – Core theory summary
- Assessing core assumptions of theory (organismal scaling)
- Extend theory – Scaling of diversity of form & function
  - relaxing many core assumptions
- Extend theory – Scaling of structure and dynamics of forests
- Extend theory – Scaling of ecosystem production
- Extend theory – Metabolic basis of Biodiversity
Models for the origin of allometric relationships

Two early and prominent models . . .

(1) Pipe- Model for plant form and function

- Relatively unknown outside of forestry
- Only for plants (?)
- Well ahead of its time (1964)

(2) Elastic similarity concept

- Biomechanical support
- Only works for metabolism for animals
- Applies to other allometries in plants
(1) Pipe-Model

Shinozaki et al. 1964

Still among the most cited general model of plant form and scaling plant function
The Pipe-Model of Plant Form

• Problem

How to estimate tree biomass (leaves, stem etc.)?

• Observation

Mass of leaves is directly proportional to the mass of stems and branches.

Relationship between photosynthetic mass \([\Gamma(z)]\) and non-photosynthetic mass \([C(z)]\) organs.

\[
\Gamma(z) = L \cdot C(z)
\]

\(L = \text{plant length}\)

A unit of leaves is supplied by ‘pipe’ with constant thickness and cross-sectional area
A leaf is supported by a constant number of pipes

- Branch consists of a ‘bunch of pipes’

- Branch area proportional to the total number of pipes!
Fig. 8. Diagrammatic representation of the pipe model of tree form, showing the successive accumulation of disused pipes in the trunk associated with the progress of tree growth.
Fig. 6. Linear relation between the area of arbitrary cross-sections $S(z)$ on a branch of *Ficus erecta* and the amount of leaves and fruits born by the parts of the branch above each section.

Leaf mass $\propto$ branch area
At each branching level, from trunk to terminal branches

- The sum of the cross-sectional area of branches is constant.
- Branching is area-preserving

For a given branching level, $k$

\[(\text{Area of branch } k) \times (\text{number of branches } k) = C\]  
\[\text{a constant!}\]

\[
N = C2 \left(\frac{1}{\pi}\right) D^{-2}
\]

\[
N \propto D^{-2}
\]

\[\left(\pi \left[\frac{n^2}{2}\right]\right) \cdot (M) = C \text{ Check – squared term on}\]
Distribution of branch sizes fits pipe-model

\[ N \propto D^{-2} \]

Number of branches

Branch diameter

Fig. 1. Frequency distribution of diameter of roots in a tree measured at 10 cm intervals, \( D \) and \( f \) respectively standing for diameter and frequency

A) Abies sachalinensis  B) Pinus Thumbergii  C) Betula platyphylla japonica  D) Betula Ermanii.
Problems:

• Most branches are mostly non-conducting (heartwood)

Solution:

Leaf area $\propto$ sapwood area$^1$ In general this is approximately correct

Problems:

• All of the hydrodynamic predictions (fluid moving through pipes) appear to be completely incorrect.
Elastic Similarity

Thomas A McMahon (1943 – 1999) Harvard University
Elastic Similarity

- Tom McMahon (1973) the 3/4 exponent of metabolism can be derived from biomechanical considerations (Elastic Similarity).

- Consider a tall cylinder of given height and radius

- If total load exceeds the strength of the column, it will fail “elastic buckling”

- How to scale body dimensions to avoid elastic buckling?

Elastic Similarity

Length dimensions must be scaled accordingly to avoid buckling

\[ L^3 \propto D^2 \]

\[ L \propto D^{2/3} \]

Because of elastic criteria height (length) and diameter must be scaled according to a specific exponent.

Critical Buckling Height

\[ L_{\text{crit}} = k \left( \frac{E}{\rho} \right)^{1/3} D^{2/3} \]

Greenhill, G 1881 Proc. Cambridge Phil. Soc. 4:65-73

Elastic Similarity

Fig. 1 (left). Metabolic heat production plotted against body weight on logarithmic scales. The solid line has slope $\frac{3}{4}$. The broken line, which does not fit the data, has slope $\frac{2}{3}$ and represents the way surface area increases with weight for geometrically similar shapes (adapted from (2)).

Fig. 2 (right). Tree height plotted against trunk base diameter on logarithmic scales for record trees representing nearly every American species. The trunk proportions are limited by elastic buckling criteria, since no points lie to the left of the solid line. Data from (18, 19).
Elastic Similarity

McMahon - elastic similarity principles applied to animals

• Mass of a given limb is

\[ M_B \propto L D^2 \]

• Elastic criteria require

\[ L^3 \propto D^2 \]
\[ L \propto D^{2/3} \]

• Therefore

\[ L \propto M^{1/4} \]
\[ D \propto M^{3/8} \] Quarter-powers!
Elastic Similarity

Work performed by contracting muscle (W)

\[ W \propto \sigma A \Delta L \]

\( \sigma = \) tensile stress (force per unit area)
\( A = \) cross sectional area of muscle
\( \Delta L = \) shortening distance

Power, \( P \), developed by muscle (work per unit time)

\[ P \propto \sigma A \frac{\Delta L}{\Delta t} \]
\[ P \propto A \]
\[ A \propto D^2 \]

\[ P \propto D^2 \propto \left( \frac{M^{3/8}}{D} \right)^2 \propto M^{3/4} \]

Derivation of Kleiber’s result!
\( \frac{3}{4} \) scaling of power (metabolism)
Elastic Similarity

- McMahon’s model, for muscles and based on elastic similarity predicts quarter-power scaling exponents

- Questions on generality . . . .

  What about other organisms - without muscle?

  What about other known allometric scaling relationships?
A Unified Theory for Allometric Scaling Relationships?
Metabolic Scaling Theory (MST)
Metabolic Scaling Theory (MST)
Several initial papers published foundation of MST (1997-2005)

Niklas and Enquist (2001) PNAS 98: 2922-2927
Gillooly et al. 2001 Science 293: 2248
Enquist and Niklas (2002) Science
A General Model for the Origin of Allometric Scaling Laws in Biology
Geoffrey B. West, James H. Brown,* Brian J. Enquist

Allometric scaling relations, including the 3/4 power law for metabolic rates, are characteristic of all organisms and are here derived from a general model that describes how essential materials are transported through space-filling fractal networks of branching tubes. The model assumes that the energy dissipated is minimized and that the terminal tubes do not vary with body size. It provides a complete analysis of scaling relations for mammalian circulatory systems that are in agreement with data. More generally, the model predicts structural and functional properties of vertebrate cardiovascular and respiratory systems, plant vascular systems, insect tracheal tubes, and other distribution networks.

The Fourth Dimension of Life: Fractal Geometry and Allometric Scaling of Organisms
Geoffrey B. West,1,* James H. Brown,2,3 Brian J. Enquist2,3

Fractal-like networks effectively endow life with an additional fourth spatial dimension. This is the origin of quarter-power scaling that is so pervasive in biology. Organisms have evolved hierarchical branching networks that terminate in size-invariant units, such as capillaries, leaves, mitochondria, and oxidase molecules. Natural selection has tended to maximize both metabolic capacity by minimizing the scaling of exchange surface areas, and internal efficiency. By minimizing the scaling of transport distances and times. These design principles are independent of detailed dynamics and explicit models and should apply to virtually all organisms.
Biology is a science comprised of vascular networks and fractal-like surface areas.
Mathematically, networks of plants and animals are similar.

Biological networks are remarkably convergent in morphology . . .

Figure 4.9:1 A silicone elastomer cast of the venous tree of a cat’s lung whose veins are subjected to a pressure difference $p_b - P_a$ of $-17 \text{ cm H}_2\text{O}$. Pleural pressure = 0 (atmospheric). Airway pressure = 10 cm H$_2$O. Blood vessel pressure was $-7 \text{ cm H}_2\text{O}$. 
Unlike the genetic code, which has evolved only once in the history of life, fractal-like distribution networks have originated many times.

Extensive surface areas of leaves, gills, lungs, guts, kidneys, chloroplasts, and mitochondria, the whole-organism branching architectures of trees, sponges, hydrozoans, and crinoids, and the treelike networks of diverse respiratory and circulatory systems.
An Analogy -
How to design a transport network?

- Optimally satisfy the needs of people
- But with a limited amount of resources
Core Assumption: Scaling of metabolism determined by the size and geometry of hierarchical vascular networks that control scaling of ‘metabolic units’ and surface areas (capillaries, leaves, etc.)

West, Brown, Enquist 1997 Science
West, Brown, Enquist 1999 Nature
Biological vascular distribution networks ultimately link fundamental ‘metabolic units’ that are embedded in/define fractal-like surface areas.
The mitochondria . . . .

But there is an important problem here
Mitochondrial Distribution Networks


Mitochondrial Clumps—Virtual networks?

We conjecture that organisms have been selected to maximize fitness by maximizing metabolic capacity, namely, the rate at which energy and material resources are taken up from the environment and allocated to some combination of survival and reproduction.

Maximize metabolic capacity . . . this has been achieved by increasing surface areas where resources are exchanged with the environment.

Minimize distances over which materials are transported (within the body) and hence the time required for transport.

“[quarter-power scaling] relationships should apply to all organisms that have been selected to maximize metabolic power under the constraint of minimizing internal transport distances and thereby having a maximally compact three dimensional body shape.”
Core Assumption - (#1) Scaling of metabolism, physiology, life history etc. determined by the size and geometry of hierarchical networks that control scaling of ‘metabolic units’ (leaves).

\[
\frac{dM}{dt} = b_0 M^\theta \propto N_L
\]

Production

Exponent governed by branching geometry (branching traits)

West, Brown, Enquist 1997 Science
West, Brown, Enquist 1999 Nature
Core Assumption (#2) – Pace of metabolism set by fundamental physiological properties of terminal metabolic units of network (leaves)

\[ \frac{dM}{dt} = b_0 M^\theta \]

Normalization governed by ‘leaf’ traits and allocation traits

Secondarily Assume - While leaf traits may vary, on average they do not systematically change with plant size
Secondary Optimizing Assumptions

In general, evolution by natural selection has shaped the geometry of biological distribution networks to follow two principles:

- **Space filling**
  - maximize resource exchange surfaces
- **Area preserving**
  - minimize transport costs, obey biomechanics
Core Assumptions
- Hierarchical Network
- Self-similar branching rules
- Symmetrical branching
- Dimensions and physiology of terminal ‘branch’ invariant of network size. (leaves etc.)

Secondary Assumptions
- Selection to ‘optimize’ network
- Space-filling branching
  + Area preserving branching
    = Biomechanical stability
Predictions –
(i) scaling exponents originate from two branching traits (rules)

\[ \frac{dM}{dt} \propto \dot{R} \propto \dot{P} \propto \dot{Q}_0 \propto N_L \propto M^\theta \]

**Whole-tree Growth**

**photosynthesis**

**Respiration**

**Network flow rate**

**Plant Size**

**# or mass of leaves**

**Plant Size**

\[ r_{k+1} / r_k \equiv n^{-a} \]

**Branch radii ratio**

\[ l_{k+1} / l_k \equiv n^{-b} \]

**Branch length ratio**

**θ Determined by Branching Traits**

\[ \theta = 1/(2a+b) \]

\[ N \] is the furcation ratio (= 2 for a bifurcating network etc.)

For large \( N \), Optimal Network

\[ a = 1/2, \quad b = 1/3, \quad \theta = 3/4 \]

Area Preserving  Volume Filling

West et al. (1999) *Nature*

Enquist et al. (2007) *Nature*

Savage et al. (2008) *PLoS Computational*
Many aspects of how morphology scales due to network geometry (branching traits)

Scaling Relationships Between Morphological Traits
Price, Enquist, Savage (2007) PNAS

\[ l_0 \propto r_0^a b \quad = \frac{2}{3} \]

\[ l_0 \propto M^{b\theta} \quad = \frac{1}{4} \]

\[ r_0 \propto M^{a\theta} \quad = \frac{3}{8} \]

For large N, Optimal Network
\[ a=1/2, \quad b=1/3, \quad \theta=3/4 \]

Area Preserving Volume Filling
The ‘da Vinci’ rules
Self similar branching rules

The total cross-sectional area of branches is constant throughout the tree

Ratio of area of mother branch to area of daughter branches = 1
Assumptions:

- Assume resources are distributed through a hierarchical branching network (*heart to cells*).

- Start with trunk (level 0) that splits into $N$ total branches across $k$ levels to terminal branches.

- At each $k$th level assume symmetrical branching
  \[ n_k = n \]

- Dimensions of terminal 'units' (capillary, cell size, leaves, mitochondria etc.) are invariant with size of network
  \[ r_c, l_c, \overline{u}_c, \Delta p_c \]

- First, assess network with large number of branching generations, $N$

Violations in any of these assumptions will cause deviations from model predictions
Scaling of network flow rates

\[ Q_0 \propto B \propto V_{Tot} \propto M^\theta \]

If \( B \propto M^a \)

Thus,

\[ \dot{Q}_0 \propto M^a \]

\[ N_c \propto M^a \]

For a self-similar network (fractal)
Number of branches increases in geometric proportion

\[ N_k = n^k \]

Branching level

Number of branches
Furcation
Scaling of network flow rates

Total flow rate $Q_0 \propto B \propto V_{Tot} \propto M^\theta$

Metabolic rate
Network volume
Organismal mass

Total Fluid Flow is conserved

Number of branches at $k^{th}$ level
Ave. flow rate through $k^{th}$ level branch

Average flow rate through $k^{th}$ level branch

$Q_0 = N_k Q_k = N_k \left( \pi r_k^2 \bar{u}_k \right) = N_c \left( \pi r_c^2 \bar{u}_c \right)$

$\dot{Q}_0 \propto B \propto N_c$

Average flow rate through final branch - the capillary or petiole of leaf

West, Brown, Enquist (1997) Science
Number of branches increases geometrically from level 0 to $N$

$$N_k = n^k$$

Number of branches at $k$th level
Furcation ratio (2 for bifurcating network)

$$N_N = N_c = n^N$$

Total number of branches in network
Total number of terminal branches (capillaries, leaves etc.)

$$N = \frac{a \ln(M/M_0)}{\ln n}$$

Figure 1. Schematic vessel architecture and branching. A vessel at level $k$ branches into two daughter vessels at level $k+1$. The branching ratio is thus $n=2$. The radii, $r_{k+1}$, and lengths, $l_{k+1}$, of the two daughter vessels are identical by Assumption 3. The ratios of the radii and lengths at level $k+1$ to those at level $k$ are defined as $\gamma$, $\beta_>$, and $\beta_<$ in Equations 2 and 3. The choice of $\beta_>$ for the radial ratio corresponds to area-preserving branching and of $\beta_<$ to area-increasing branching. In the WBE model, the cardiovascular system is composed of successive generations of these vascular branchings, from level 0 (the heart) to level $N$ (the capillaries).

doi:10.1371/journal.pcbi.1000171.g001
Characterize Network Branching Structure

Need to determine how $n_k$, $r_k$, and $l_k$ change throughout the network.

Introduce scale factors: Branching Traits

Ratio of lengths

$$\gamma \equiv \frac{l_{k+1}}{l_k}$$

Ratio of radii

$$\beta \equiv \frac{r_{k+1}}{r_k}$$

Furcation ratio

$$n_k$$

Figure 1. Schematic vessel architecture and branching. A vessel at level $k$ branches into two daughter vessels at level $k+1$. The branching ratio is thus $n=2$. The radii, $r_{k+1}$, and lengths, $l_{k+1}$, of the two daughter vessels are identical by Assumption 3. The ratios of the radii and lengths at level $k+1$ to those at level $k$ are defined as $\gamma$, $\beta_>$, and $\beta_<$, in Equations 2 and 3. The choice of $\beta_>$ for the radial ratio corresponds to area-preserving branching and of $\beta_<$ to area-increasing branching. In the WBE model, the cardiovascular system is composed of successive generations of these vascular branchings, from level 0 (the heart) to level $N$ (the capillaries).

doi:10.1371/journal.pcbi.1000171.g001
Volume of fluid in the network, $V_b$, depends upon size of network and the geometry of network branching

$$V_b = \sum_{k=0}^{N} N_k V_k = \sum_{k=0}^{N} \pi r_k^2 l_k n_k$$
Geometric Series
A handy trick for summations Involving a power-law

When $n$ is small

$$S_n = \sum_{k=0}^{n} r^k = \frac{1 - r^{n+1}}{1 - r}.$$  

When $n$ is large then

$$S = S_\infty = \sum_{k=0}^{\infty} r^k = \frac{1}{1 - r}.$$
Volume of fluid within the network, \( V_b \)

\[
V_b = \sum_{k=0}^{N} V_k V_k = \sum_{k=0}^{N} \pi R_k^2 l_k n_k
\]

\[
V_b = \frac{\pi R_{k+1}^2 l_{k+1} n_{k+1}}{k+1}
\]

Beta

\[
\beta_k = \beta \frac{R_{k+1}}{R_k} \Rightarrow R_k = \frac{R_{k+1}}{\beta}
\]

Gamma

\[
\gamma_k = \gamma \frac{l_{k+1}}{l_k} \Rightarrow l_k = \frac{l_{k+1}}{\gamma}
\]

\[
V_b = \sum_{k=0}^{N} \pi R_k^2 l_k n_k
\]

From copy of notes explaining derivation with Choy Huang
Volume of fluid in the network, $V_b$, depends upon size of network and the geometry of network branching.

\[
V_b = \sum_{k=0}^{N} N_k V_k = \sum_{k=0}^{N} \pi r_k^2 l_k n^k
\]

Geometry of branching \hspace{2cm} Number of branching generations

\[
= \left( \frac{n \gamma \beta^2}{\left( n \gamma \beta^2 \right)^{-1}} \right)^{-(N+1)} - 1 \approx n^N V_c
\]

Total volume of all terminal branch
Thus, the derivation of scaling exponent, \( \alpha \), from the traits of the branching network

\[
V_b = \sum_{k=0}^{N} N_k V_k = \sum_{k=0}^{N} \pi n_k^2 l_k n^k = \frac{(n \gamma \beta^2)^{(N - 1)}}{(n \gamma \beta^2)^{-1} - 1} n^N V_c \tag{4}
\]

where the last expression reflects the fractal nature of the system. As shown below, one can also prove from the energy minimization principle that \( V_b \sim M \). Because \( n \gamma \beta^2 < 1 \) and \( N \gg 1 \), a good approximation to Eq. 4 is

\[
V_b = V_0/(1 - n \gamma \beta^2) = V_c (\gamma \beta^2)^{-N}/(1 - n \gamma \beta^2).
\]

From our assumption that capillaries are invariant units, it therefore follows that \( (\gamma \beta^2)^{-N} \sim M \). Using this relation in Eq. 3 then gives

\[
M \sim (\gamma \beta^2)^{-N}
\]

\[
\dot{Q}_0 \sim M^\alpha
\]

\[
N_c \sim M^\alpha
\]

\[
M \sim (\gamma \beta^2)^{-N}
\]
Secondary Optimizing Assumptions

In general, evolution by natural selection has shaped the geometry of biological distribution networks to follow two principles:

- **Space filling**
  - maximize resource exchange surfaces

- **Area preserving**
  - minimize transport costs, obey biomechanics
Branching Rule 1: Branching is Space Filling (Volume Preserving)

Network must branch to supply all cells and/or fill space

Total Volume of Network

At all branching levels, network ‘fills a volume’ and branch volume is constant:

\[ N_k l_k^3 = N_{k+1} l_{k+1}^3 \]

\[ \gamma_k^3 \equiv \left( \frac{l_{k+1}}{l_k} \right)^3 \approx \frac{N_k}{N_{k+1}} = \frac{1}{n} \]

\[ V \approx N_k \gamma_k \propto N_k l_k^3 \]

\[ \gamma \equiv n^{-1/3} \]
The ‘da Vinci’ rules
A self similar branching rules

The total cross-sectional area of branches is constant throughout the tree
Branching Rule 2: Branching is Area Preserving

Natural selection to minimize resistance through network

Proving this is quite technical - depends on dynamics of system

Total cross-sectional area at each branching level is constant (area-preserving)

\[ \pi r_k^2 = n \pi_{k+1}^2 \]

\[ N_k r_k^2 = N_{k+1} r_{k+1}^2 \]

\[ \beta \equiv \frac{r_{k+1}}{r_k} = n^{-1/2} \]
Prediction: A network that is space-filling and area-preserving will be characterized by a $\frac{3}{4}$ metabolic scaling exponent

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

$$\gamma \equiv \frac{l_{k+1}}{l_k} = n^{-1/3}$$

$$(\gamma \beta^2)^{-N} \propto M$$

$$\dot{Q}_0 \propto B \propto M^a$$

$$\theta = -\frac{\ln n}{\ln(\gamma \beta^2)}$$

Independent of $n$

$$\theta = \frac{3}{4}$$
Predictions –

(i) scaling exponents originate from three branching traits (rules)

\[ \theta \text{ Determined by Branching Traits} \]

\[ \theta = \frac{1}{2a+b} \]

\[ \frac{r_{k+1}}{r_k} = n^{-a} \]

\[ \frac{l_{k+1}}{l_k} = n^{-b} \]

For large \( N \), Optimal Network

\( a = 1/2, \quad b = 1/3, \quad \theta = 3/4 \)

West et al. (1999) Nature
Enquist et al. (2007) Nature
Savage et al. (2008) PLoS Computational

Growth \( \dot{G} \propto R \propto \dot{P} \propto \dot{Q}_0 \propto N_L \propto M^\theta \)

Respiration
Net photosynthesis
Network flow rate
# or mass of leaves
Plant Size

Area Preserving
Volume Filling
Predictions:

- As the number of cells in body, $N_{\text{cell}}$ increases $M^1$, $N_{\text{cell}} \propto V \propto M$
- The optimal network can only supply resources so fast $(M^{3/4})$ . . .
- As a result - the demand of cells must match the rates at which the network can deliver $\dot{Q}_0 \propto B \propto M^{3/4}$
- $B/N_{\text{cell}} \propto M^{-1/4}$
Biological Networks Control Biological Rates and Times

Determines how fast a cell can run and hence the pace of biological time

The metabolic potential of a cell
Place cell in the middle of a large network
The same cell but placed within a network with few limits
Consistent with the prediction that constraints of network limits metabolic potential of cells.
Core Assumptions
- Hierarchical Network
- Self-similar branching rules
- Symmetrical branching
- Dimensions and physiology of terminal ‘branch’ invariant of network size.

Secondary Assumptions
- Selection to ‘optimize’ network
- Space-filling branching
- Area preserving branching

Biomechanical stability
Many aspects of how morphology scales due to network geometry (branching traits)

Scaling Relationships Between Morphological Traits

\[ l_0 \propto r_0^a \quad = \frac{2}{3} \]

\[ l_0 \propto M^{b\theta} \quad = \frac{1}{4} \]

\[ r_0 \propto M^{a\theta} \quad = \frac{3}{8} \]

For a large optimal network
\[ a = 1/2, \quad b = 1/3, \quad \theta = 3/4 \]

Price, Enquist, Savage (2007) PNAS

Area Preserving    Volume Filling

Length \( l_0 \)
Stem radius, \( r_0 \)
Mass (M)
Interpecific Scaling of Leaf Biomass

\[ \dot{G} \propto \dot{R} \propto \dot{P} \propto \dot{Q}_0 \propto N_L \propto M^\theta \]

Enquist and Niklas (2002) *Science*
Enquist et al. (2007) *Nature*
Whole organism metabolic rates scale as $M^{3/4}$
## Predicted Relationships for Plant Vascular Networks

### Table 1 Predicted values of scaling exponents for physiological and anatomical variables of plant vascular systems.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Plant mass</th>
<th>Branch radius</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Exponent</td>
<td>Exponent</td>
</tr>
<tr>
<td>Predicted</td>
<td>Symbol</td>
<td>Symbol</td>
</tr>
<tr>
<td>Number of leaves</td>
<td>$\frac{3}{4}$ (0.75)</td>
<td>$n_0^c$</td>
</tr>
<tr>
<td>Number of branches</td>
<td>$\frac{3}{4}$ (0.75)</td>
<td>$N_0$</td>
</tr>
<tr>
<td>Number of tubes</td>
<td>$\frac{3}{4}$ (0.75)</td>
<td>$n_0$</td>
</tr>
<tr>
<td>Branch length</td>
<td>$\frac{4}{3}$ (0.25)</td>
<td>$l_0$</td>
</tr>
<tr>
<td>Branch radius</td>
<td>$\frac{3}{4}$ (0.375)</td>
<td>$r_0$</td>
</tr>
<tr>
<td>Area of conductive tissue</td>
<td>$\frac{4}{3}$ (0.875)</td>
<td>$A_0^{ct}$</td>
</tr>
<tr>
<td>Tube radius</td>
<td>$\frac{1}{2}$ (0.0625)</td>
<td>$a_0$</td>
</tr>
<tr>
<td>Conductivity</td>
<td>1 (1.00)</td>
<td>$K_0$</td>
</tr>
<tr>
<td>Leaf-specific conductivity</td>
<td>$\frac{4}{3}$ (0.25)</td>
<td>$L_0$</td>
</tr>
<tr>
<td>Fluid flow rate</td>
<td>$Q_k$</td>
<td>2 (2.00)</td>
</tr>
<tr>
<td>Metabolic rate</td>
<td>$\frac{3}{4}$ (0.75)</td>
<td>$Q_0$</td>
</tr>
<tr>
<td>Pressure gradient</td>
<td>$\frac{1}{4}$ ($-0.25$)</td>
<td>$\Delta P_0/l_0$</td>
</tr>
<tr>
<td>Fluid velocity</td>
<td>$\frac{1}{4}$ ($-0.125$)</td>
<td>$u_0$</td>
</tr>
<tr>
<td>Branch resistance</td>
<td>$\frac{3}{4}$ (0.75)</td>
<td>$Z_0$</td>
</tr>
<tr>
<td>Tree height</td>
<td>$\frac{1}{4}$ (0.25)</td>
<td>$h$</td>
</tr>
<tr>
<td>Reproductive biomass</td>
<td>$\frac{3}{4}$ (0.75)</td>
<td></td>
</tr>
<tr>
<td>Total fluid volume</td>
<td>$\frac{1}{2}$ (1.0415)</td>
<td></td>
</tr>
</tbody>
</table>
Insights into cancer and disease?

• Notable pattern of cancer cells is that metabolism increases.

• Suggests that cancer cells are cells that forget they are part of a network . . .

• How do diseases and parasites interact with constraints on the allometric scaling of rates of cellular processing??

• Their replication depends upon host metabolism and/or metabolic machinery . . .
Other Important Points

Theory is quantitative and mechanistic

• Predicts values for exponent and also is capable of predicting the allometric intercept . . . .

• Provides the framework to explore many ramifications of allometry in biology.

Temperature, Stoichiometry, life-history

Begin to explore residual variation . . . .
The importance of scaling

- All living things use the same basic chemical structures and processes
  
  **molecules:** DNA, RNA, ATP, NAD, rubisco
  
  **reactions:** replication, transcription, translation, TCA cycle, photosynthesis

- As biological systems vary from molecules to the biosphere, scaling laws reflect how natural selection has shaped integration of structure and function

- Biological scaling laws have two features:
  1) “invariant” units (approximate constant with body size)
     - molecules, organelles, cells, capillaries, leaves
  2) scaled attributes
     - **structural:** skeletons, bodies/organs, exchange surfaces, distribution networks
     - **functional:** rates of processes, times of activities
Difference between Theory and Model

A theory is aimed at a generalized statement aimed at explaining a phenomenon (mechanism).

A model is a purposeful specific representation of reality. A model can be an applied aspect of a given theory

For example: metabolic scaling theory -> model of scaling of mammalian network -> model of scaling of plant vascular networks.

You can have models without theory (usually these are statistical models where mechanism is unclear or unspecified. Know the difference between statistical and mechanistic models).

The evolution of a successful theory is for it to become more general, through the development of detailed models that apply the theory to a wider class of phenomena.

On Theory in Ecology

PABLO A. MARQUET, ANDREW P. ALLEN, JAMES H. BROWN, JENNIFER A. DUNNE, BRIAN J. ENQUIST, JAMES F. GILLOOLY, PATRICIA A. GOWATY, JESSICA L. GREEN, JOHN HARTE, STEVE P. HUBBELL, JAMES O’DWYER, JORDAN G. OKIE, ANNETTE OSTLING, MARK RITCHIE, DAVID STORCH, AND GEOFFREY B. WEST

We argue for expanding the role of theory in ecology to accelerate scientific progress, enhance the ability to address environmental challenges, foster the development of synthesis and unification, and improve the design of experiments and large-scale environmental-monitoring programs. To achieve these goals, it is essential to foster the development of what we call efficient theories, which have several key attributes. Efficient theories are grounded in first principles, are usually expressed in the language of mathematics, make few assumptions and generate a large number of predictions per free parameter, are approximate, and entail predictions that provide well-understood standards for comparison with empirical data. We contend that the development and successive refinement of efficient theories provide a solid foundation for advancing environmental science in the era of big data.

Keywords: theory unification, metabolic theory, neutral theory of biodiversity, maximum entropy theory of ecology, big data

The grand aim of all science is to cover the greatest number of empirical facts by logical deduction from the smallest number of hypotheses or axioms. (Albert Einstein)
Role of mathematical theory in biology (e.g. how to build a theory/model)

- Start simple – only add complexity kicking and screaming!
- Start with well-understood first principles of biology, physics, and chemistry
- Make deliberate oversimplifications of a more complex reality
- Metabolic scaling theory (MST) elucidates the fundamental unity of life: microbes to sequoia trees, molecules to ecosystems
- It makes precise, quantitative, empirically testable predictions
- Predictions provide baselines for evaluating residual variation due to other factors
- Starting point for more detailed models that includes more variables and biological reality
MST Caveats and qualifications

- Metabolic Scaling Theory – and its applications (models) are deliberate oversimplifications of a more complex reality

- Substantial unexplained variation exists (biology/reality not incorporated into theory):
  - experimental/measurement error
  - stoichiometry
  - phylogenetic constraints
  - environmental conditions and evolutionary adaptations

- Factors not included in the model can be evaluated as deviations from predictions

- Example: stoichiometry (C:P ratio) explains variation in development rates
Predictions –

(i) scaling exponents originate from two branching traits (rules)

\[ \frac{dM}{dt} \propto \dot{R} \propto \dot{P} \propto \dot{Q}_0 \propto N_L \propto M^\theta \]

Whole-tree Growth

Respiration

photosynthesis

Network flow rate

Plant Size

# or mass of leaves

Branch radii ratio

\[ r_{k+1} / r_k \equiv n^{-a} \]

Branch length ratio

\[ l_{k+1} / l_k \equiv n^{-b} \]

\[ \theta = 1/(2a + b) \]

\[ \theta \text{ Determined by Branching Traits} \]

For large N, Optimal Network

a = 1/2, \quad b = 1/3, \quad \theta = 3/4

Area Preserving

Volume Filling

West et al. (1999) Nature

Enquist et al. (2007) Nature

Savage et al. (2008) PLoS Computational
Intraspecific Scaling of Leaf Biomass

\[ \frac{dM}{dt} \propto \dot{R} \propto \dot{P} \propto \dot{Q}_0 \propto N_L \propto M^\theta \]

Whole-tree growth

Photosynthesis

Respiration

Network flow rate

\# or mass of leaves

*Pinus ponderosa*

\[ y = 1.928x^{0.738} \]

*Observed \( \theta = 0.738 \)*
Inter-specific Scaling of Leaf Biomass

\[
dM/dt \propto \dot{R} \propto \dot{P} \propto \dot{Q}_0 \propto N_L \propto M^\theta
\]

Enquist and Niklas (2002) Science
Enquist et al. (2007) Nature
Extend metabolic theory to prediction allocation of plant biomass and carbon

**Scaling Plant Organ Biomass**
*(or how much biomass is below ground?)*

\[
M_L (\text{Leaf Mass})
\]

\[
M_S (\text{Stem Mass})
\]

\[
M_R (\text{Root Mass})
\]

**Predictions**

- \(M_L = \beta_{12} M_S^{3/4}\)
- \(M_L = \beta_{13} M_R^{3/4}\)
- \(M_S = (\beta_{12}/\beta_{13}) M_R\)

**Observed**

- \(M_L \propto M_S^{0.75}\)
- \(M_L \propto M_R^{0.79}\)
- \(M_S \propto M_R^{1.09}\)

Less root mass than predicted by theory

Application of MST to plants (plant specific model and some background on some esoteric xylem anatomy natural history and basic hydraulics)
How do plants scale the transport water to such great heights through their vasculur networks?
How to minimize resistance to xylem flow?

- Remember the Hagen-Poiseuille equation
- Assuming a constant pressure gradient, the resistance to fluid flow within a xylem conduit is given by:

\[ Z_i = \frac{8\eta l_i}{\pi r_i^4} \]

\[ J_i = \frac{\pi r_i^4}{8\eta l_i} \Delta \psi \]
Tapering of Xylem Radii??

What controls the scaling of xylem resistance?

Hagen-Poiseuille equation

\[ Z_i = \frac{8\eta l_k}{\pi r_k^4} \]

If \( r \) is constant then \( Z \) increases directly with \( l \)!
Coordinated and General Scaling of Xylem Traits?

KARL SANIO (1832-1891)

‘Sanio’s Laws’

Tracheid length increase from the inside to the outside of stem and distally up to some Maximum height (from the base to the top of stems).

Sherwin Carlquist 1972

Tracheary cell diameters in the most recent growth ring tend to decrease from the bottom to the top of trees.

thought to reflect adaptive compromises to competing developmental and functional demands.
If xylem elements are scaled so that they taper along path length then resistance is a constant!

Specifically, $D_{\text{xylem}} \propto D^\alpha$, where $\alpha > 1/6$
Starting Assumptions

• **Selection for space-filling branching geometries** in order to maximize carbon uptake by leaves and sap flow through xylem conduits

• **Selection to minimize the scaling of hydraulic resistance** which is equivalent to maximizing the scaling of hydraulic conductance and resource supply to leaves

• **Selection to protect against embolism** and associated decreases in vascular conductance

• **Selection to enforce biomechanical stability** uniformly across the plant branching network

• **Within plants during ontogeny and across species**, terminal leaf size, physiological rates, and internal architecture are independent of increases in plant size.

Violations of any of these assumptions will lead to calculable deviations from predictions.
Extend theory to integrating external and ‘internal’ networks to predict scaling of xylem traits and plant hydraulics.

External branching network

Internal vascular network (xylem)

Principles of Minimizing resistance, space-filling & while protecting against embolism can predict scaling of plant hydraulics.

Savage et al (2010) PNAS
Savage et al. (2010) *PNAS* - > Xylem ‘tubes’ fill branch space or cross-sectional area (principle of space filling also applied to xylem network)
Elaboration of MST to make detailed prediction for scaling whole-plant hydraulics and anatomy of internal vascular network

<table>
<thead>
<tr>
<th>Plant xylem &amp; Hydraulic traits</th>
<th>Theory predicted exponent for scaling trunk or stem radius</th>
</tr>
</thead>
<tbody>
<tr>
<td>Packing (conduit frequency vs. conduit radius, ( r_{\text{int},k} ), not branch radius)</td>
<td>-2</td>
</tr>
<tr>
<td>Conduit radius taper (( r_{\text{int},k} ))</td>
<td>1/3 ( \approx 0.33 )</td>
</tr>
<tr>
<td>Conduits in branch segment (( N_{\text{seg}}^{\text{int},k} ))</td>
<td>4/3 ( \approx 1.33 )</td>
</tr>
<tr>
<td>Fluid velocity (( u_k ))</td>
<td>0 or n.s.</td>
</tr>
<tr>
<td>Conducting-to-nonconducting ratio</td>
<td>0 or n.s.</td>
</tr>
<tr>
<td>Network conductance (( k_k ))</td>
<td>1.84 (finite) 2 (infinite)</td>
</tr>
<tr>
<td>Branch segment conductivity (( K_k ))</td>
<td>8/3 ( \approx 2.67 )</td>
</tr>
<tr>
<td>Leaf-specific conductivity (( K_k/N_{\text{leaves}} ))</td>
<td>2/3 ( \approx 0.67 )</td>
</tr>
<tr>
<td>Volume flow rate (( Q_k ))</td>
<td>2</td>
</tr>
<tr>
<td>Pressure gradient along branch segment (( \Delta P_k/\bar{k} ))</td>
<td>-2/3</td>
</tr>
<tr>
<td>Branch segment conductance (( Z_k/N_{\text{int},k} ))</td>
<td>2</td>
</tr>
</tbody>
</table>

Hydraulic trade-offs and space filling enable better predictions of vascular structure and function in plants

V. M. Savage, L. P. Bentley, B. J. Enquist, J. S. Sperry, D. D. Smith, P. B. Reich, and E. I. von Allmen

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Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved November 9, 2010 (received for review August 17, 2010)

- Integrate scaling of external and internal networks
- Principle of space-filling appears general and also key to understanding scaling of plant hydraulics
Further updated plant scaling model – includes more detail on anatomical, physiological differences between species and individuals

More detailed and more parameterized than WBE 1999 but can predict species-level scaling normalization and scaling exponents

Fig. 1. Elements of metabolic scaling theory. Self-similar and symmetric branching architecture (left) that is area-preserving (central column) yields trunk diameter ($D_{B0}$) by mass ($M^c$) scaling. Xylem conduit architecture (shown in column cross-sections) yields water use ($Q$, flow rate) by $D_{B0}^{-q}$ scaling. Combining mass and water use yields $Q$ by $M^{c_q}$ scaling. If growth rate ($G$) is isometric with $Q$ (metabolic isometry), then the theory yields growth rate ($G$) by $M^{c_q}$ scaling. Asterisked components represent novel parameters that were not explicit in the Savage et al. (2010) model. See Table 1 for other symbols.

From Sperry et al. 2012 Functional Ecology
Paradox – how can there be diversity if everything scales according to metabolic scaling theory?
Paradox – how can there be diversity if everything scales according to metabolic scaling theory?

Global - interspecific - Leaf economic spectrum

Fast Life histories

Slow Life histories

Leaf mass per unit area

Wright et al. 2004 Nature
Limitations of Theory?
Biological networks are rarely (if ever?) symmetrical - Cross Kingdom Analysis

Quantifying Branching Asymmetry

\[ \lambda_R = \frac{r_{\text{child, small}}}{r_{\text{child, large}}} \]

\[ \lambda_L = \frac{l_{\text{child, small}}}{l_{\text{child, large}}} \]

Child Diameter Ratios for Human Cardio-Torso

Mammal network

Symmetrical Network = 1.0

Brummer et al. (ms submitted)
Limitations of Theory?

• Unclear if theory can be applied to understand trait variation within integrated phenotypes

• What about variation in scaling exponents?

• What about variation in scaling intercept?

• What causes residual variation?

• Tree branching model is static – dynamics of branching (birth, growth, death) not explicitly modeled? How do branching structures emerge over the ontogeny of an individual?
Limitations of Theory?

• Unclear if scaling theory can be applied to trait variation within and between species
• What about variation in scaling exponents?
• What causes residual variation about scaling?

But . . .

Most studies focused on optimized predictions – i.e. the ‘quarter-power’ scaling exponents

Missing from debate since 1997 is a focus on the core assumptions and evolutionary basis of the theory fundamental role of vascular networks in the origin of biological scaling relationships.
Theory can better apply to the diversity of life by 

- Relaxing optimality assumptions
- Pointing to the key traits to measure to predict whole organism function
- Integrating MST with other theories

Goal - make MST more predictive and extend range of predictions
BUT! There is variation in allometric exponents. Some species differ from theory predictions.

Distribution of allometric exponents

Number of studies

Allometric Exponent, $\theta$

Savage et al. 2004
Advancing the theory – Relax assumptions of a symmetrical and optimal network to account for trait variation predict more of the variation

Metabolic theory

Assumptions

1. Hierarchical, symmetric branching network
2. Minimization of hydraulic resistance
3. Mechanical stability
4. Space filling architecture
5. Petioles have constant size

Scaling Predictions

1. Number of leaves
2. Number of branches
3. Number of tubes
4. Fluid volume flow rate
5. Metabolic rate
6. Pressure gradient
7. Branch length
8. Tree height
9. Branch radius
10. Area conducting tissue
11. Tube radius
12. Conductivity
13. Leaf-specific conductivity
14. Fluid velocity
15. Branch resistance

How does variation in leaf size and leaf traits, branching asymmetry, influence branching architecture and whole-tree allometry?

Enquist and Bentley (2012) in Metabolic Ecology
Advancing theory by relaxing and detailing secondary assumptions in the study of plant biology (Price et al. 2007 PNAS).
Improving allometric predictions by allowing for branching diversity - asymmetry -

WE TAKE THIS MODEL... ...AND IMPOSE IT ONTO THESE DIFFERING NETWORKS

CAN WE DO BETTER WITH MODELS THAT INCORPORATE ASYMMETRY?

Does incorporating asymmetric branching violate the predictions of metabolic scaling?
Questions/Goals

• Does incorporating asymmetric branching change the predictions of metabolic scaling? Do asymmetric networks follow quarter power scaling?

• Relax the symmetric assumption by defining and exploring two candidates for asymmetrically bifurcating networks.

• Incorporate asymmetric branching into the WBE model as an extension beyond the original symmetric design.

• As was originally done in the original WBE model, minimize hydrodynamic power loss while maximizing fractal space-filling for asymmetrical networks.

Brummer, Savage, Enquist (2017) PLoS Computational Biology
**Branching Rule 3:** Daughter branch asymmetry constrained by rules 1 & 2 (area preserving and volume preserving)

**Symmetric vs. Asymmetric Theories**

**SYMMETRIC:** All child branches within a given generation are identical

**ASYMMETRIC:** Child branches can be wider/thinner and longer/shorter

### Predicted Metabolic Scaling Exponent

**Symmetric**

\[ \Theta \approx - \left( \frac{\ln(\beta^2 \gamma)}{\ln(n)} \right)^{-1} \]

**Asymmetric**

\[ \theta = - \left\{ \frac{\ln(\beta^2 \gamma)}{\ln(2)} + \frac{\ln \left( 1 + \frac{2\Delta \beta \Delta \gamma}{\beta \gamma} + \frac{\Delta \beta^2}{\beta^2} \right)}{\ln(2)} \right\}^{-1} \]

Brummer, Savage, Enquist (2017) PLoS Computational Biology
Important take home messages:

- Incorporating branching asymmetries can possibly explain more variation in scaling.
- Branching networks with differing asymmetries can yield similar \( \frac{3}{2} \) allometric scaling exponents.
- In principle you can predict allometric scaling by measuring branching traits (mother-daughter branch radii, lengths, and asymmetries)

Brummer et al. (2017) *PloS Comp. Bio*
Further applications of MST via more detailed models of branching architectures.

Species are more variable in length ratios than radii ratios.

Smith et al. (2014) *New Phytologist*
Advance scaling theory but adding another key branching trait (asymmetry)

Can create the diversity of plant branching with three branching traits

- Length ratios (WBE model)
- Radii ratios (WBE model)
- Path fraction (NEW! branching asymmetry)

Trade off (Resource Acquisition)

Hydraulic conductance Light Interception

Mean path length of all branches

\[ P_f = \frac{\bar{L}}{L^*} \]

Maximum path length within a tree
Optimal branching architecture (asymmetry) maximizes light intercepted per unit volume of network.

Fig. 6: Volume normalized light interception for the same trees shown in Fig. 4d. Shading corresponds to mean absorption at each zenith angle from horizontal (black) to directly overhead (white). The peaks observed at each zenith angle are suggestive of optimal architectures that maximize carbon gain per carbon spent.

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New Phytologist © 2013 New Phytologist Trust
Some detail on application of MST to branching networks with asymmetry
Symmetric vs. Asymmetric Theories

**SYMMETRIC:** All child branches within a given generation are identical

\[ \Theta \approx -\left(\frac{\ln(\beta^2 \gamma)}{\ln(n)}\right)^{-1} \]

**ASYMMETRIC:** Child branches can be wider/thinner and longer/shorter

\[ \theta = -\left\{ \frac{\ln(\beta^2 \gamma)}{\ln(2)} + \frac{\ln\left(1 + \frac{2\Delta \beta \Delta \gamma}{\beta \gamma} + \frac{\Delta \beta^2}{\beta^2}\right)}{\ln(2)} \right\}^{-1} \]

Brummer, Savage, Enquist (2017) PLoS Computational Biology
• Asymmetric networks can also attain $\frac{3}{4}$ scaling

• Differing network geometries can attain similar scaling exponents

• Different branching geometries can converge on $\frac{3}{4}$ scaling

• Deviation from $\frac{3}{4}$ stem from different branching architectures

Brummer, Savage, Enquist (2017) PLoS Computational Biology
Brummer, Savage, Enquist (2017) PLoS Computational Biology
• Differing network geometries can attain similar scaling exponents

• All of these branching networks – total leaf area scales with network volume or mass to the $3/4$ power

• Different branching geometries can converge on $3/4$ scaling

Brummer, Savage, Enquist (2017) PLoS Computational Biology