

1 Ecological organization

In these lectures we investigate some ways in which organisms assemble themselves into an ecosystem.

We address two types of questions:

- *Geometry*. How can we characterize the topological assembly—i.e., the *connectivity of the components* of a complex system?
- *Physics*. How do rates of resource consumption influence the assembly?

We begin with some observations about the flow of energy through ecosystems.

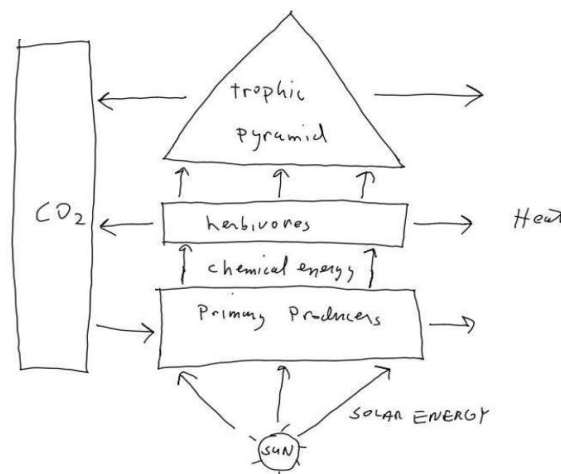
1.1 Energy flow

An *ecosystem* is a biological community and its physical environment.

The *community* is made up of the organisms living in a particular habitat (valley, lake, island, etc).

Within and across communities, one can study the flow of matter and energy.

In this way the ecosystem is not only a major component of the carbon cycle, but also a mechanism for energy dissipation:



Between the sun and the dissipation of heat, and between the input and output of CO_2 , lies a chemical reaction network called a *food web*.

Food webs describe which kind of organisms eat which other kinds.

The simplest food web is a *food chain*.

At the base of the food chain are *producers*, or *autotrophs*.

At the next *trophic level* one finds *consumers*, or *heterotrophs*, which live off of primary producers.

At the next higher trophic level are the consumers of consumers, etc.

Given this simple description, we can ask a simple question: *How long is a typical food chain?*

1.1.1 Food chains

In the simplest food chain,

- Individuals of species S_0 are eaten by those of S_1 ;
- those of S_1 are eaten by those of S_2 , etc.

Schematically there is a flow of energy like

$$S_0 \rightarrow S_1 \rightarrow S_2 \rightarrow \text{etc.}$$

In such an idealization, S_0 is typically a plant, S_1 an herbivore, S_2 a carnivore, S_3 a bigger carnivore, etc.

Now suppose that a fraction $0 < \phi < 1$ of the energy that passes from S_{i-1} to S_i is available to pass to link S_{i+1} .

After n trophic steps,

$$\text{available energy} \propto \phi^n.$$

A decent guess might be that $\phi = 0.2$.

Then S_4 has available to it only

$$\phi^4 = (0.2)^4 = 0.16\%$$

of primary production.

To get a better idea of what that might mean, suppose that each predator has twice the mass of its prey.

This is not so much: the linear dimension of the predator is then only

$$2^{1/3} = 1.26$$

times greater than the prey.

Then species S_n is 2^n times larger than S_0 , and if we can equate its mass to the energy it provides the next trophic level, the ratio of its population P_n to the population P_0 of S_0 is

$$\frac{P_n}{P_0} = \frac{\text{mass}_n/\text{size}_n}{\text{mass}_0/\text{size}_0} = \frac{\phi^n/2^n}{1/2^0} = 10^{-n} \quad (\phi = 0.2).$$

Thus if there are $n + 1 = 5$ trophic levels, species S_4 at the top of the food chain has a population 1/10,000 of S_0 .

This is the basis of the *trophic pyramid*, suggesting that populations and the energy available to them exponentially decrease with each trophic level.

Such reasoning is often invoked to explain why food chains rarely exceed about 5 trophic levels.

The reasoning may be wrong—among other problems, food chain length does not appear to depend on primary production.

But to illustrate why the reasoning may not be completely incorrect, consider an extreme example:

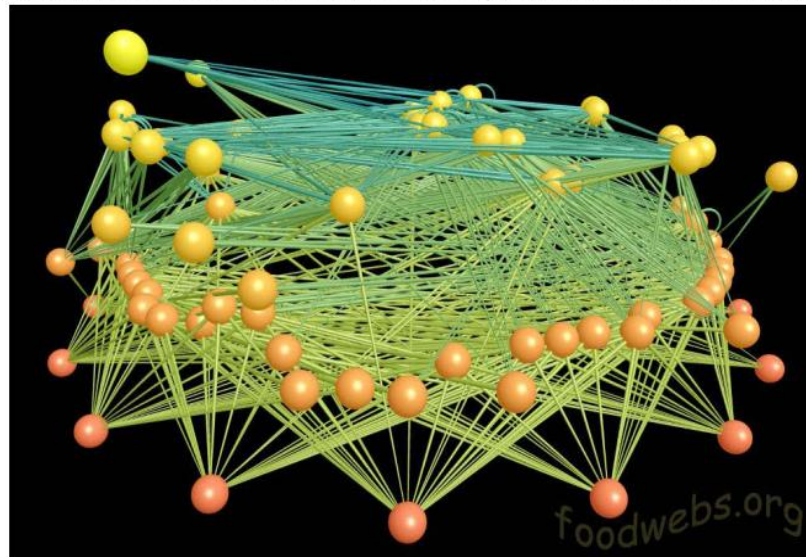
- A protozoan feeds on algae with a density of 10^6 /ml.
- Assuming 30 trophic levels and size ratios as above, the population density of the top predator would be 10^{-24} /ml.

- But the oceans have a size of $\sim 10^9 \text{ km}^3 = 10^{24} \text{ ml}$.
- So the top predator would have a population of size 1!

1.1.2 Food webs

As one might expect, real food webs exhibit a complexity—and presumably an evolutionary history—that far exceeds that of a simple food chain.

Here's an example, from the East River Valley, 120 miles southwest of Denver:



Each node represents a *trophic species*, i.e. a functional group that contains organisms that appear to eat and be eaten by the exact same species within a food web.

The web structure in the image is organized vertically, with node color representing trophic level. Red nodes represent basal species, such as plants and detritus, orange nodes represent intermediate species, and yellow nodes represent top species or primary predators.

Note that this image has 4 trophic levels, with some species well connected

and others not so much.

In what follows, we focus on models that predict distributions of connectivity to see if we can learn more.

1.2 Random networks

A perfectly plausible null hypothesis is to imagine that species represent nodes and predator-prey relationships represent links (edges) that are chosen randomly.

For simplicity, we ignore the *directed* nature of the predator-prey link, and seek information only about the existence of the link.

We then define a *random network* as follows:

- We specify n nodes (i.e., species).
- We specify the probability p that any two nodes are connected.

Note that for any given node, there are

$n - 1$ possible connections.

Since there are n possible starting points for those $n - 1$ connections, there are

$$\frac{n(n-1)}{2} \text{ possible links,}$$

where the factor of $1/2$ arises because we care only about the existence of the link, not its direction (i.e, we don't count links twice).

The expected number of links $\ell(n)$ in the random graph is

$$\begin{aligned} \ell(n) &= p \cdot (\text{number of possible links}) \\ &= p \frac{n(n-1)}{2}. \end{aligned}$$

Define

$$k_i = \text{number of links to node } i.$$

k_i is called the *degree* of node i .

The mean number of links attached to a node is

$$\langle k \rangle = 2 \frac{\ell(n)}{n}$$

The factor of 2 arises because each link is attached to 2 nodes. We thus have

$$\langle k \rangle = \frac{2pn(n-1)}{2n} = p(n-1) \simeq pn.$$

$\langle k \rangle$ is called the *mean degree* of the random network.

We seek the *degree probability distribution*: the probability of observing a node with degree k .

To obtain a node with degree k , we must have k “successful” connections, each with probability p , and $(n-1-k)$ unsuccessful connections.

The number of possible combinations of such connections is given by the binomial coefficient

$$\binom{n-1}{k} = \frac{(n-1)!}{(n-1-k)! k!}.$$

The probability P_k of observing k connections at a given node is then given by the binomial distribution

$$P_k = \binom{n-1}{k} p^k (1-p)^{n-1-k}.$$

The binomial distribution is a bell-shaped curve. If $n \rightarrow \infty$ and $p \rightarrow 0$ while $\langle k \rangle = np$ remains constant, then the binomial distribution converges to the Poisson distribution

$$P_k = \frac{\langle k \rangle^k e^{-\langle k \rangle}}{k!},$$

the mean and variance of which are both $\langle k \rangle$.

The *random-network* null-hypothesis thus makes a specific prediction: degree distributions are bell-shaped, with a mean and variance of $\langle k \rangle$.

Real food web data is, however, inconsistent with this prediction [6].

1.3 Scale-free networks

We now consider a model of a *growing* network. It too should be considered a null hypothesis rather than a mechanistic model of food webs.

There are two ingredients:

- *Growth.* We start with m_0 nodes with pre-existing connections. At each time step we add a new node with $m \leq m_0$ links to pre-existing nodes.
- *Preferential attachment.* New links tend to attach to already well-attached nodes. Specifically: the probability Π that a new node is connected to node i is proportional to k_i :

$$\Pi(k_i) = \frac{k_i}{\sum_j k_j}.$$

We can easily see that after t time steps, there are

$$t + m_0 \text{ nodes and } mt \text{ new links.}$$

To derive the degree distribution, we assume that k_i and t are continuous.

Then the rate at which k_i changes is proportional to $\Pi(k_i)$:

$$\frac{dk_i}{dt} = m\Pi(k_i).$$

The factor of m arises by identifying the units of time with the interval between time steps and recalling that m links are added at each time step.

We next substitute for $\Pi(k_i)$:

$$\frac{dk_i}{dt} = m \frac{k_i}{\sum_j k_j}.$$

Since there are mt new links after t units of time, the sum

$$\sum_j k_j(t) \simeq 2mt,$$

where the factor of 2 comes from counting each link twice (both “incoming” and “outgoing”), and the approximation ignores the small correction (for large t) that would arise from not counting the initial links.

Substituting the sum into the growth equation above, we obtain

$$\frac{dk_i}{dt} = \frac{k_i}{2t}.$$

Separating variables, we have

$$\frac{dk_i}{k_i} = \frac{dt}{2t}.$$

Integrating both sides, we have

$$\ln k_i(t) = \frac{1}{2} \ln t + \text{const.} \quad \Rightarrow \quad k_i = Ct^{1/2}.$$

Now define

$$t_i = \text{time of inception of the } i\text{th node.}$$

The initial condition is then $k_i(t_i) = m$, and therefore

$$k_i(t) = m \left(\frac{t}{t_i} \right)^{1/2}. \quad (1)$$

The number of links attached to the i th node therefore grows like $t^{1/2}$, but the prefactor $m/\sqrt{t_i}$ depends on its time of inception.

We seek the continuous probability density function $p(k)$ that a node has degree k .

To do so, we first define the cumulative probability distribution function

$$P[k_i(t) < k] = \text{probability that the } i\text{th node has fewer than } k \text{ links.}$$

We rewrite this expression using (1):

$$P[k_i(t) < k] = P \left[m \left(\frac{t}{t_i} \right)^{1/2} < k \right] \quad (2)$$

$$= P \left(t_i > \frac{m^2 t}{k^2} \right). \quad (3)$$

Now recall that there are $m_0 + t$ nodes, and one node is added at each time step.

Thus the time t_i at which the i th node is added is uniformly distributed between 0 and $m_0 + t$ (assuming the same rate for the first m_0 nodes).

The probability density function $p(t_i)$ is therefore constant over that interval. Since it must integrate to unity, we have

$$p(t_i) = \frac{1}{m_0 + t}.$$

Consequently the RHS of (3) is

$$\begin{aligned} P\left(t_i > \frac{m^2 t}{k^2}\right) &= \int_{m^2 t/k^2}^{m_0+t} p(t_i) dt_i \\ &= 1 - \int_0^{m^2 t/k^2} \frac{dt_i}{m_0 + t} \\ &= 1 - \frac{m^2 t}{k^2(m_0 + t)}. \end{aligned}$$

Inserting this into (3), we obtain

$$P[k_i(t) < k] = 1 - \frac{m^2 t}{k^2(m_0 + t)}.$$

We can now obtain $p(k)$ by noting that

$$\begin{aligned} p(k) &= \frac{d}{dk} P[k_i(t) < k] \\ &= -\frac{d}{dk} \left(\frac{m^2 t}{k^2(m_0 + t)} \right) \\ &= \frac{2m^2 t}{m_0 + t} k^{-3}, \end{aligned}$$

which in the limit of large t becomes

$$p(k) \sim 2m^2 k^{-3}.$$

This degree distribution is distinctive for two reasons:

- Unlike the bell-curve of random networks centered at $\langle k \rangle$, here the degree distribution is one-sided, with its maximum at 0.
- The power-law form of the distribution means that it is *scale-free*.

We say that the distribution is scale-free because its form is independent of scale (and therefore time).

To be precise, note that if we have a power-law distribution

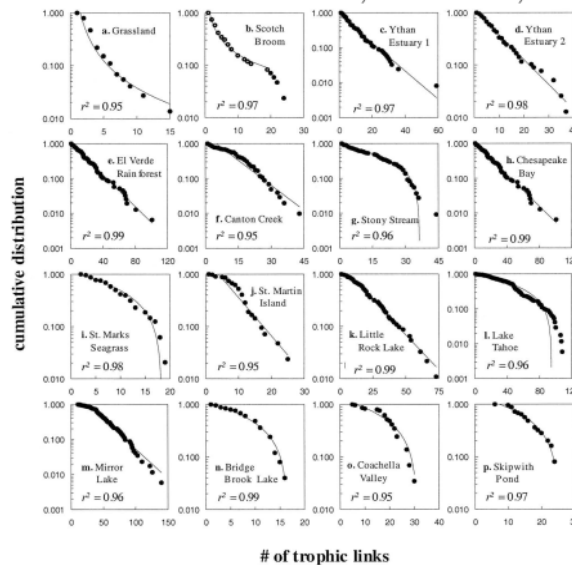
$$p(x) = x^{-\alpha},$$

then it is invariant, except for a prefactor, under the change of scale $x \rightarrow bx$:

$$p(bx) = (bx)^{-\alpha} = b^{-\alpha}p(x).$$

The power law is the only distribution of this type [8].

Are real food webs scale-free? The answer, it seems, is *sometimes*:



In this figure, power-law degree distributions are concave upward, exponential distributions are straight lines, and uniform distributions are concave downward.

Though hardly the rule in ecology, a great deal of other networks are apparently scale free. Some examples [7]:

- The World Wide Web and the internet.
- Scientific citations and co-authorship networks.
- Metabolic networks.

In the case of metabolic networks, one considers the nodes to be substrates (e.g., ATP, H₂O) and the links represent chemical reactions.

The scale-free nature of metabolic networks naturally raises the question of whether scale-invariance carries over to the scale of entire ecosystems and therefore biogeochemical cycles.

We don't know, but we now turn to discuss some interesting ways metabolism expresses itself at the scale of ecosystems.

1.4 Metabolic scaling

Metabolism is a complex network of biochemical reactions, by which energy is provided for an organism and new material is assimilated.

Metabolic rate is the rate of energy uptake, transformation, and allocation.

For an autotroph, metabolic rate = photosynthetic rate.

For a heterotroph, metabolic rate = respiration rate, i.e., the rate at which



since energy is derived from the oxidation of organic carbon.

Metabolic rates vary from organism to organism, but their dependence on body size and temperature, to which we now turn, is a well-established empirical fact.

1.4.1 Body size

Define

$$\begin{aligned} I &= \text{metabolic rate of an individual organism} \\ M &= \text{mass of the organism} \end{aligned}$$

Empirical studies show that, from unicellular organisms to elephants,

$$I = I_0 M^\alpha \quad (4)$$

where I_0 is a constant that is independent of mass.

The exponent α is widely believed to be $\alpha = 3/4$. However all theories supporting $\alpha = 3/4$ are controversial.

To understand α a bit more, we consider a dimensional argument:

- Heat is lost through the surface of a body.
- Metabolic rate is limited by surface area.

Noting that

$$(\text{surface area}) \propto (\text{volume})^{2/3} \propto M^{2/3}$$

we find that our dimensional argument predicts $\alpha = 2/3$.

Because it is often difficult to distinguish an exponent of $2/3$ from one of $3/4$, in the following we merely assume that the scaling law (4) holds but we do not specify the value of α .

Much more secure than the actual value of α , however, is the virtual fact that

$$\alpha < 1.$$

Now consider the *mass-specific metabolic rate*

$$B = I/M = M^{\alpha-1}.$$

We find the remarkable result that, per unit mass, the metabolic rate of small organisms is faster than that of large organisms.

These scaling laws are called *allometric* because, as in the case of river basins, a fundamental property (here, metabolic rate) does not scale proportionately with size.

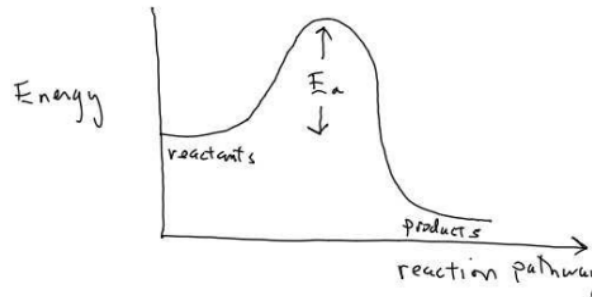
Consequently, as we shall soon show, the rate at which carbon passes through small organisms, is, per unit mass of the organisms, much greater than that of large organisms.

In this sense one can say that small organisms dominate the flux of carbon through the biosphere.

1.4.2 Temperature

Classical equilibrium chemical kinetics predicts reaction rate constants k in terms of activation energies E_a .

The activation energy is a potential barrier that is surmounted by a sufficient thermal fluctuation.



Arrhenius kinetics predicts that the rate constant

$$k = \omega e^{-E_a/k_B T},$$

where

- T = temperature
- k_B = Boltzmann's constant; and
- ω = the "attempt frequency" or "frequency factor."

In the classical interpretation of Arrhenius kinetics, the fraction of reactant molecules with a kinetic energy greater than E_a is proportional to the Boltzmann factor $\exp(-E_a/k_B T)$.

In this essentially phenomenological characterization, the temperature defines the characteristic size of a thermal fluctuation, E_a is the energy barrier that must be overcome by the fluctuation, and ω is the frequency at which the fluctuations lead to reaction.

For a heterotroph, E_a varies between about 0.2 and 1.2 eV, with a typical value of

$$E_a \simeq 0.65 \text{ eV}$$

The commonality of the measured activation energies for organisms ranging from microbes to large mammals reflects the kinetics of ATP synthesis.

Since

$$\frac{1 \text{ eV}}{k_B} = 11604.5 \text{ kelvins,}$$

we have typically that

$$\frac{E_a}{k_B} \simeq 7500 \text{ kelvins}$$

For a temperature change of ΔT ,

$$\begin{aligned} \frac{k(T + \Delta T)}{k(T)} &= \exp \left[-\frac{E_a}{k_B} \left(\frac{1}{T + \Delta T} - \frac{1}{T} \right) \right] \\ &= \exp \left[\frac{E_a}{k_B T} \left(\frac{\Delta T}{T + \Delta T} \right) \right]. \end{aligned}$$

For $\Delta T = 10^\circ \text{ C}$ and a base temperature $T = 15^\circ \text{ C} = 288^\circ \text{ K}$, we have

$$\frac{k(T + \Delta T)}{k(T)} \simeq 2.4,$$

indicating that the metabolic rate of a typical heterotroph increases by about a factor of two for a 10° C increase in temperature.

Combining size and temperature

Combining the Arrhenius law for biological rates with the size dependence of metabolism, the individual metabolic rate is

$$I = i_0 M^\alpha e^{-E_a/k_B T}$$

where i_0 is constant independent of both size and temperature.

We now compare this with measurements.

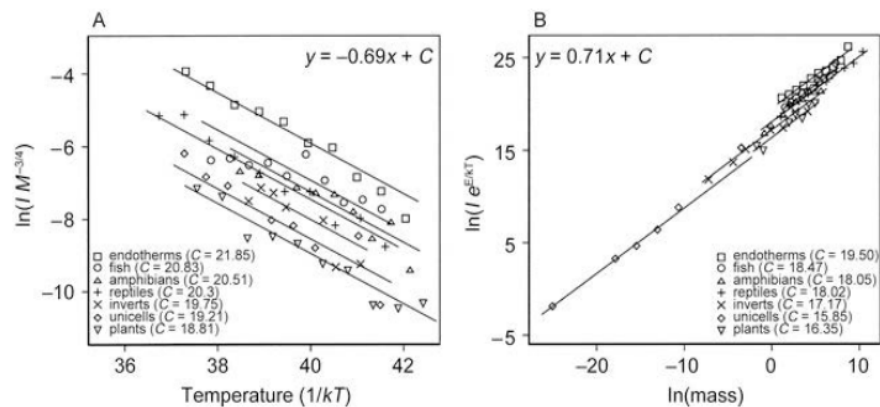
In one case, we correct I by size to expose temperature dependence:

$$I \cdot M^{-\alpha} = i_0 e^{E_a/k_B T}$$

In the other case we correct I by temperature to expose size dependence:

$$I \cdot e^{E_a/k_B T} = i_0 M^\alpha$$

These scalings work remarkably well:



In this case we find, on average, that

$$E_a = 0.69 \text{ eV} \quad \text{and} \quad \alpha = 0.71.$$

Note that the allometric exponent α is midway between $2/3$ and $3/4$, reflecting some indeterminacy in its origin. However there is no doubt that $\alpha < 1$.

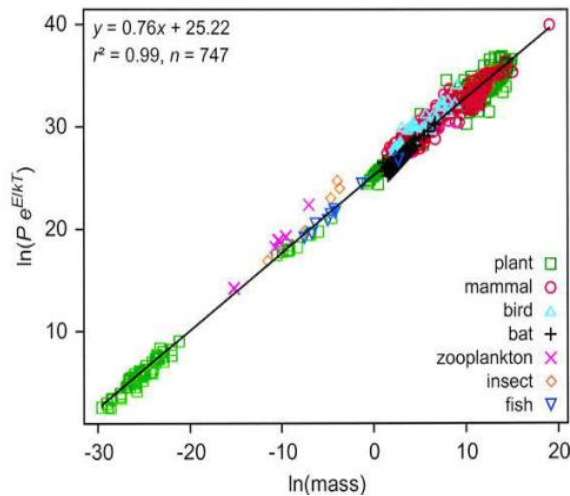
Individual expressions of metabolic scaling

Set

$P =$ biomass production rate.

We expect $P \propto$ metabolic rate, and therefore

$$P \cdot e^{E_a/k_B T} \propto M^\alpha$$



Here $\alpha \simeq 0.76$.

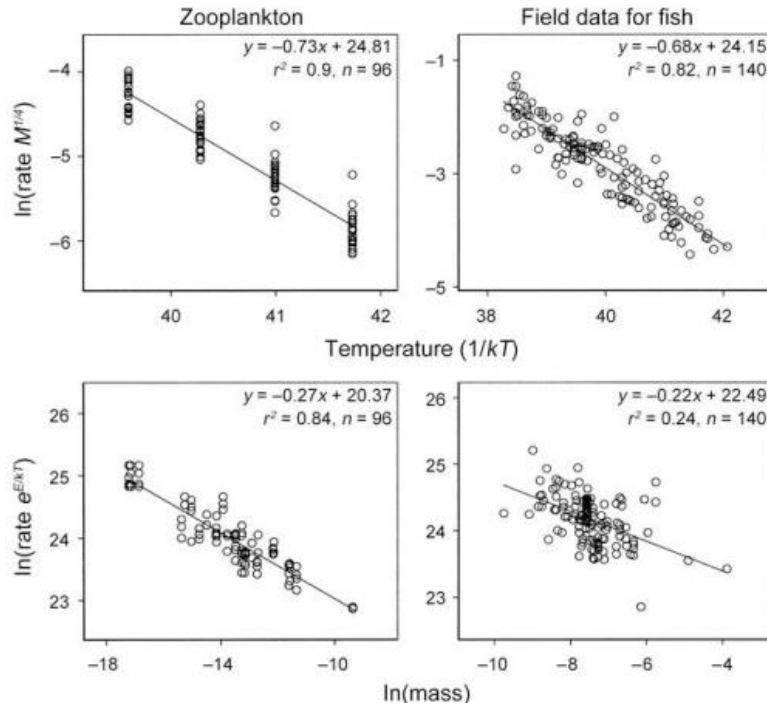
Recalling that $\ln 10 \simeq 2.3$, we note that mass ranges over about 21 orders of magnitude, and therefore the linear dimension of size ranges over $21/3 = 7$ orders of magnitude.

Expressing the mass-specific metabolic rate B in terms of both size and temperature, we have

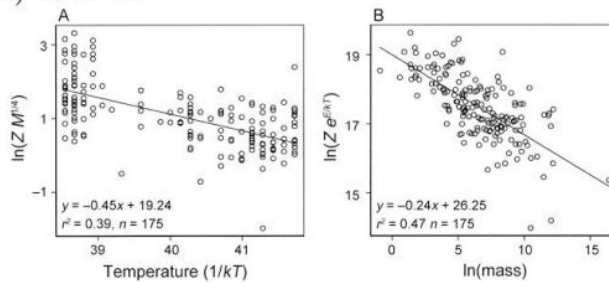
$$B \propto M^{\alpha-1} e^{-E_a/k_B T}.$$

B sets a great variety of the time scales relevant to the life history of an individual organism.

Consider, for example, the time scale for development (e.g., the time it takes for an egg to hatch):



The mass-specific mortality rate Z (measured in units of year^{-1}) scales similarly (here, for fish) like $M^{\alpha-1}$:



Heart rates also turn out to scale like the mass-specific metabolic rate. Consequently the number of heartbeats in an individual's life time scales like

$$\begin{aligned}
 \text{number of heart beats} &\propto \frac{\text{metabolic rate}}{M} \times \text{lifetime} \\
 &\propto M^{\alpha-1} \times \frac{1}{\text{mass-specific mortality rate}} \\
 &\propto M^{\alpha-1} \times (1/M^{\alpha-1}) \\
 &= \text{constant}
 \end{aligned}$$

showing that the number of heartbeats in the typical lifetime of a mouse and an elephant are equal!

Metabolic scaling of populations

Consider the population size N of a particular species.

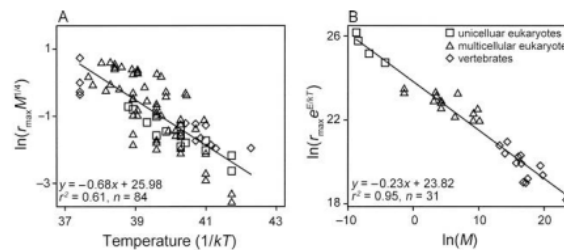
When resources are abundant, we expect

$$\frac{dN}{dt} = \mu N,$$

where μ is the (maximal) growth rate. Solving for N , growth is exponential:

$$N(t) \propto e^{\mu t}.$$

This maximal growth rate also scales like the metabolic rate:



Population growth, however, is always limited. A frequently employed model suggests that

$$\frac{dN}{dt} = \mu N \left(1 - \frac{N}{K} \right),$$

where K is called the *carrying capacity*.

In steady state there is neither growth nor decay, so that the steady population size is given by

$$N = K.$$

Now set

$r_0 =$ constant rate of supply, per unit area, of a limiting resource.

These resources should be consumed at a rate given by the population size and its individual metabolic rate; i.e.,

$$(\text{consumption rate}) \propto (N \times \text{metabolic rate}).$$

In steady state the consumption rate should equal the rate of resource supply, so that (ignoring temperature effects)

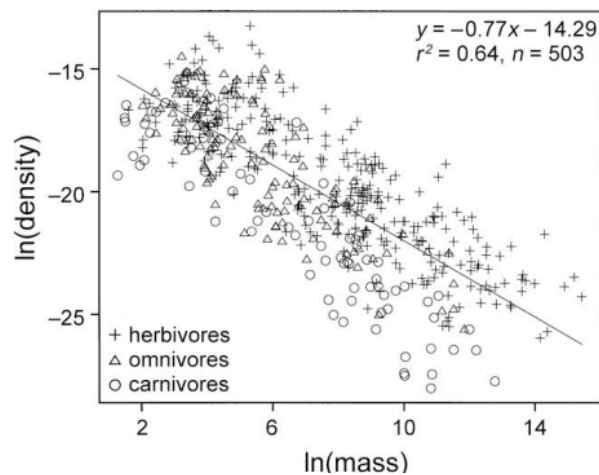
$$r_0 \propto nM^\alpha$$

where n , the population density, is the number of individuals per unit area.

Consequently n scales like

$$n \propto r_0 M^{-\alpha}$$

Observations of terrestrial mammals show just this behavior, for $\alpha \simeq 0.77$:



The scatter along the vertical axis may be due to different resource requirements at different trophic levels. (Organisms at higher trophic levels tend to require lower rates of resource supply.)

Now consider the rate of energy use per unit area for each size class:

$$\begin{aligned} \frac{\text{energy use}}{\text{area}} &\propto n(M) \cdot M^\alpha \\ &\propto r_0 M^{-\alpha} \cdot M^\alpha \\ &= r_0. \end{aligned}$$

Thus for a constant rate of resource supply, the energy flux per unit area due to organisms of different size is independent of their size!

We thus find a size-independent equipartition of resources, called the *energetic equivalence* rule.

Note that this remarkable balance of resources does not depend on a particular value of α .

However it does require that r_0 —the rate of resource supply (usable energy) per unit area—be the same for each size class.

Why is this so? We don't know.

1.7 Metabolic scaling of carbon stocks and turnover times

We now consider the size of carbon stocks and the rate at which they are consumed. Define

$w =$ standing stock or stored biomass per unit area

For each size class, w is the product of the population density n and the mass M of individuals:

$$\begin{aligned} w &\propto n(M) \cdot M \\ &\propto r_0 M^{-\alpha} \cdot M \\ &= r_0 M^{1-\alpha} \end{aligned}$$

We have already shown that the biomass production rate P for an organism of size M scales like

$$P \propto M^\alpha.$$

Then

$$\begin{aligned} nP &= \text{production rate per unit area} \\ &\propto (r_0 M^{-\alpha}) M^\alpha \\ &\propto r_0 \end{aligned}$$

and as a consequence

$$\frac{\text{production rate}}{\text{biomass}} \propto \frac{nP}{w} = M^{\alpha-1}.$$

Thus the mass-specific production rate increases with decreasing size.

Now recall that we have previously established that mass-specific mortality rates scale similarly.

This should be no surprise, as production and consumption are balanced in steady state.

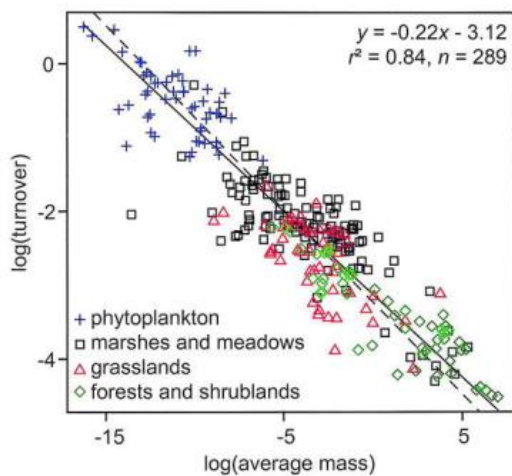
Now define

$$\text{turnover rate} = \frac{\text{production rate}}{\text{biomass}} = \frac{\text{mortality rate}}{\text{biomass}}.$$

We find that

$$\text{turnover rate} \propto M^{\alpha-1}$$

Data for plants in aquatic and terrestrial ecosystems display this relation over about 7 orders of magnitude in mass, with $\alpha \simeq 0.22$:



Turnover times are simply the inverse of the turnover rate; so that

$$\text{turnover time} \propto M^{1-\alpha}.$$

1.8 Scaling from individuals to the globe

Finally, we take a bold step and extrapolate these results to the global marine ecosystem.

We return to thermal effects.

Studies indicate that the activation energy E_a for plants is smaller than that of heterotrophs.

Then, neglecting size effects, we have

$$\frac{\text{production rate}}{\text{respiration rate}} \propto \frac{\exp[-E_a(\text{plants})/k_B T]}{\exp[-E_a(\text{heterotrophs})/k_B T]}$$

We have already noted that

$$E_a(\text{heterotrophs}) \simeq 0.65 \text{ eV}.$$

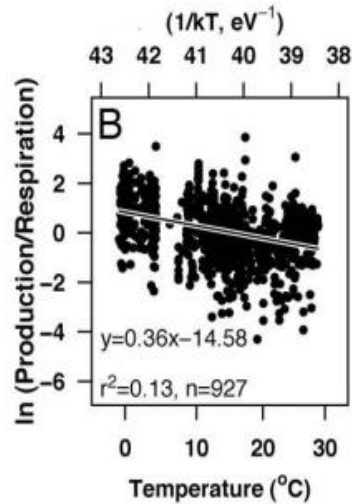
For plants,

$$E_a(\text{plants}) \simeq 0.33 \text{ eV}.$$

Plugging these numbers in above, we obtain

$$\frac{\text{production rate}}{\text{respiration rate}} \propto e^{(0.32 \text{ eV})/k_B T}$$

Remarkably, this is strikingly close to what is found for marine ecosystems:



Taking this result at face value and assuming no other changes, we would conclude that as temperatures increase, increases in respiration rates would outpace those of production, leading to a net increase of CO_2 levels and further warming.

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