Ecosystem Concepts:
Allometry, Scaling/Complexity,
and Power Laws

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Topics

• Allometry
  – Measuring Complicated Variables with the Simple Metrics

• Scaling Theory
  – Emerging Rules of Ecology

• Power Laws
  – Bringing Order to Chaos: A Tool for Quantifying Attributes of Ecosystems

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Allometry

- The study of the Relationship between Size and Shape
- Non-Destructive
- Practical
  - Measure easy variables, like tree diameter, can infer difficult to measure quantities, like leaf area, height, and productivity
Allometry, a Tool of Ecology and Forest Management

![Graph showing allometric relationship](image)

**Figure 1**—Allometric relationship between measured whole-tree leaf mass and trunk diameter at breast height for 14 blue oak trees harvested from a native stand in the Sierra Nevada foothills.

Karluk and MacKay, 2002, USFS

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Not precise, but bounds system. For tropical forests, less than 2500 trees have been cut and weighed to derived these functions (Chave et al. 2005 Oecologica)
Shows the relation between power law functions and log log plots. The slope of the log log plot is the exponent of the power law.
Overarching Concepts

• Emergent Features of Complex Systems
  – Allometries provide useful Rules for Ecological Assessments; they bring order of the complex diversity of ecosystems
  – Many Biological Allometries have exponents that are multiples of $\frac{1}{4}$
  – Are Associated with the Physics of Hierarchal Systems and Fractal Nature of Branching Systems

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Ecological Power Law Scaling Rules

• Individual
  – Leaf Mass scales w/ Tree Diameter
  – Leaf Area scales w/ Sapwood Area
  – Metabolism scales w/ Mass
  – Photosynthesis scales w/ tree diameter
  – Respiration scale w/ Mass
  – Nitrogen scales w/ Mass

• Community
  – Biomass scales w/ Number of Trees per unit Area
  – Density scales inversely with Size
    • Number of trees per unit area ~ Mass
  – Biodiversity scales with Area
  – Home Range scales with Mass
  – Mortality scales with Mass

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List of potential power law functions
Examples of power law scaling in plants
Tree Allometry \[ y = ax^b \]

<table>
<thead>
<tr>
<th>y</th>
<th>x</th>
<th>Exponent, b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter</td>
<td>Mass</td>
<td>3/8</td>
</tr>
<tr>
<td>Mass</td>
<td>Diameter</td>
<td>8/3</td>
</tr>
<tr>
<td>Height</td>
<td>Mass</td>
<td>1/4</td>
</tr>
<tr>
<td>Height</td>
<td>Diameter</td>
<td>2/3</td>
</tr>
<tr>
<td>Leaf Mass</td>
<td>Diameter</td>
<td>2</td>
</tr>
<tr>
<td>Mass/plant</td>
<td>Number/area</td>
<td>-4/3</td>
</tr>
</tbody>
</table>

West et al, 1997; Enquist et al
On one hand I find utility in these power laws but I also recognize their limits. Use, but use with caution. They work better for problems across scales that those within scale

Caveat Emptor

• Scaling Laws Don’t Work Everywhere and All of the Time
  – There Remain Debates on the Values of the Power Law Exponents

• There Remains Large Variability in y at a given x, at a given scale, as the plots are on log-log scales
Why do these power laws seem to have $\frac{1}{4}$ fractions of exponents. One may think $1/3$ due to geometry.
Fractal Geometry, Space-Filling Perspective, adds 4th spatial dimension

Area (a), Volume (v), Length (l), Density (ρ) Scaling: 1/4 Power Law Dependency

End member size is finite, leading to 4th power scaling.
Here is a simple thought experiment packing cubes. I nested groups of more and bigger cubes and observe they produce a $1/4$ power law between the area of the cube and the total area of the space filling cubelets.
West and colleagues made fundamental advances on explaining their power law findings.

**Fundamentals of ¼ scaling**

- Living things are sustained by transport of materials (water, nutrients) through networks of paths.
- For the network to function, it must be space filling throughout the volume.
- The final branch is scale invariant.
- The energy required to transport material must be minimized.
  - The hydrodynamic resistance must be minimized.

West et al 1997 Science

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Using Scaling Laws to Infer Information on the Properties and Performance of Ecosystems

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Size vs. Number Density transcends 9-12 orders of magnitude in an Orderly Manner

Physics Wins:
You can only be so big and sustain so many individuals for the resources available

Corollary 1: You can only grow so Big and So Fast; an Ecological lesson for the Stock Market and the Federal Reserve.

Corollary 2: Don’t Eat anything Bigger than your Head (Morn)

Or density is a function of mass to the \(-3/4\) power, getting back to a situation with scaling being a multiple of \(1/4\).
This relation is important to recognize from various standpoints. The classic one is what happens when you plant a tree. I think we all have in our minds eye it will grow big and tall and take up carbon. Yet in a real forest most small trees will die and be crowded out by the bigger ones. There is only so much sunlight per unit area and only so many trees to be sustained in that area. Either lots of little trees or a few big trees results.
Nice visual of the change in density with size and time.
This scaling shows how biomass increases with fewer, but bigger, trees
Kleiber’s Law

Metabolic rate (B) of an organism scales to the 3/4 power of its mass (M)

\[ B = M^{3/4} \]

The Metabolic Energy needed to Sustain an organism INCREASES with Mass, to the ¾ power

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Powerful law on metabolic rates
Life spans +20 Orders of Magnitude in Mass; Blue Whale $10^{18}$g
phytoplankton, $10^{-13}$g
Net Primary Production Scales with Size

Woodwell and Whittaker, 1968 Am Zoo

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EcoPhysiological Scaling:
Metabolism vs Life Span, Specific Leaf Area and Nitrogen

Ecology: Reich et al.  

Net photosynthesis (mmol m⁻² d⁻¹)

Leaf nitrogen (mg/g)

Mean annual temperature (°C)

Mean annual precipitation (cm)

Specific leaf area (cm²/g)

Leaf life-span (months)

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Ecological Scaling Rules for Metabolism, Size and Nitrogen Economy in Plants.

\[ N \sim M^{+1} \quad R_{\text{dark}} \sim N^{+1} \]

Reich et al 2006 Nature

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Summary of EcoPhysiological Scaling Laws

<table>
<thead>
<tr>
<th>Y</th>
<th>X</th>
<th>Power exponent</th>
<th>citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{\text{dark}}$</td>
<td>$[\text{N}]$</td>
<td>+1</td>
<td>Reich et al. 2006 Nature</td>
</tr>
<tr>
<td>$[\text{N}]$</td>
<td>Mass</td>
<td>+1</td>
<td>Reich et al. 2006 Nature</td>
</tr>
<tr>
<td>$\text{Ps-mass}$</td>
<td>Life Span</td>
<td>-3/4</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$\text{Ps-area}$</td>
<td>Life Span</td>
<td>-1/3 (-0.29)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$R_{\text{dark}}$</td>
<td>Life Span</td>
<td>-2/3 (-0.58)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$\text{Ps}$</td>
<td>SLA</td>
<td>-4/3 (1.31)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$R_{\text{dark}}$</td>
<td>SLA</td>
<td>+1 (1.02)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$[\text{N}]$</td>
<td>SLA</td>
<td>+2/3 (0.61)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$\text{Ps-mass}$</td>
<td>$[\text{N}]$</td>
<td>+7/4 (1.73)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$R_{\text{dark}}$</td>
<td>$[\text{N}]$</td>
<td>+4/3 (1.36)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
<tr>
<td>$\text{Ps-mass}$</td>
<td>$R_{\text{dark}}$</td>
<td>+1 (1.08)</td>
<td>Reich et al 1997 PNAS</td>
</tr>
</tbody>
</table>

Ps: photosynthesis; $R_{\text{dark}}$: dark respiration; $[\text{N}]$: nitrogen concentration; SLA: specific leaf area (area/mass)

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Metabolic scaling of populations is Scale Invariant: an Emergent Property of the System

Energy flux of a population per unit area ($B_i$) is invariant with mass of the system ($M$):

$$B_T = N_i B_i \propto a \cdot M_i^{-3/4} b \cdot M_i^{3/4} \sim abM^0$$

$$B_T \neq N \cdot \langle B \rangle$$

Remember there is only so much Sunlight/Energy available to a given Meter of Land

Allen et al. (2002)  ESPM 111 Ecosystem Ecology

Metabolic scaling of populations is
Ecosystem Transpiration is Scale-Free

Transpiration is not equal to the number of trees times their average Transpiration rate

Enquist et al 1998 Nature

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Fire, Scaling and Cellular Automata Theory

- Patch either has Tree, Empty or Fire
- Tree catches fire if Neighbor is burning
- Empty site becomes occupied with a tree by prob, b(t)
- Tree without a burning neighbor may burn with prob, f(t)
- Power Law occurs because small fires are common and frequent; large fires are rare

Moritz et al PNAS 2005

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Scaling Fire Frequency and Size/Area Follows Power Law Scaling

\[ \text{Number of Fires per unit area} \]
\[ \text{Area} \]

REPORTS

A USFG

B Western US

C Alaska

D Australia

\text{Slope} = -1.31

\text{Slope} = -1.34

\text{Slope} = -1.43

\text{Slope} = -1.49

Malamud et al 1998, Science

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Distance to Nearest Neighbor Scales with Diameter, exponent is one

Small Trees are close together; Big Trees are Spaced Farther Apart

Enquist et al 2009 PNAS

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Home-Range Scales with Body Size:

Bigger Animals have to go Farther for Food, and vice versa

\[ H \sim M^{+1} \]

Holling 1992 Ecol Monograph

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Trophic Energetics Deems that Predator Mass Scales with Prey's Mass and Fewer Bigger Predators (Top Trophic Level) tend to eat smaller and More Abundant Prey (Basal and Intermediate Trophic Levels)

Cohen et al 1993 J Animal Ecology
Cohen et al 2009, PNAS
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Scaling Does Not Work All of the Time

Examples where it Fails:

- Mortality
- Biodiversity
Mortality

Mortality Scaling was Proven Not to be Universal Periodic Disturbance by Hurricanes

Muller-Landau et al 2006, Ecology Letters

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Biodiversity May Follow Power Law Scaling, too

\[ \# \text{Species} = cA^{1/4} \]

But Use with Caution, Caveat Emptor

MacArthur and Wilson, 1963 Evolution
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Power Law behavior only arises in the limit of increasing abundance and its power law approaches zero, not one-fourth.
### Summary of Ecological Scaling Laws

<table>
<thead>
<tr>
<th>Dependent variable, $y$</th>
<th>Independent variable, $x$</th>
<th>Power exponent</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Metabolism, $B$</td>
<td>Mass, $M$</td>
<td>+3/4</td>
<td>Kleiber</td>
</tr>
<tr>
<td>Mass</td>
<td>#/area</td>
<td>-4/3</td>
<td>Enquist et al. 1996 Nature</td>
</tr>
<tr>
<td>Plant Mass</td>
<td>Stem Diameter</td>
<td>+2 to +3</td>
<td>Gower et al. 1997 JGR</td>
</tr>
<tr>
<td>Home Range: carnivores,</td>
<td>Body mass</td>
<td>+1</td>
<td>Hollings 1992 Ecol Monograph</td>
</tr>
<tr>
<td>carnivores and herbivores</td>
<td>Basal diameter</td>
<td>+1</td>
<td>Enquist et al. 2009 PNAS</td>
</tr>
<tr>
<td># Fire</td>
<td>Area</td>
<td>-4/3</td>
<td>Malamud et al. 1998 Science</td>
</tr>
<tr>
<td>Ecosystem Water Use</td>
<td>Mass</td>
<td>0</td>
<td>Enquist 2002 Tree Physiology</td>
</tr>
<tr>
<td>Species #</td>
<td>Area</td>
<td>+1/4 -0</td>
<td>MacArthur-Wilson/Marte</td>
</tr>
<tr>
<td>Mortality</td>
<td>Mass</td>
<td>-1/4</td>
<td>Brown et al. 2004</td>
</tr>
</tbody>
</table>

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Summary

- Many Ecological Processes follow Power Law behavior for
  - Size vs density: density decreases with increasing mass
  - Metabolism vs Size: metabolism increases with size
- The Power Law Exponent follows Multiples of $\frac{1}{4}$
- Complexity is an attribute of Ecosystem Function and Behavior and leads to Emergent Scale Behavior
Thoughts to Ponder

- Based on the Self-Thinning Rule does planting is ‘Tree Planting’ an effective way to stem the growth of CO$_2$ in the Atmosphere?

$$B_T = N_i B_i \propto M_i^{-3/4} M_i^{3/4} = M^0$$

- Do the unique and additive contributions of Individual Species Matter in Scaling and Ecosystem Ecology?
Scaling Rules of Thumb

- Biological Allometries scale with multiples of $\frac{1}{4}$ power
- Annual rate of growth, $G$, scales as a $\frac{3}{4}$ power of body mass, $M$, for over 20 orders of magnitude ($G \sim M^{3/4}$).
- Plant body length scales as $\frac{1}{4}$ power of mass.
- Photosynthetic body mass, $M_p$, scales with $\frac{3}{4}$ power of non-photosynthetic body mass, $M_n$ ($M_p \sim M_n^{3/4}$).
- Organism Metabolism scales with $\frac{3}{4}$ power of mass
- Together they find that growth rate is directly proportional to photosynthetic body mass, $M_p$ ($G \sim M_p$).
Background, after Notes from Geoffrey West

- Metabolic Rate, $B$, scales with fluid flow, $Q_0$
- Fluid Flow is equal to the number of capillaries times the flow rate through the Capillaries, $Q_0 = Q_c N_c$
- The number of Capillaries scales with mass to the $3/4$ power, $N_c \sim M^{3/4}$
- Number of branches ($N_k$) times length of branches ($l_k$) is volume preserving (d=3)
- Area Preserving Branching ($\beta = r_k/r_{k+1}$)
- Invariant terminal size, capillary size is same for all organisms

Volume preserving

$$N_k l_k^d \approx N_{k+1} l_{k+1}^d$$
$$N_k l_k^3 \approx N_{k+1} l_{k+1}^3$$
$$\gamma_k = \frac{l_{k+1}}{l_k} = \left(\frac{N_{k+1}}{N_k}\right)^{1/d}$$

Branch Doubling

$$\gamma_k = \frac{1}{2^{1/3}}$$

Area preserving

$$\pi r_k^2 = \pi r_{k+1}^2$$
$$\beta_k = \frac{r_{k+1}}{r_k} = \left(\frac{N_{k+1}}{N_k}\right)^{1/d}$$

$$V_r = \sum_{k} N_k V_{r_k} = \sum_{k} \pi r_k^2 l_k$$

$$a = \frac{-\log a}{\log (r_f)} = \frac{d}{d+1}$$

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Mass ($M$) and Area ($A$) of Trees scale with Diameter ($D$) of Trunk

\[ M = aD^b \]
\[ A = cD^c \]

Gower et al., 1999

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Density scales inversely with a 1/3 power law (-1/3) of length
Volume Filling and Surface Area

1 Cube is 6-sided and 1 by 1 by 1 m². Surface Area: 1 * 1 * 6; Unit Sfc Area = 6 m²

Many cube-lettes: M * x * y * 6, x = X/N; y = Y/N; z = Z/N; M = 5 * 5 * 5;
Unit Sfc Area = 5 * 6 = 30 m²
= 5 * 5 * 5 * 1/5 * 1/5 * 6

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Assumptions of West/Brown/Enquist ¼ Power Theory

- Distribution Network Determines the Scaling Relationship
- The Distribution Network is Hierarchal
- Vessels within the same Hierarchy are equal
- Branching Ratio is Constant
- Network is Space Filling
- Energy Loss of Fluid Flow through the network is Minimized
- Capillary size across species are the same
- Capillaries are the only exchange surface of O₂

Savage et al 2006 PLOS Computational Biology

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