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

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

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Allometry, a Tool of Ecology and Forest Management

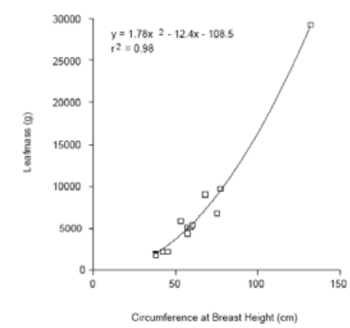

Figure 1—Allometric relationship between measured whole-tree leaf mass and trunk diameter at breast height for 14 blue oak trees harvested from a native stand in the Sierra Nevada foothills.

Karlik and MacKay, 2002, USFS

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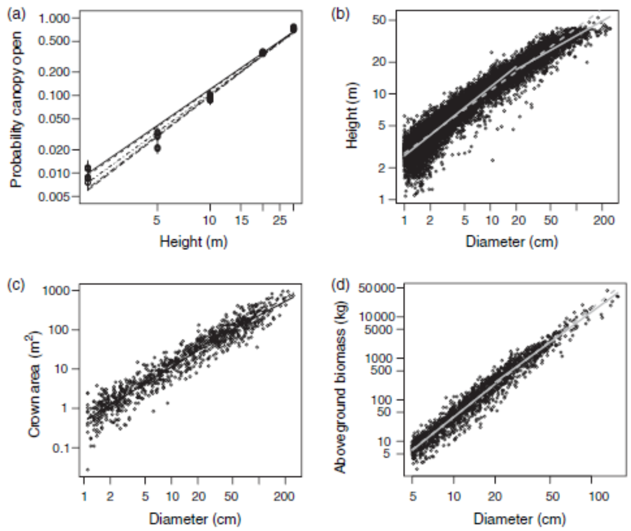
Scaling from 1000s of Tropical Trees



Muller-Landau et al 2006 Ecol Letters

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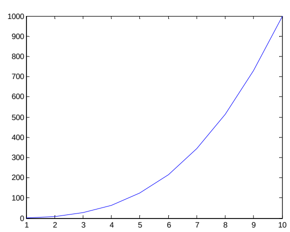
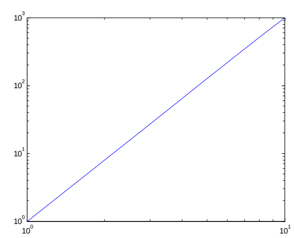
Fundamental Power Laws



$$y = ax^b$$



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

The Exponent, b, equals the Slope of the Log-Log plot of x and y

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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 ¼
  - Are Associated with the Physics of Hierarchal Systems and Fractal Nature of Branching Systems

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

Tree Allometry $$y = ax^b$$

y	x	Exponent, b
Diameter	Mass	3/8
Mass	Diameter	8/3
Height	Mass	1/4
Height	Diameter	2/3
Leaf Mass	Diameter	2
Mass/plant	Number/area	-4/3

West et al, 1997; Enquist et al

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, as the plots are on log-log scales

Fundamentals of Scaling: Euclidian vs Fractal Scaling

- Euclidian scaling relates to exterior shape
  - power law exponents are multiples of 1/3
- Biological Scaling is Fractal
  - Associated with internal shapes and networks
  - Power Law exponents are multiples of ¼

West et al 1999 Science; Brown et al 2002 Phil Trans Roy Soc;
Agutter and Wheatley, 2004, Theor Biological Med Modelling
Savage et al 2008 PLOS Computational Biology

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Fractal Geometry, Space-Filling Perspective, adds 4th spatial dimension

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

West et al 1999 Science

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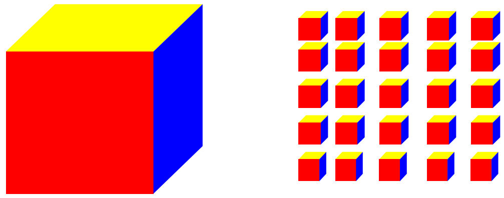
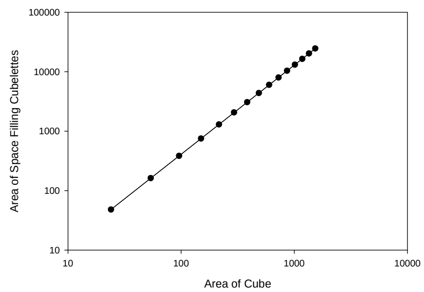
Volume Filling and Surface Area

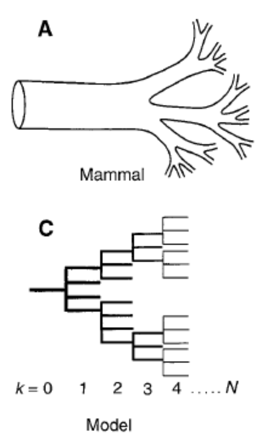




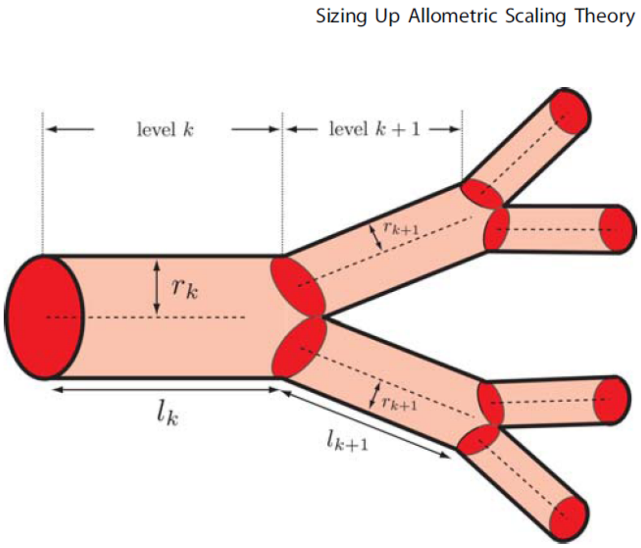
Slope = +6/4 = +3/2

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



Savage et al 2008, PLOS Computational Biology

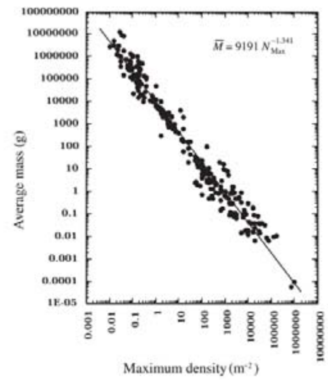
Using Scaling Laws to Infer Information on the Properties and Performance of Ecosystems

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.

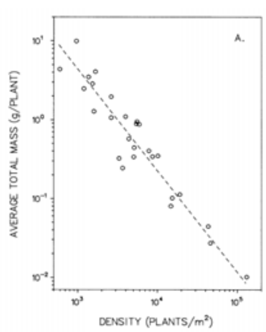
Corollary 2: Don't Eat anything Bigger than your Head (Mom)



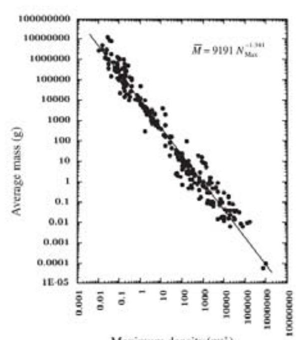
Enquist et al. 1998. Nature, 395

Yoda's Self-Thinning Law

- Conventional Wisdom: Tree Size (Mass) of Forest Plantations follows -3/2 power law with plant density

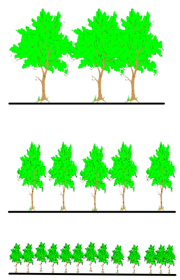


- Newer Analyzes reveal a -4/3 power law dependence based on energetics of metabolism (Weller, 1987; Enquist et al., 1998)



$$Mass \approx a\, Number^{-4/3}$$

$$Number \approx \frac{Mass}{a}^{-3/4}$$



A Forest can only sustain a few Large trees, or many small trees

Pine Seedlings in Finland

Old Growth Forest in Finland

http://www.helsinki.fi/~korpela/forestphotos.html

Forests Self-Thin with Size and Age

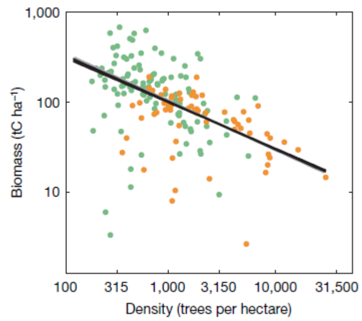
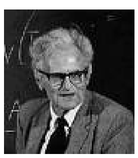


Figure 2 | **Biomass accumulation as a function of stand density.**

Recognize Scaling is Imperfect; Much Scatter Exists

Luyssaert et al. 2008 Nature



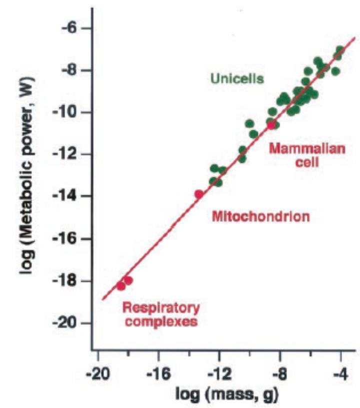
Kleiber's Law

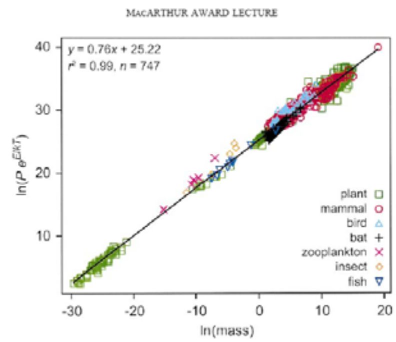
Metabolic rate (B) of an organism scales to the 3/4 power of its mass (M)

$$B = M^{3/4}$$

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

Basal Metabolic Rate (B) of uni-cellular and multi-cellular organisms scales to the 3/4 power of their mass (M)





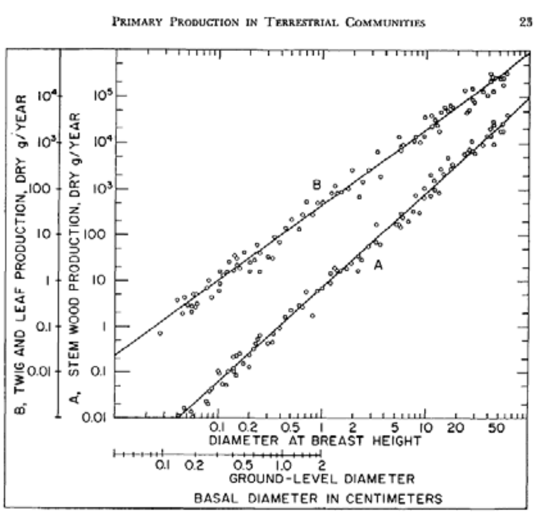
10^{-14} kg

10^{8} kg

West et al 2002 PNAS

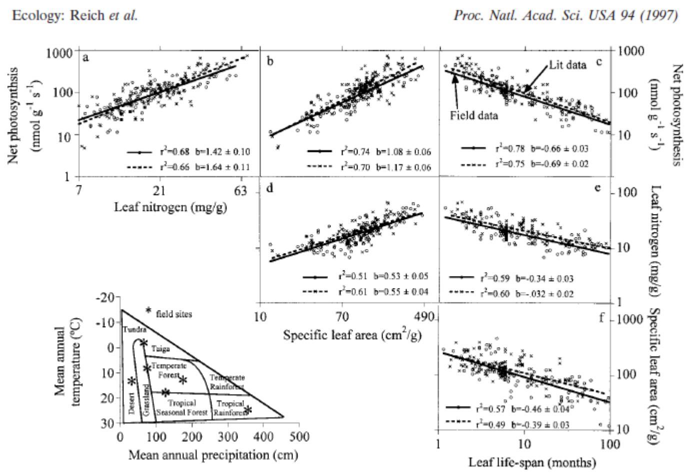
Brown 2004, Ecology

Net Primary Production Scales with Size



Woodwell and Whittaker, 1968 Am Zoo

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



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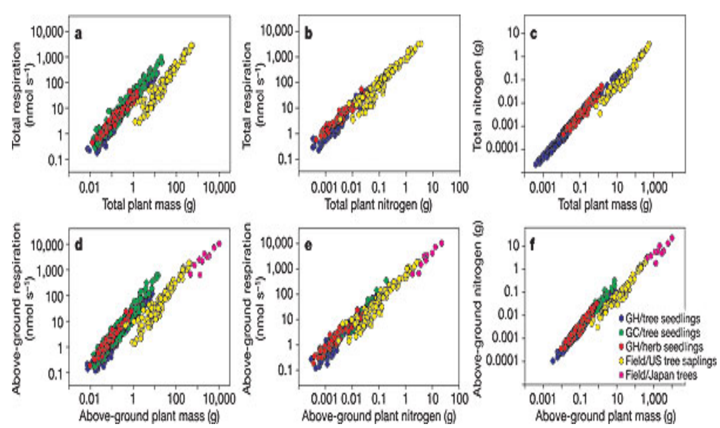
Ecological Scaling Rules for Metabolism, Size and Nitrogen Economy in Plants.



$$N \sim M^{+1} \qquad R_{dark} \sim N^{+1}$$

Reich et al 2006 Nature

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Summary of EcoPhysiological Scaling Laws

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

Ps: photosynthesis; Rdark: dark respiration; [N]: nitrogen concentration; SLA: specific leaf area (area/mass)

Metabolic Scaling of Populations of Organisms is Scale Invariant:
an Emergent Property of the System

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

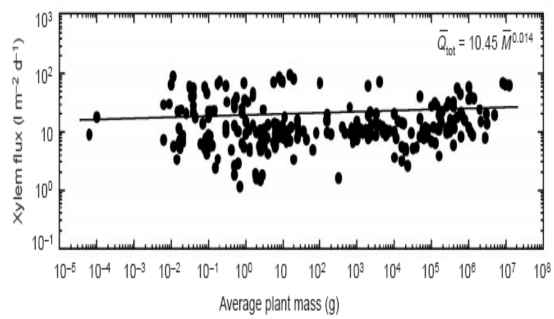
$$B_T = N_i B_i \propto a \cdot M_i^{-3/4} \, b \cdot M_i^{3/4} \sim a\, b M^0$$

$$B_T \neq N \cdot < B >$$

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

Allen et al. (2002)

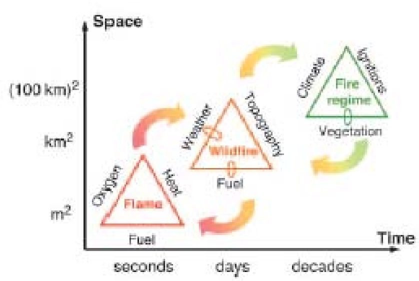
Ecosystem Transpiration is Scale-Free



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

Enquist et al 1998 Nature

Fire,Scaling and Cellular Automata Theory

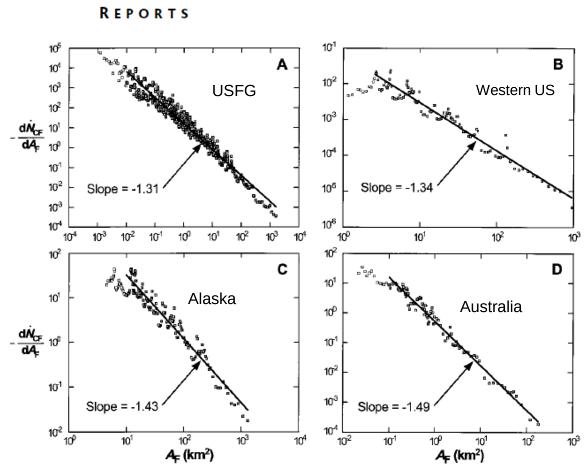


Moritz et al PNAS 2005

- 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

Scaling Fire Frequency and Size/Area Follows Power Law Scaling

Number of Fires per unit area

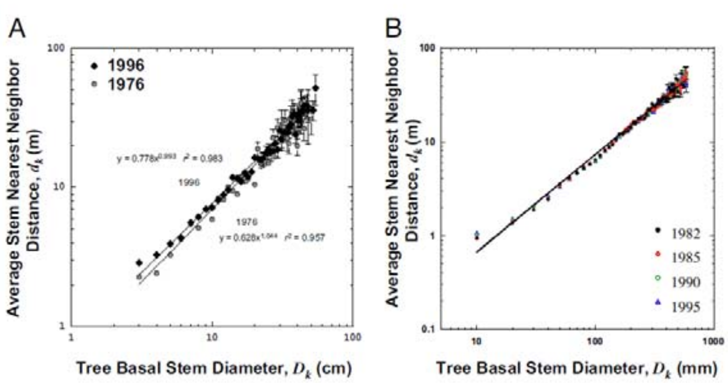


Area

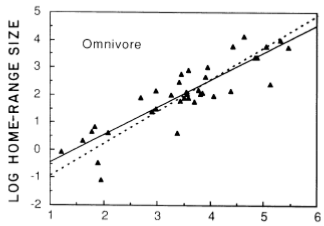
Malamud et al 1998, Science

Distance to Nearest Neighbor Scales with Diameter, exponent is one

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



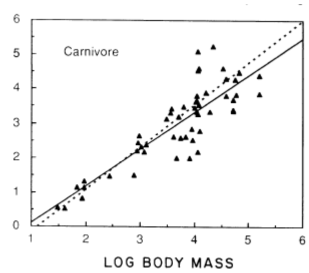
Enquist et al 2009 PNAS

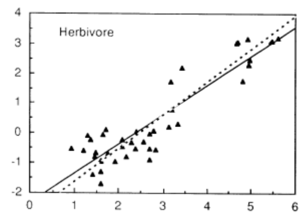


Home-Range Scales with Body Size:

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

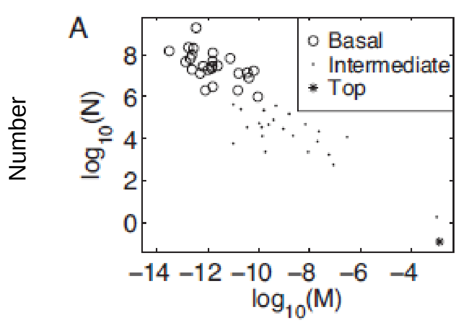
$$H \sim M^{+1}$$





Holling 1992 Ecol Monograph

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)



Mass

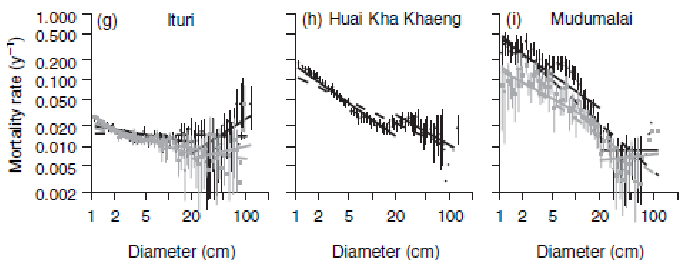
Cohen et al 1993 J Animal Ecology
Cohen et al 2009, PNAS

Scaling Does Not Work All of the Time

Examples where it Fails:

- Mortality
- Biodiversity

Mortality

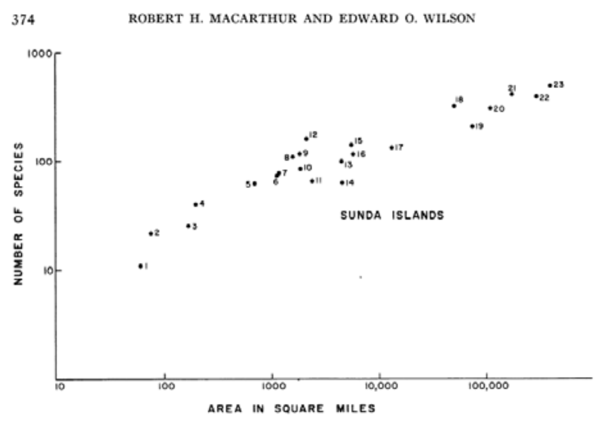


Mortality Scaling was Proven Not to be Universal
Periodic Disturbance by Hurricanes

Muller-Landau et al 2006, Ecology Letters

Biodiversity May Follow Power Law Scaling, too

•# Species = c $A^{1/4}$



But Use with Caution, *Caveat Emptor*

MacArthur and Wilson, 1963 Evolution

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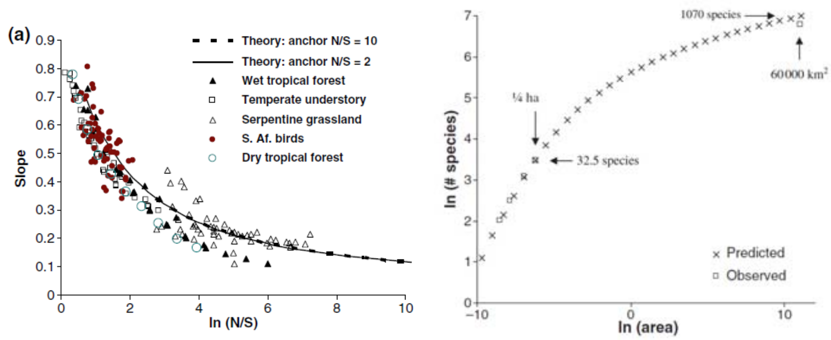
Limits to Biodiversity, Species-Area Scaling



S: # species; N # individuals

Harte et al 2009 Ecology Letters

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Summary of Ecological Scaling Laws

Dependent variable, y	Independent variable, x	Power exponent	
Metabolism, B	Mass, M	+3/4	Kleiber
Population/Area	Mass	-3/4	Enquist et al 1998 Nature
Mass	#/area	-4/3	Enquist et al 1998 Nature
Plant Mass	Stem Diameter	+2 to +3	Gower et al 1997 JGR
Mass Mammals	Mass Birds	+2	Hollings 1992 Ecol Monograph
Home Range: omnivores, carnivore and herbivores	Body mass	+1	Hollings 1992 Ecol Monograph
Nearest plant	Basal diameter	+1	Enquist et al 2009 PNAS
# Fire	Area	-4/3	Malamud et al 1998 Science
Ecosystem Water Use	Mass	0	Enquist 2002 Tree Physiology
Species #	Area	+¼ -> 0	Mac Arthur-Wilson/Harte
Mortality	Mass	-1/4	Brown et al 2004

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 ¼
- 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?

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Scaling Rules of Thumb

- Biological Allometries scale with multiples of ¼ power
- Annual rate of growth, G, scales as a ¾ power of body mass, M, for over 20 orders of magnitude ($G \sim M^{3/4}$).
- Plant body length scales as ¼ power of mass.
- Photosynthetic body mass, M_p scales with ¾ power of non-photosynthetic body mass, M_n ($M_p \sim M_n^{3/4}$).
- Organism Metabolism scales with ¾ power of mass
- Together they find that growth rate is directly proportional to photosynthetic body mass, *Mp*. (G~Mp).

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 ¾ 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 ($\beta = r_{k+1}/r_k$)
- Invariant terminal size, capillary size is same for all organisms

Volume preserving

$$N_k l_k^d \approx N_{k+1} l_{k+1}^d$$

$$N_k l_k^3 \approx N_{k+1} l_{k+1}^3$$

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

Branch Doubling

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

Area preserving

$$\pi r_k^2 = n\pi r_{k+1}^2$$

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

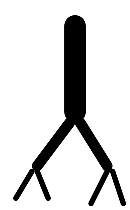
$$V_b \approx M$$

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

$$\approx (\gamma\beta^2)^{-N} V_c$$

$$B \approx M^a$$

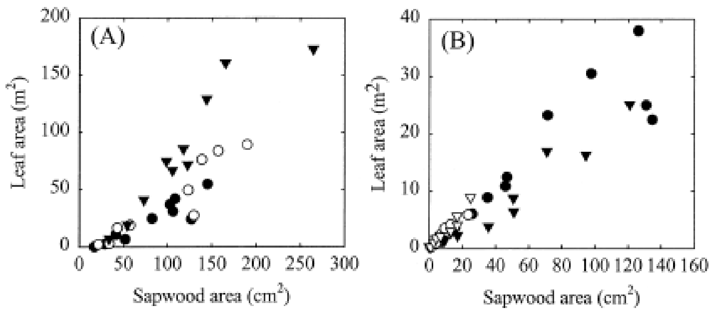
$$a = \frac{\log n}{\log(\gamma\beta^2)} = \frac{d}{d+1}$$



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

$$M = aD^b$$

$$A = cD^e$$

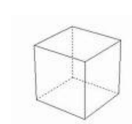


Gower et al., 1999

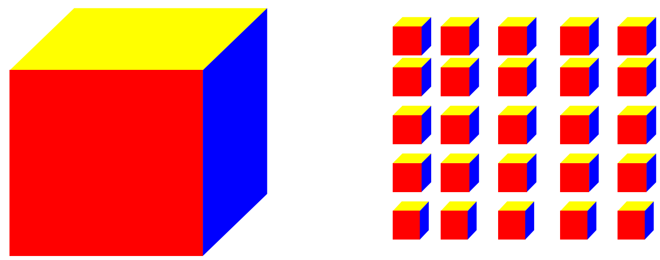
Euclidian Geometry Perspective

Area (A), Volume (V), Length (l), Density (ρ) Scaling:
1/3 Power Law Dependency

$$A \sim l^2 \therefore l \sim A^{1/2}$$
$$V \sim l^3 \therefore l \sim V^{1/3}$$
$$A \sim V^{2/3}$$
$$\rho \sim M / V \sim g \cdot l^{-3}$$



Volume Filling and Surface Area



1 Cube is 6-sided and 1 by 1 by 1 m^2: 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 m^2
= 5 * 5 *5 * 1/5 *1/5 * 6

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 O_2

Savage et al 2008 PLOS Computational Biology