The Metabolic Theory of Ecology

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Biol 417: Evolutionary Ecology

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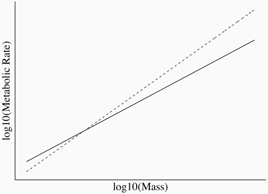
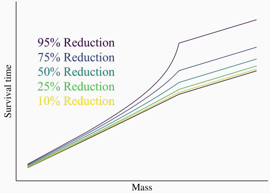
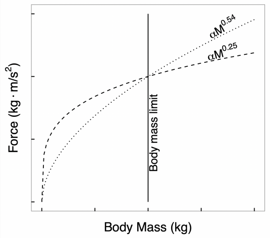
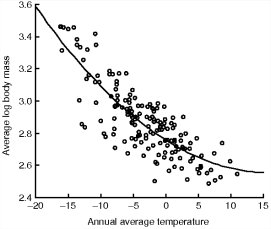
Review

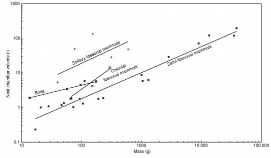
Throughout the course we have used allometric relationships to help understand evolutionary patterns in ecological systems.



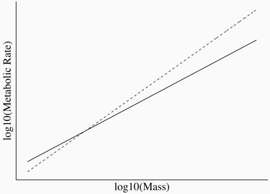


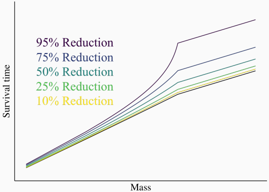


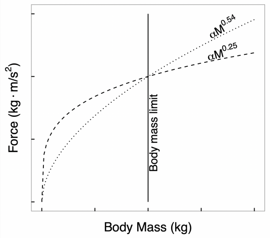


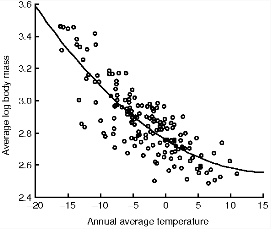


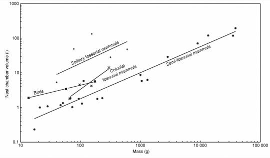
These relationships are only meaningful if there are underlying mechanisms (otherwise it's just correlation without causation).



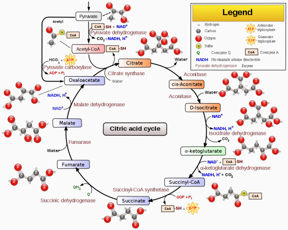




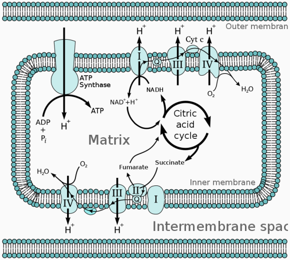




Metabolism and Metabolic Rate



Source: Wikipedia

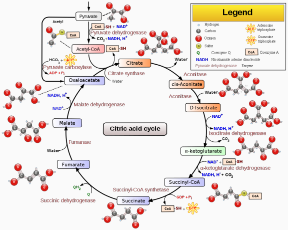


Source: Wikipedia

Metabolism is the biological processing of energy and materials and involves a complex network of biochemical reactions.

Organisms have different rates of uptake, transformation, and allocation, but the same basic machinery (i.e., TCA cycle and Ox. Phosph.) is conserved.

Metabolic rate



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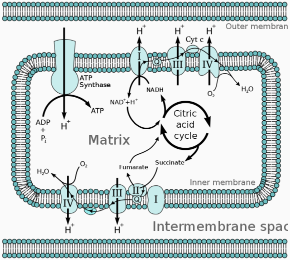
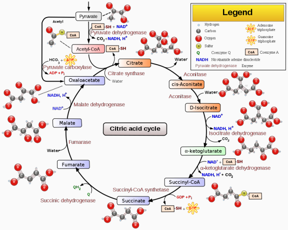


Source: Wikipedia

Brown *et al.* (2004) argue that because the metabolic rate underpins the uptake, transformation, and allocation of energy it is **the** fundamental rate

… and that metabolic rates will, therefore, underpins **every** aspect of a species' ecology.



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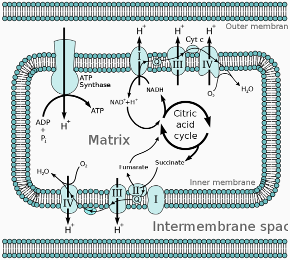


Source: Wikipedia

Individuals have some plasticity in the expression of metabolism (e.g., dormancy)

... but the conserved machinery means trends should emerge across taxa.

Many traits change with body size according to power functions of the form:

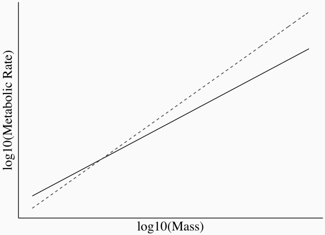
$$Y = \alpha M^{b}$$

Most biological scaling exponents (b) are multiples of $\frac{1}{4}$

Metabolic rate scales with body size as:

$$I = \alpha M^{\frac{3}{4}}.$$

α will have different values for basal, field, and maximal rates, but the exponent is conserved.



Temperature dependent reactions

Essentially all biological processes are temperature dependent (e.g., individual/population growth rates, life spans, development).

Biochemical reaction rates increase exponentially with temperature according to the Boltzmann factor:

$$e^{-\frac{E}{kT}}$$

where E is the activation energy, k is Boltzmann's constant, and T is absolute temperature in K (Boltzmann, 1872).

This exponential form governs the temperature dependence of whole-organism metabolism.

The combined effects of body size and temperature on metabolic rates can be expressed via:

$$I = \alpha M^{\frac{3}{4}} e^{-\frac{E}{kT}}$$

Taking natural logarithms and rearranging we can obtain mass-corrected metabolic rates:

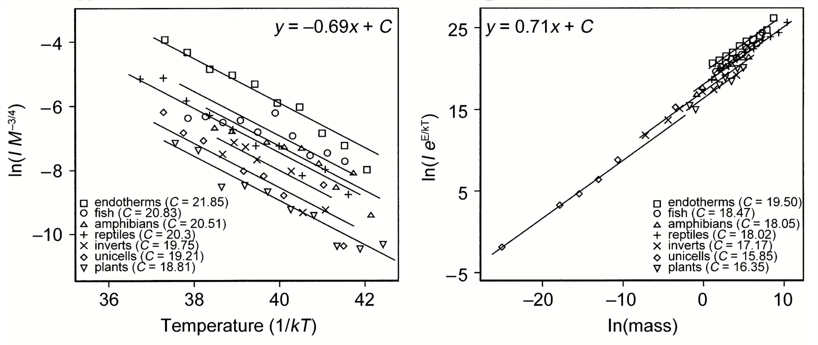
$$\ln(I\ M^{-\frac{3}{4}}) = -\frac{E}{kT} + \cancel{\ln(\alpha)}$$

... and temperature-corrected metabolic rates:

$$\ln(I\ e^{\frac{E}{kT}}) = \frac{3}{4}\ln(M) + \cancel{\ln(\alpha)}$$

Temperature and allometry

These relations can accurately predict metabolic rates over 20 orders of magnitude in body size from single-celled microbes to large vertebrates and trees.



Brown *et al.* (2004)

Temp. and Metabolism Take Homes

The vast majority of organisms share the same metabolic pathways, which are a series of temperature dependent biochemical reactions.

The combined effects of body size and temperature on whole-organism metabolic rates can be expressed as:

$$I = \alpha M^{\frac{3}{4}} e^{-\frac{E}{kT}}$$

This equation accurately predicts metabolic rates across the kingdom of life (!).

... but what does this imply for other ecological processes?

Individual Life History

The combined effects of body size and temperature on whole-organism metabolic rates can be expressed as:

$$I = \alpha M^{\frac{3}{4}} e^{-\frac{E}{kT}}$$

Mass-specific metabolic rate, B, can be obtained by dividing both sides by M.

$$\frac{I}{M} = \frac{\alpha M^{\frac{3}{4}} e^{-\frac{E}{kT}}}{M} \quad \rightarrow \quad B \propto M^{-\frac{1}{4}} e^{-\frac{E}{kT}}$$

… which implies that mass-specific biological **rates** that are underpinned by metabolism should scale according to a power of $-\frac{1}{4}$.

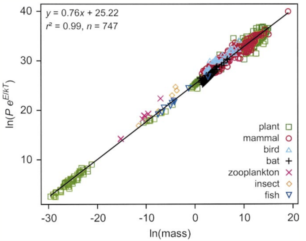
Individual biomass production

Organisms devote some prop. of their metabolism to catabolism, and the remainder to anabolism, growth, and reproduction.

Whole-organism P and mass-specific $\frac{P}{M}$ rates of biomass production should be tightly linked to metabolism and scale as:

$$P \propto M^{\frac{3}{4}} e^{-\frac{E}{kT}} \quad \& \quad \frac{P}{M} \propto M^{-\frac{1}{4}} e^{-\frac{E}{kT}}$$

The rate of biomass production (in g individual^{-1} year^{-1}) for aerobic eukaryotes scales with body-size with a slope of $\sim \frac{3}{4}$.



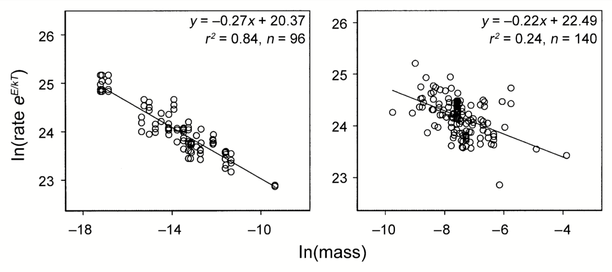
Brown *et al.* (2004), data from Ernest *et al.* (2003)

Ontogenetic growth

Metabolism thus sets the pace of life and life-history schedules.

Source: Biology Dictionary

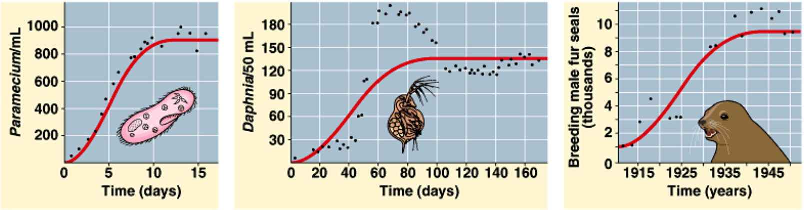
Source: Nat Geo



Brown *et al.* (2004), with data from Pauly & Pullin (1988) & Gillooly & Dodson (2000)

Birth and mortality rates

At carrying capacity most populations have stable size, which implies that births $\propto$ deaths.



(a) A *Paramecium* population in laboratory culture

(b) A *Daphnia* population in laboratory culture

(c) A fur seal (*Callorhinus ursinus*) population on St. Paul Island, Alaska

Because metabolic rates underpin biomass production, metabolism should also underpin birth, and therefore, mortality rates.

Birth and mortality rates cont.

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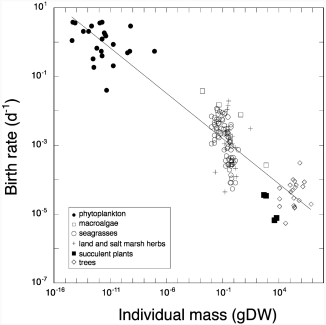
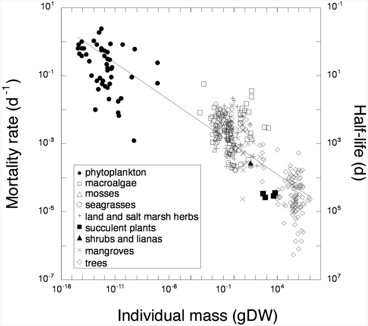
Marbà *et al.* (2007) showed that plant birth and mortality rates scale with slopes of $-\frac{1}{4}$.



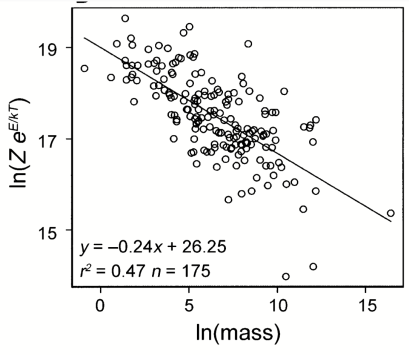
Marbà *et al.* (2007)



Marbà *et al.* (2007)

Birth and mortality rates cont.

The $-\frac{1}{4}$ slope also holds for fish mortality rates Z (ind. year^{-1}).

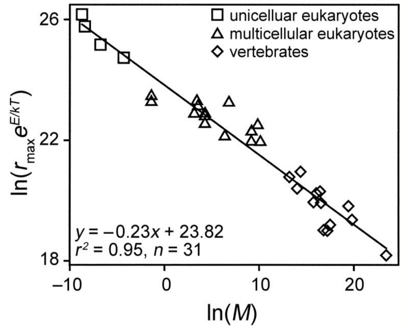


Brown *et al.* (2004), data from Pauly & Pullin (1988)

Source: Wikipedia

Population & Community Dynamics

A metabolic basis for biomass production, development, and birth and mortality rates implies a metabolic basis for population growth rates $r_{\max}$.



Brown *et al.* (2004), data from Pauly & Pullin (1988)

Eukaryotic $r_{\max}$ follows the $-\frac{1}{4}$ slope predicted by metabolic theory.

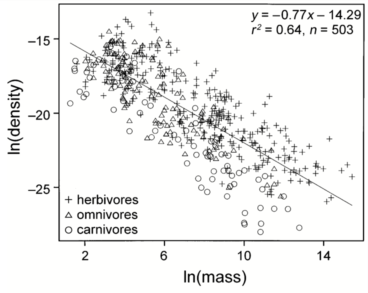
...which implies the r, K spectrum involves selection for metabolic rates.

Population densities

Solving the logistic growth equation, $\frac{dN}{dt} = rN(\frac{K-N}{K})$, for the steady state when $\frac{dN}{dt} = 0$ yields a prediction for metabolically driven carrying capacities, K:

$$K \propto M^{-\frac{3}{4}} e^{\frac{E}{kT}}$$

for derivations see Brown *et al.* (2004)

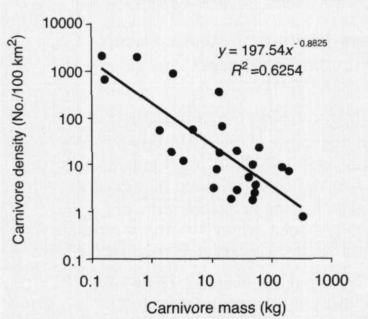


Brown *et al.* (2004), data from Ernest *et al.* (2003)

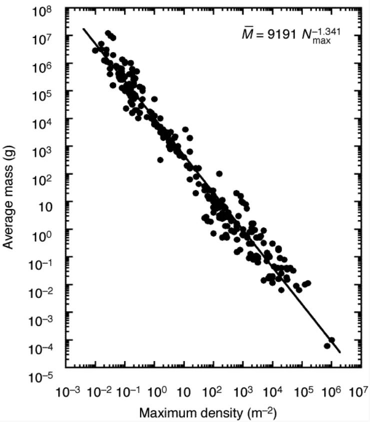
Mammalian population densities follow the $-\frac{3}{4}$ slope predicted by metabolic theory.

Metabolic rates scales as $M^{\frac{3}{4}}$ and pop. densities as $M^{-\frac{3}{4}}$, total energy used per area is $M^{\frac{3}{4}} M^{-\frac{3}{4}} \propto M^0$ (i.e., resources are used at similar rates).

The $M^{-\frac{3}{4}}$ scaling holds in carnivores and plants.



Carbone & Gittleman (2002)

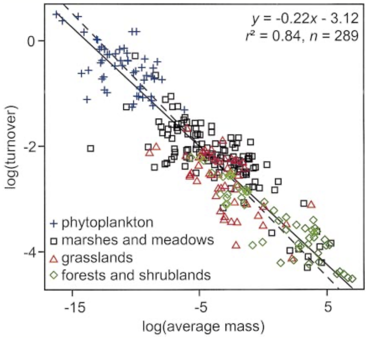


Enquist *et al.* (1998)

Biomass turnover

Because production and consumption should, theoretically, be $\sim$ equal for systems in steady states, turnover should be $\propto$:

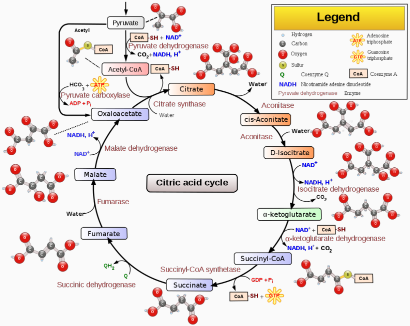
$$M^{-\frac{1}{4}}e^{-\frac{E}{kT}}$$



Brown *et al.* (2004), data from Cebrian (1999)

Carbon turnover rates in terrestrial and aquatic ecosystems closely follow the metabolically predicted $M^{-\frac{1}{4}}$ scaling (!).

Take homes



Source: Wikipedia

The vast majority of organisms share the same metabolic pathways.

Because metabolic rate underpins the uptake, transformation, and allocation of energy, it also underpins many (most?) ecological rates.

Take homes cont.

Metabolism predictably links individual-level processes with whole-ecosystem processes and acts as a unifying theory (like genetic inheritance for evolution).

Most of an individual's ecology is constrained by metabolism, making it a potent target for selection.

Metabolic theory can help us understand how to manage species, populations, and whole ecosystems.

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