Slide 1

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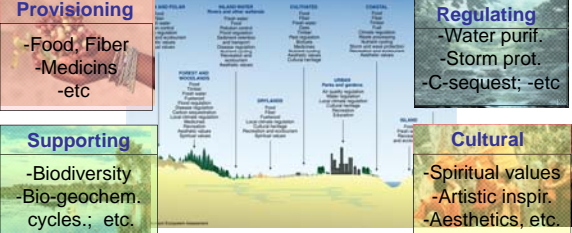# Ecological Allometry and Stability

towards a bioenergetic foundation for assessing

ecosystem services

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Slide 2

Millennium Ecosystem Assessment

Millennium Ecosystem Assessment (2001-2005)
Consequences of Ecosystem Change for Human Well-being
1360 scientists from 95 countries   www.MAweb.org

"Everyone in the world depends on nature and ecosystem services to provide the conditions for a decent, healthy, and secure life"

10 (Eco)systems -> 20 different services

Provisioning
-Food, Fiber
-Medicins
-etc

Regulating
-Water purif.
-Storm prot.
-C-sequest; -etc

Supporting
-Biodiversity
-Bio-geochem. cycles.; etc.

Cultural
-Spiritual values
-Artistic inspir.
-Aesthetics, etc.

From natural and cultivated ecosystems

Slide 3

# Body Size vs. Metabolic Rate

Slide 4

- Body size is probably the single most obvious feature of an organism, and it profoundly affects structure and function.
- On average, larger organisms have higher metabolic rate R but lower population density D than smaller ones.
- The dependencies of R and D on body size determine the pattern of energy partitioning within an ecological community.

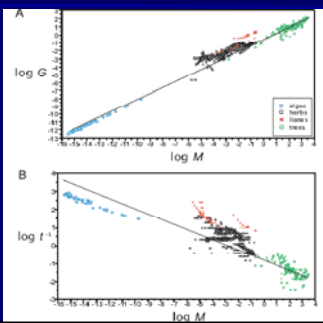Basal metabolic rate *vs.* body mass for various mammalian species
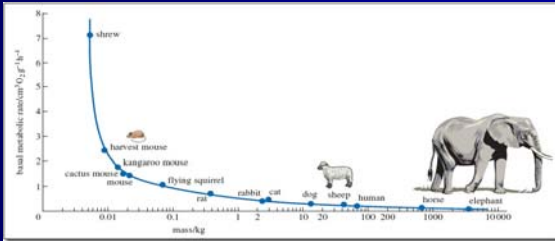
Adapted from Schmidt-Nielson (1975), Animal Physiology, Adaptation and Environment, Cambridge University Press

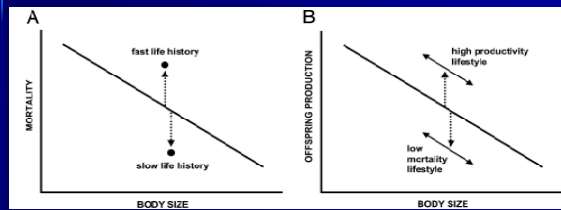## The dependence of individual territory on body mass in mammals
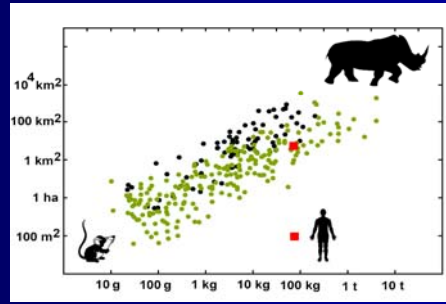
Plant growth rate vs. body mass

(Niklas, 2007)

A lifestyle view of life-history evolution

(Dobson, 2007)

2

Allometric Scaling

- The D-M relationship, $D \propto M^a$;

  Damuth (1981, 1987) pointed out that in mammals and several other higher taxa D decreases proportionally to $M^{-0.75}$, where M is body mass. Assuming that metabolic rate R increases as $M^{0.75}$ (Kleiber, 1932), Damuth put forward the idea of energetic equivalence of species, i.e. that every species consumes the same amount of energy per unit time per unit area irrespective of its body size.
- The B-M relationship, $B \equiv DM \propto M^b$ (e.g., the biomass equivalence rule (Damuth 1994)).
- The number of species in an ecological community is also a function of body size (e.g., Harvey & Lawton 1986)

Scaling exponents

- Both similar to Damuth's -0.75 and significant different from it were found.
- Studies of aquatic communities traditionally operating with size-class rather than species population density are on average characterized by D-M scaling exponents clustering around -1 rather than around -0.75.
- size-class biomass of other animals, e.g., tropical arthropods (Stork and Blackburn, 1993) or microscopic soil organisms (Lin and Brookes, 1999), was shown to grow conspicuously with body size.

- In the view of the substantial uncertainty that is associated with the scaling exponents of the D-M and B-M relationships, as well as with the dependence of species number on body size (e.g., global versus local patterns, see Brown and Nicoletto, 1991), one has to conclude that so far there is no general answer to the question of whether the larger organisms consume greater or smaller portions of the community's energy flux than the smaller ones.

Diversity-Stability

- The species body size and the share of community's energy flux allocated to different-sized organisms are at best marginal parameters or completely absent from the numerous models developed for the study of ecosystem stability (Leigh, 1965; DeAngelis, 1980; Moore *et al.*, 1993).

A new theoretical approach that links the allometry of energy partitioning among different-sized organisms in ecological community to community stability is needed.

The theoretical problem of energy partitioning over different-sized organisms is central to the ecosystem stability problem, and vice versa.

ENERGY PARTITIONING BETWEEN DIFFERENT-SIZED ORGANISMS AND ECOSYSTEM STABILITY

Bai-Lian Li,[1,3] Victor G. Gorshkov,[2] and Anastassia M. Makarieva[2]

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ECOLOGICAL COMPLEXITY

Ecological Complexity 1 (2004) 139–175

http://www.elsevier.com/locate/ecocom

Body size, energy consumption and allometric scaling: a new dimension in the diversity–stability debate

Anastassia M. Makarieva [a,b,*], Victor G. Gorshkov [a], Bai-Lian Li [b]

We proposed that natural ecological communities are organized in a way maximizing their stability and minimizing the fluctuations of all life-important environmental parameters, including nutrient concentrations and live biomass.

Some key equations

To account for the change of body size l we introduce the linear spectral density of the share of energy consumption and squared relative biomass fluctuation:

$$\beta_l = \frac{1}{\Delta l} \sum_{l}^{l+\Delta l} \beta_i, \qquad \varepsilon_l^2 = \frac{1}{\Delta l} \sum_{l}^{l+\Delta l} \varepsilon_i^2, \qquad (7)$$

where summation is made over all heterotrophic individuals with body size confined between l and $l + \Delta l$.

The condition that fluctuations introduced by highly mobile heterotrophs of all body sizes, from minimum l_{min} to maximum l_{max} in total do not exceed the fluctuations of plant biomass introduced by plants themselves (Appendix 1), thus assumes the form:

$$\int_{l_{min}}^{l_{max}} \varepsilon_l^2 \, dl \le \varepsilon_1^2. \qquad (8)$$

The linear spectral density β_l has the dimension of inverse length. It is not convenient for the quantitative analysis of the available empirical data, which usually refer to logarithmic intervals of body size. The transition from linear β_l to logarithmic $\beta(l)$ spectral density of the share of energy consumption can be performed as

$$\beta(l) = \int_l^{kl} \beta_l \, dl, \qquad (11)$$

where k is the base of the logarithm used.

From Eqs. (10) and (11) we have

$$\beta(l) = \left(1 - \frac{1}{k}\right) \frac{1}{l} \frac{\varepsilon_i^2 s_i}{l_{max} \bar{S}}. \qquad (12)$$

For population density $D(l)$ and biomass $B(l)$ of highly mobile heterotrophs from logarithmic body size intervals we have

$$D(l) = \frac{\beta}{R} P_i \propto \frac{1}{lR}. \qquad (13)$$

$$B(l) = DM \propto \frac{M}{lR}. \qquad (14)$$

As long as $R \propto M^\alpha$, where the value of α is normally not less than 2/3, Eq. (14) suggests either a constant biomass $B \propto M^0$ (if $\alpha = 2/3$, as is the case in birds, for example (Nagy, 1987; Dodds *et al.*, 2001)) or a decrease of biomass at a rate of $B \propto M^{1-(3/3+\alpha)}$ (if $\alpha > 2/3$).

Stable versus unstable ecological communities

- The basis for the theoretical predictions formalized by Eqs. (12)-(14) is formed by the idea that elementary ecosystem units (e.g., in forest ecosystems these were defined by us as trees with the attached local biota) are organized so as to minimize fluctuations of all life-important environmental characteristics.
- Plant biomass is responsible for the primary flux of energy in the ecosystem, which drives the local biogeochemical cycles of all nutrients.
- Hence, fluctuations of plant biomass due to its consumption by plant-feeding animals lead to fluctuations of local fluxes and stores of organic and inorganic nutrients. The plant biomass fluctuations introduced by individual animals grow rapidly with increasing body size.

- For the stability of the ecosystem unit's functioning to be conserved, the absolute amount of primary productivity allocated to large heterotrophs should decrease with increasing body size.
- Such a principle of community organization is only meaningful if the abiotic fluctuations of the community's environment are small. This is the case when the abiotic processes fluxes of matter for environmental fluctuations are less powerful than the biological fluxes of synthesis and decomposition.


- The situation is different in environments where the power of abiotic processes significantly exceeds the community's productivity. If the community's environment fluctuates due to powerful abiotic processes, the minimization of biotic fluctuations is of no use, as it will not lead to a stable environment anyway.
- Our approach predicts that in such unstable communities the ecological restrictions on fluctuations of plant biomass due to consumption by heterotrophs are either significantly lessened or completely absent. This leads to disappearance of the dependence of the share of energy consumption over body size, which in stable ecosystems is dictated by Eq. (8).

■ Hence, we can expect that in unstable ecosystems the energy partitioning among organisms of different body size should be more irrigular and, on average, more equitable. The logarithmic β-M, D-M and B-M distributions, Eqs. (12)-(14), should be on average flatter in unstable as compared to stable ecological communities.

Stable ecological communities of boreal forests

■ Equation (13) predicts that population density D of animals from each size class should decline as $D \propto 1/(lR) \propto M^{-1.06}$, where M is the mean mass for size class and $l \propto M^{1/3}$.

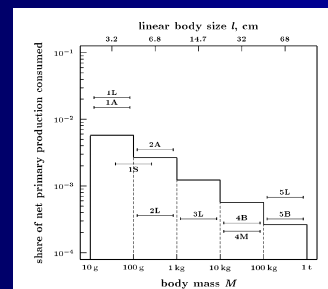**Population density of plant-feeding animals versus size-class body mass in boreal forest communities**
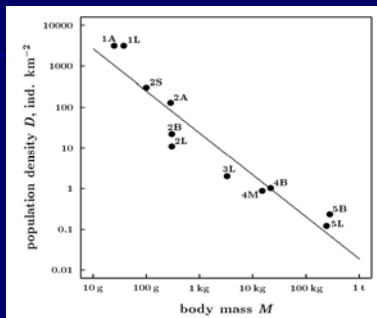
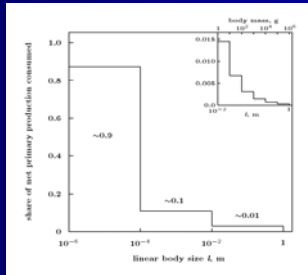b=-1.03
SD=0.11
R^2=0.9

b_L=-1.06
SD=0.3
R^2=0.86

(Makarieva, Gorshkov & Li, 2004. Ecol. Complexity, 1(2).)

Relative share $\beta(l)$ of net primary production consumed by plant-feeding organisms from different body size classes.

Order-of-magnitude energy consumption portrait of a stable ecological community
(estimation from the data available in the literature)

Size spectra in aquatic ecosystems

- Despite fundamental differences in biological organization, aquatic ecosystems appear to conform to the same rule: ecosystem stability is associated with lower energy flow through larger individuals

- Sprules and Munawar (1986) compared scaling exponents in the *D-M* relationships for 67 plankton samples (fresh particle weight from 10–10 to 10–3 g, *D* is the number of individuals per unit volume in a logarithmic size class) from the Central Gyre in the North Pacific Ocean, inland Ontario lakes and Laurentian Great Lakes Superior, Huron, St.-Clair, Erie and Ontario.

- The observed scatter of *D-M* scaling exponents ranged from $b = -0.76$ (central stations in Lake Erie) to $b = -1.16$ (open ocean);
- The most stable ecosystems like those of the open ocean, $b = -1.16$, and large oligotrophic lakes like Lake Superior, $b = -1.10$, are not only characterised by the lowest values of the scaling exponent, but also by the highest correlation coefficients describing the *D-M* spectra ($r^2 = 0.97$ and 0.94-0.98, respectively);
- Unstable and destabilised aquatic ecosystems, like shallow lakes receiving major nutrient discharges from the inflowing rivers (Lake St. Clair) or lakes with a high degree of contamination (Lakes Ontario and Erie), demonstrate the shallowest logarithmic *D-M* slopes *b* and the lowest correlation coefficients.

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A similar difference between energy partitioning patterns in stable versus unstable ecosystems within separate trophic groups

- In the most stable ecosystem of Lake Superior and other oligotrophic lakes bacterial respiration accounts for more than 90% (from 91% to 98%) of the total planktonic respiration.
- With increasing eutrophy, the share of bacterial respiration decreases down to 9% (Lakes Medicine and Mitchell), indicating the growing role of larger heterotrophs in such ecosystems.

Ecological stability and productivity

- Where external matter fluxes shaping the community's environment are low, like in stable oligotrophic systems, a low biotic productivity is enough to keep the environment under control.
- Where such fluxes are high (e.g., nutrient discharges from the coastal zone), the more productive the ecological community, the more control it can impose on the environment.
- Hence, in highly fluctuating environments there appears a natural selection gradient towards higher biological productivity

Summary (I)

- A new theoretical approach is developed that links the allometry of energy partitioning among different-sized organisms in ecological community to community stability.
- The magnitude of fluctuations of plant biomass introduced by plant-feeding heterotrophs is shown to grow rapidly with increasing body size.
- To keep these fluctuations at a low level compatible with ecosystem stability, the share of ecosystem primary productivity claimed by plant-feeding heterotrophs should decrease with increasing body size.

- In unstable environments the ecological restrictions on biotic fluctuations are lessened and net primary productivity can be distributed more evenly among different-sized organisms.
- Within the developed approach it is possible to quantitatively estimate not only the scaling exponents in the dependence of population density and biomass of heterotrophs on body size, but also the absolute values of energy fluxes claimed by organisms of a given size in stable communities.
- Theoretical predictions are tested against diverse sets of empirical data.
- It is shown that in stable ecological communities the largest heterotrophs are allowed to consume no more than several tenths of percent of net primary productivity.

Allometry of Home Range and Population Density

Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability

Anastassia M. Makarieva [a,b], Victor G. Gorshkov [a], Bai-Lian Li [b,*]

Home range

- Home range is defined as the area accommodating all regular activities of the animal, including consumption of energy from the environment (feeding).
- Already early research in mammals revealed that home range grows significantly more rapidly with body mass than does individual metabolic rate. Recent comprehensive works confirmed this pattern.
- Several theoretical studies sought to quantitatively account for the observed mass scaling exponents of home range that typically approximate or somewhat exceed unity, but lack of a general explanation.

Some key equations
1. Primary consumers

We have shown (Makarieva et al., 2004) that the condition that in stable ecosystems plant biomass fluctuations introduced by herbivores do not grow with herbivore body size makes the share of primary productivity $\beta_h(l)$ claimed by herbivores of linear body size l decline inversely proportionally to l (energetic dominance of the smallest animals):

$$\beta_h(l) \propto \frac{1}{l}. \tag{1}$$

Here, $\beta_h(l) \equiv P_h(l)/P_1$, where P_1 is ecosystem's primary productivity (W m^{-2}) and $P_h(l)$ is the cumulative flux of energy consumption by all herbivorous animals of body size l in a logarithmic body size interval.

The absolute population-level energy consumption P_h of herbivores is related to population density N_h as $P_h = N_h Q_h$, where Q_h is individual metabolic rate (W ind^{-1}) and N_h (ind km^{-2}) is the cumulative population density of herbivores of a given body size. Assuming $Q_h \propto M^{m(Q_h)}$ and $l_h \propto M^{1/3}$, where M_h is herbivore body mass and l_h is its linear body size, we, using Eq. (1), obtain for the mass scaling of population density, $N \propto M^{m(N_h)}$, that $m(N_h) = -(m(Q_h) + 1/3)$. For solitary animals home range H equals inverse population density N, if the latter is measured on contiguous areas inhabited by the species, $H = N^{-1}$, so we have:

$$m(H) = -m(N) = m(Q_h) + 1/3 \qquad (2)$$

Field metabolic rate of mammals scales as body mass in the power 0.73 (Nagy et al., 1999). Setting $m(Q_h) = 0.73$ in Eq. (2) gives $m(H_h) = 1.06$ for herbivorous mammals.

2. Secondary consumers

Assuming that under natural conditions carnivores (denoted as low index c) exempt a size-independent fraction β_c of productivity of their herbivorous prey (low index h), we have $N_c Q_c = \beta_c N_h Q_h$, where N_c and Q_c are population density and metabolic rate of carnivores. This assumption is supported by the available observations. For example, Carbone and Gittleman (2002) found that at mass-independent $N_h Q_h \propto M^0$, the population density of carnivores per unit productivity of their prey scales inversely proportionally to metabolic rate Q_c, which means that β_c is also size-independent, $\beta_c \propto M_c^0 \propto M^0$. From this, we obtain under the assumption that metabolic rate scales similarly in carnivores and herbivores, $m(Q_h) = m(Q_c) \equiv m(Q)$:

$$N_c \propto N_h \left(\frac{M_h^{m(Q)}}{M_c^{m(Q)}} \right). \qquad (3)$$

Here, M_c is carnivore body mass and M_h is body mass of its herbivorous prey. The scaling of carnivore population density will, therefore, depend on how prey mass scales with predator mass. We denote the corresponding scaling exponent as m_{pp} (prey–predator), $M_h/M_c \propto M_c^{m_{pp}}$. Remembering that in stable ecosystems Eq. (2) takes place we obtain from Eq. (3):

$$m(H_c) = -m(N_c) = m(Q) + \frac{1}{3} + \left(\frac{1}{3} \right) m_{pp} \qquad (4)$$

Home range in carnivores should grow more rapidly with body mass than home range of herbivores, $m(H_c) = m(H_h) + (1/3)m_{pp}$. This effect becomes stronger with growing m_{pp}, that is, the more rapidly prey size grows with predator size, the more rapidly predator home range grows with predator size.

Home range scaling in carnivores
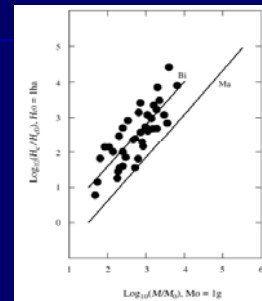
■ This result is consistent with the observation that birds are generally by far less abundant than equally sized mammals.

Summary (II)

- We have proposed that home range size is an inherent species property, while population density is a more flexible parameter reflecting ecosystem state.
- With the onset of ecosystem disturbance (cutting, burning, invasions, habitat fragmentation etc.) animal population density is the first spatial variable to distort from its ecologically stable value.
- Animals should be able to tolerate changes in population density more easily than those of home range. For example, animals can survive overcrowding on areas equal to or exceeding their natural home range, but should rapidly become extinct if concentrated on areas significantly smaller than their natural home range.
- One can expect, for example, that large carnivores, featuring the largest home territories among vertebrates, will be the first victims of habitat loss and habitat fragmentation. This prediction is consistently supported by observations (Primm and Clark, 1996; Woodroffe and Ginsberg, 1998).

- In stable (s) ecosystems population density N_h and inverse home range H_h of herbivores decline with growing body size more rapidly than the reciprocal of individual metabolic rate Q, , can be explained under the assumption that natural ecological communities are organized such as to stabilize local energy and matter fluxes.
- In disturbed (d) ecosystems with distorted species composition the ecological mechanisms of population control fail, and some species can claim a major part of primary productivity or even fully destroy vegetation.
- Where ecological limitations on fluctuations of local fluxes of matter and energy are absent or weakened, energy consumption can be on average independent of body size, , and herbivore population density N_h is not proportional to inverse home range H_h. Scaling of home range area, representing a species-specific property rather than an indicator of ecosystem state, does not depend on the degree of ecosystem disturbance.

- The difference between the absolute values of the scaling exponents $m(H_h)$ and $m(N_h)$ describing scaling of herbivore population density and home range with body mass observed in a particular ecosystem can serve as an indicator of ecosystem state, with $m(H_h) = -m(N_h)$ corresponding to stable and $m(H_h) > -m(N_h)$ to unstable (disturbed) ecosystems.

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Mathematical Models
of Dynamics and Control of Environmental Change:

Scaling from Genomes to Ecosystems

April 26 - May 1, 2009

Conclusions

Thank you