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Towards a Biophysically-Sounded Approach to Ecological Complexity and Sustainability

B. Larry Li

(In collaboration with: A. M. Makarieva, V. G. Gorshkov
and many others)

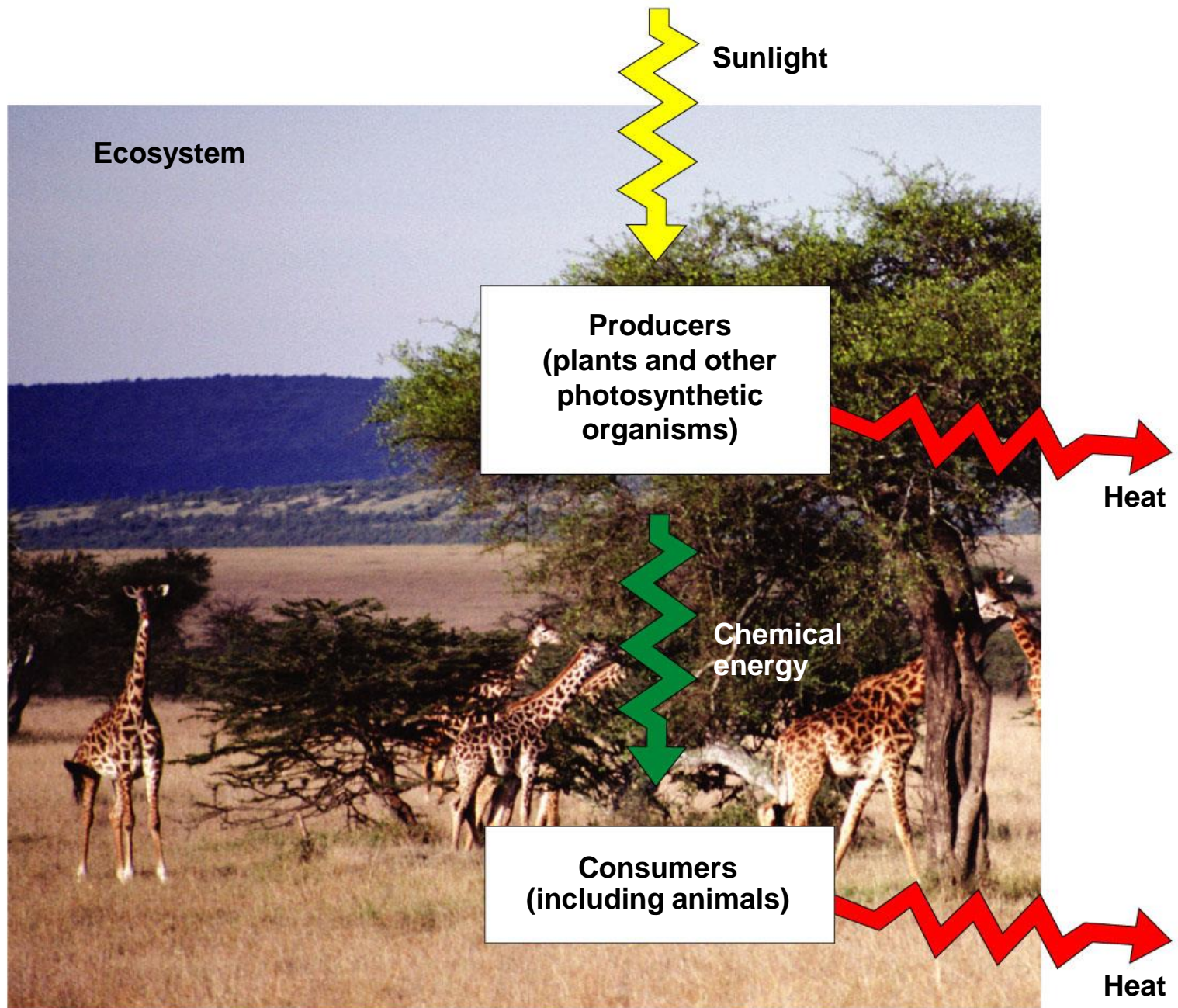
All the biological sciences rest on two central principles:

- One is that all life processes have an entirely physical and chemical (i.e., material) basis
- The other is that all organisms and their characteristics are products of evolution

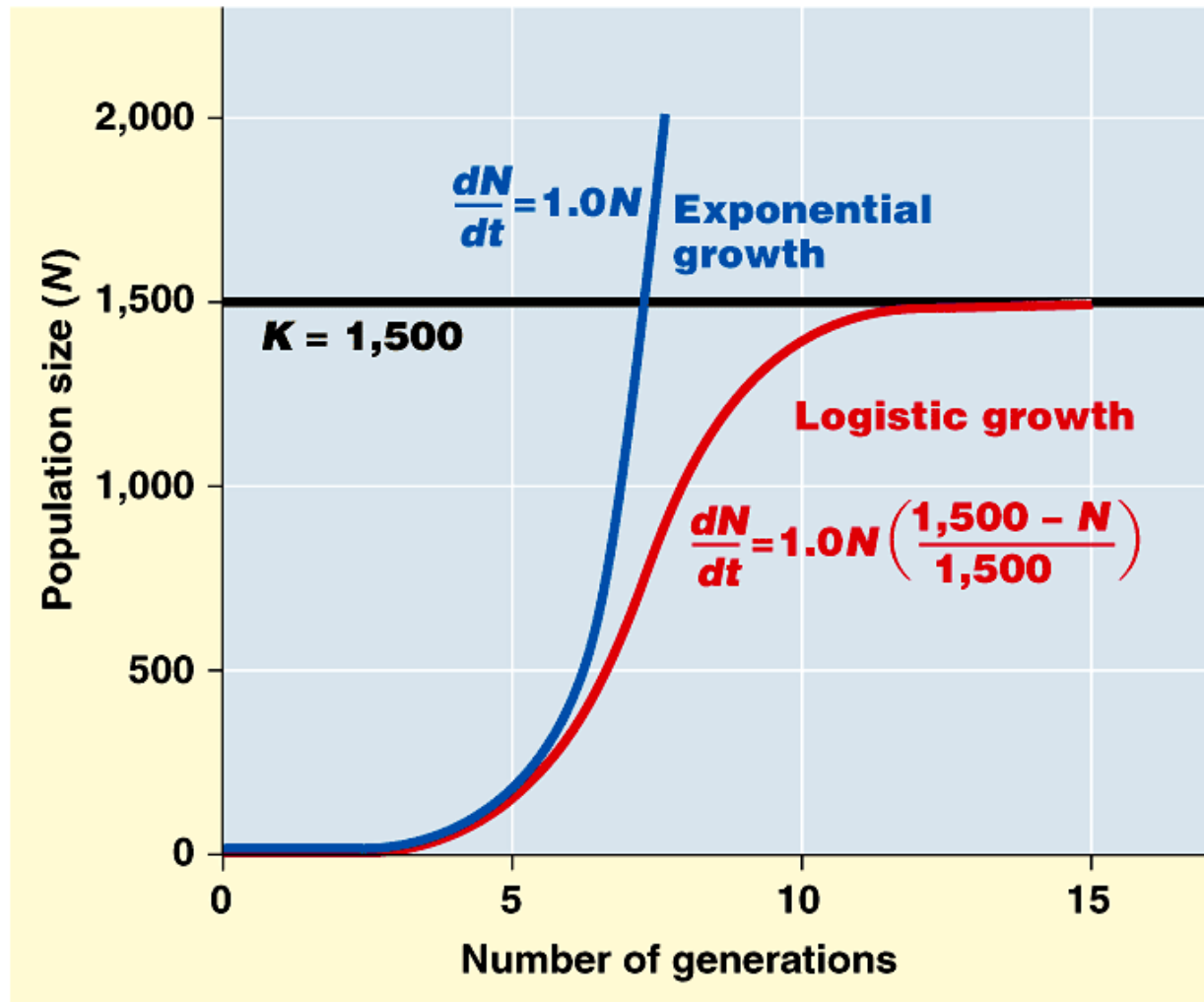
Energy and life



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Logistic Equation



Question

- How well is our commonly used Logistic equation biophysically sounded (e.g., energy conservation)?

Population dynamics without resource replenishment

$$\frac{1}{N} \frac{dN}{dt} = \lambda g(R) - \mu,$$

and

$$\frac{dR}{dt} = - \frac{\lambda g(R) N}{\xi},$$

The underlying basic assumption is that a constant proportion of consumed resource transforms into the form of reproduced population.

$$\xi R + N = \xi E_0 - \beta(t), \quad (8)$$

where subscript '0' denotes $t = 0$, $\xi E_0 = \xi R_0 + N_0$ represents the original potential population density that bio-energy per gram dry soil can support and $\beta(t) = \mu \int_0^t N(\tau) d\tau$ is the cumulative population loss (energy dissipated) per gram dry soil. Eq. (8) can be interpreted as conservation of energy relationship. The current total unit vital energy in the form of available resource and population density is equal to the initial total vital energy less the energy being dissipated.

$$\frac{dN}{dt} = \{\xi^{-1}\lambda[\xi E_0 - N - \beta(t)] - \mu\}N, \quad (11)$$

which can be reduced to the form similar to classical logistic equation (form (2))

$$\frac{1}{N} \frac{dN}{dt} = r(t) \left[1 - \frac{N}{K(t)} \right], \quad (12)$$

where $r(t)$ and $K(t)$ are the time-dependent specific growth rate and carrying capacity, respectively:

$$r(t) = \xi^{-1}\lambda[\xi E_0 - \beta(t)] - \mu = \chi K(t), \quad (13a)$$

where $\chi = \lambda/\xi$ represents a birth-rate parameter and

$$K(t) = \xi \left(E_0 - \frac{\mu}{\lambda} \right) - \beta(t). \quad (13b)$$

From Eq. (13a), it is clear that the specific growth rate changes with the carrying capacity, which in turn decreases with the non-recyclable energy loss of $\beta(t)$.

Population dynamics with a constant rate of resource replenishment

$$\xi R + N = \xi E_0 + \xi \gamma t - \beta(t),$$

$$\frac{1}{N} \frac{dN}{dt} = r_{\gamma(\text{CL})}(t) \left(\frac{1 - N/K_{\gamma(\text{CL})}(t)}{1 - N/K_{\gamma}^*(t)} \right)$$

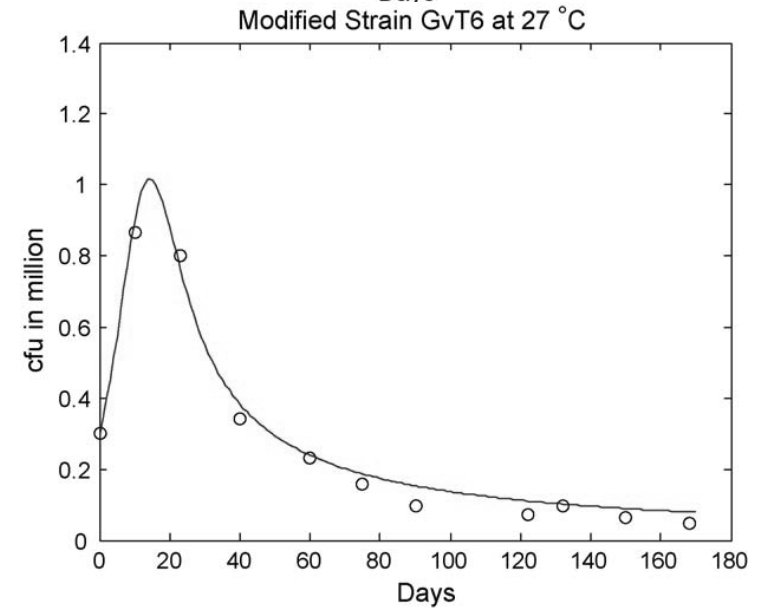
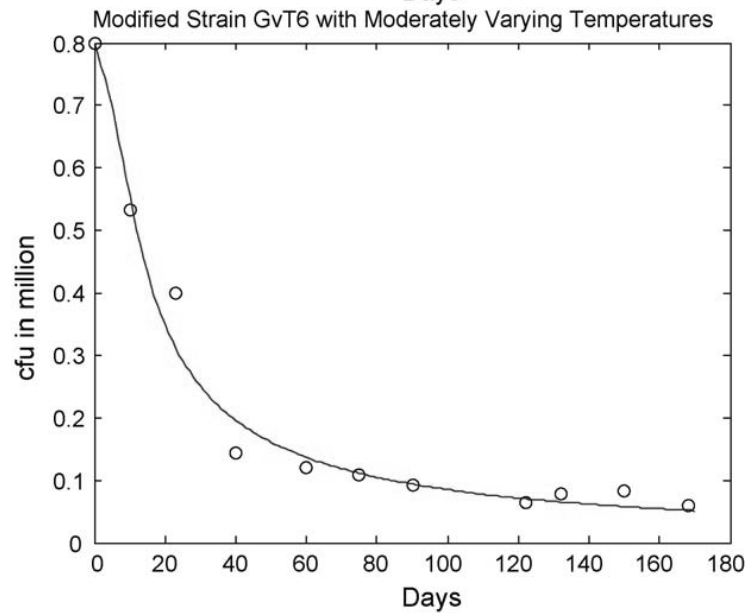
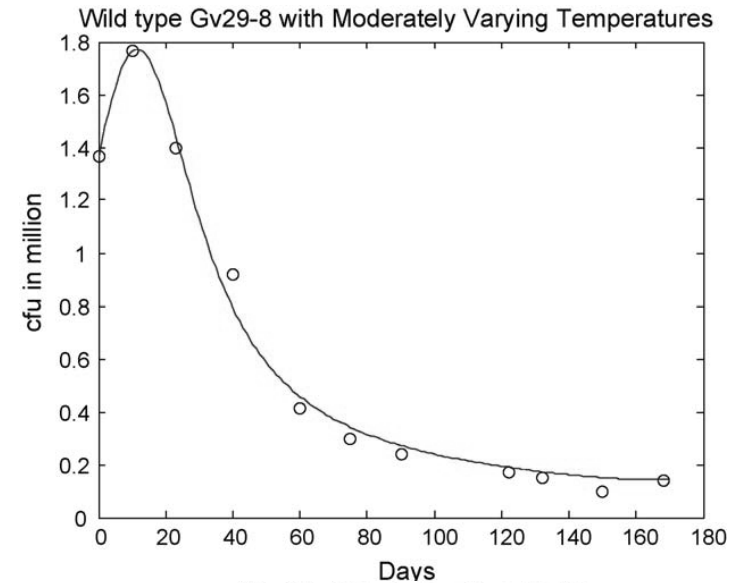
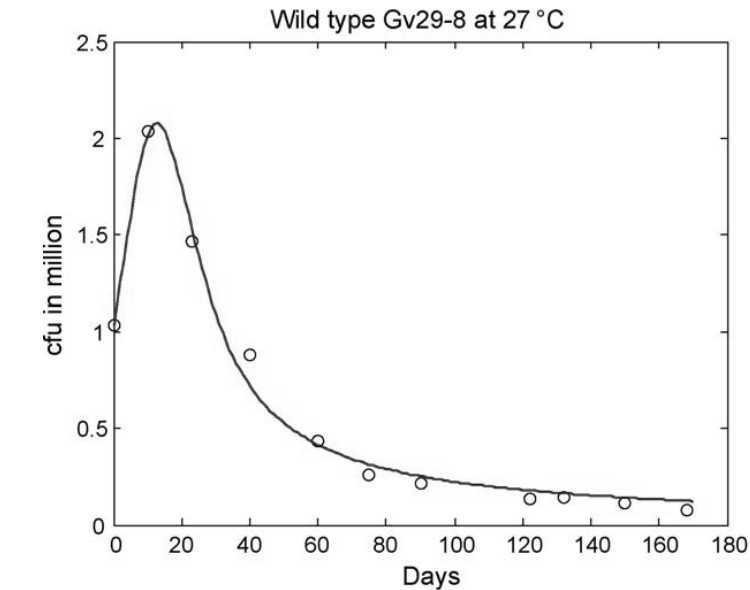
where

$$r_{\gamma(\text{CL})}(t) = (\lambda - \mu) K_{\gamma(\text{CL})}(t) / K_{\gamma}^*(t),$$

$$K_{\gamma(\text{CL})}(t) = K_{\gamma}^*(t) - S \xi \frac{\lambda}{\lambda - \mu},$$

$$K_{\gamma}^*(t) = \xi(E_0 + \gamma t + S) - \beta(t)$$

Some examples of biophysically-sounded Logistic equation





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Formulating variable carrying capacity by exploring a resource dynamics-based feedback mechanism underlying the population growth models

Hsin-i Wu^a, Amit Chakraborty^{b,*}, Bai-Lian Li^b, Charles M. Kenerley^c

Some of fundamental, but unanswered biological questions

- How much energy, on average, Earth's different life forms spend per unit mass per unit time to remain alive?
- Why do we breath?
- Why do animals move and why plant stay where they are? Why plant leaves are never as thick as some animal bodies?
- and so on.

We start from the premise that

- *life is organized in such a manner that it is capable of maintaining optimal conditions of its functioning, ensuring the needed fluxes of matter and energy at every scale of its organization, from cells to ecosystems.*

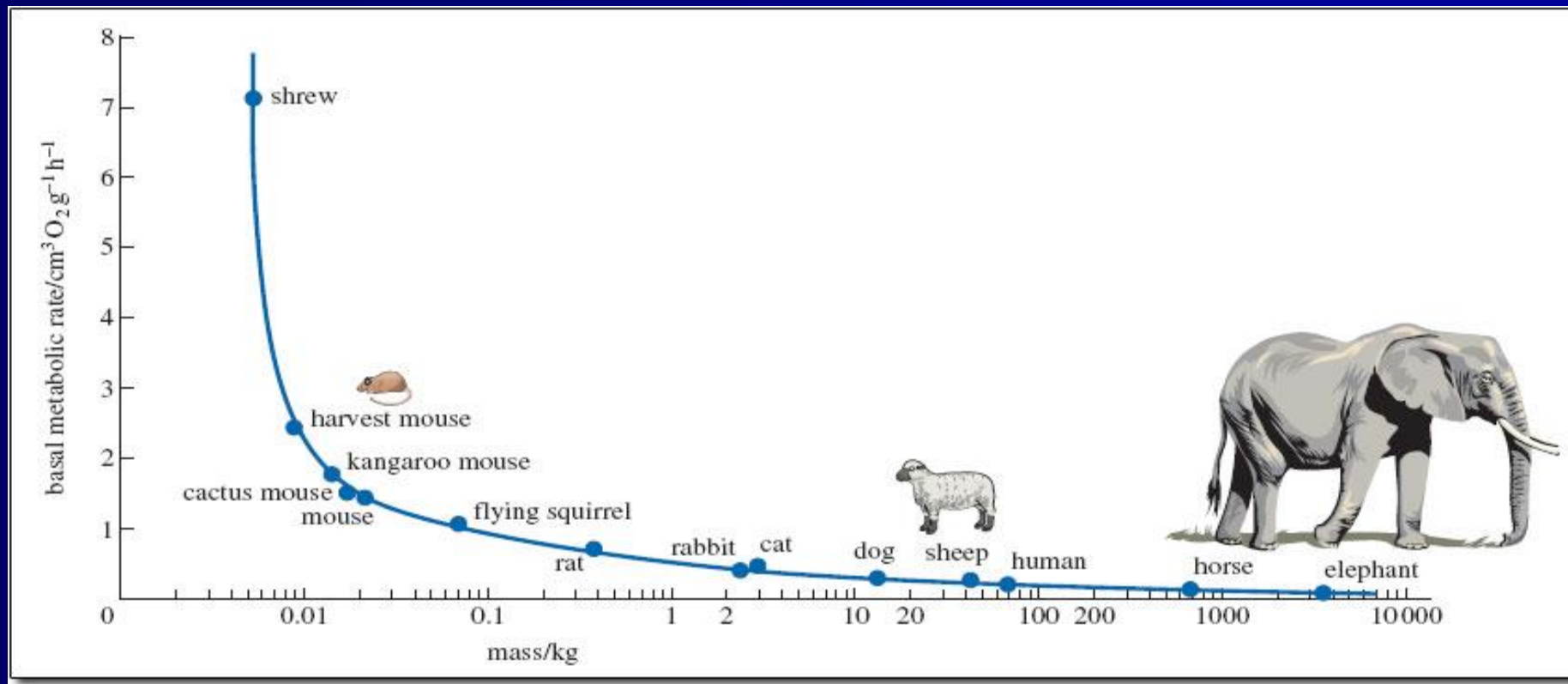
Broader impact

- Besides offering a new conceptual dimension in the current views on life, we can provide insights into several specific problems, for example:
- **At the ecosystem scale**, that forest cover plays a major role in the spatial scaling of the water supply rate on land, suggesting a good potential for forest-mediated solutions of the global desertification and water security problems.
- **At the cellular scale**, the proposed analysis of optimal functioning of distributive networks will, e.g., provide a theoretical basis for the use of body mass index in obesity-related analyses of cardiovascular diseases.
- **At the organismal scale**, the research of breathing cost limitations will provide essential theoretical basis for, e.g., the possible use of fossils in reconstructing paleoclimates (e.g., Head et al. Nature 2009; MGL, Nature, 2009).

Body Size vs. Metabolic Rate

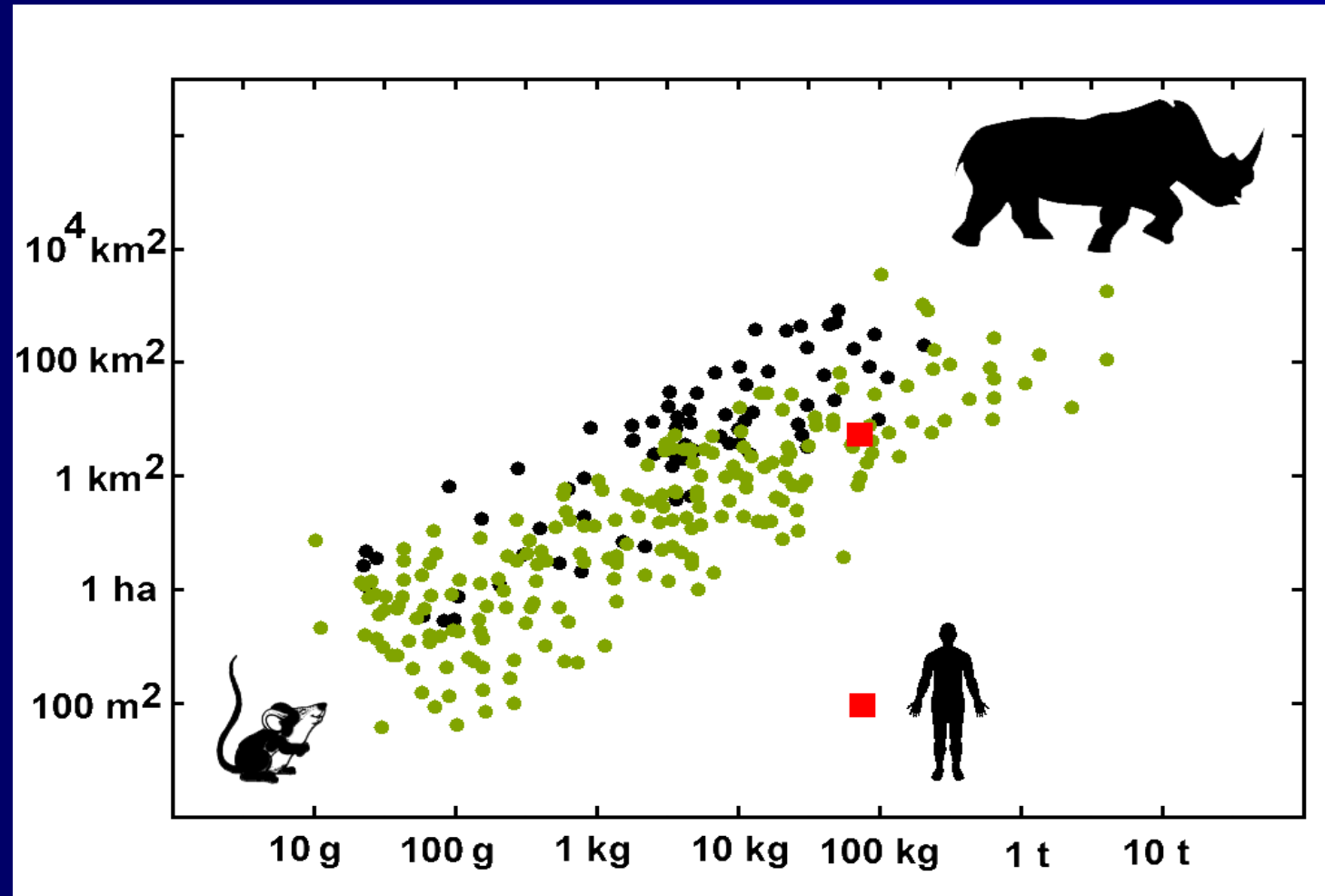


Basal metabolic rate vs. body mass for various mammalian species

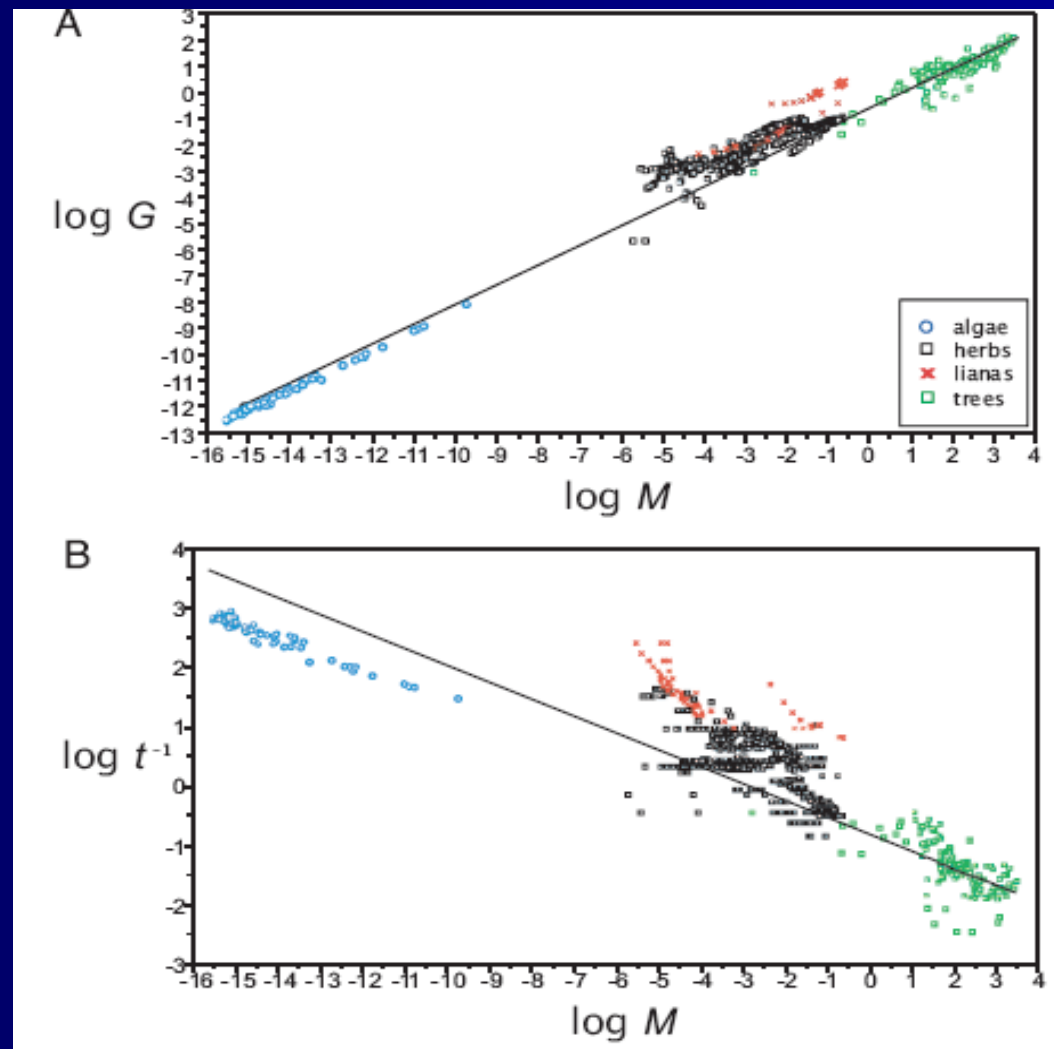


Adapted from Schmidt-Nielson (1975), Animal Physiology, Adaptation and Environment, Cambridge University Press

The dependence of individual territory on body mass in mammals

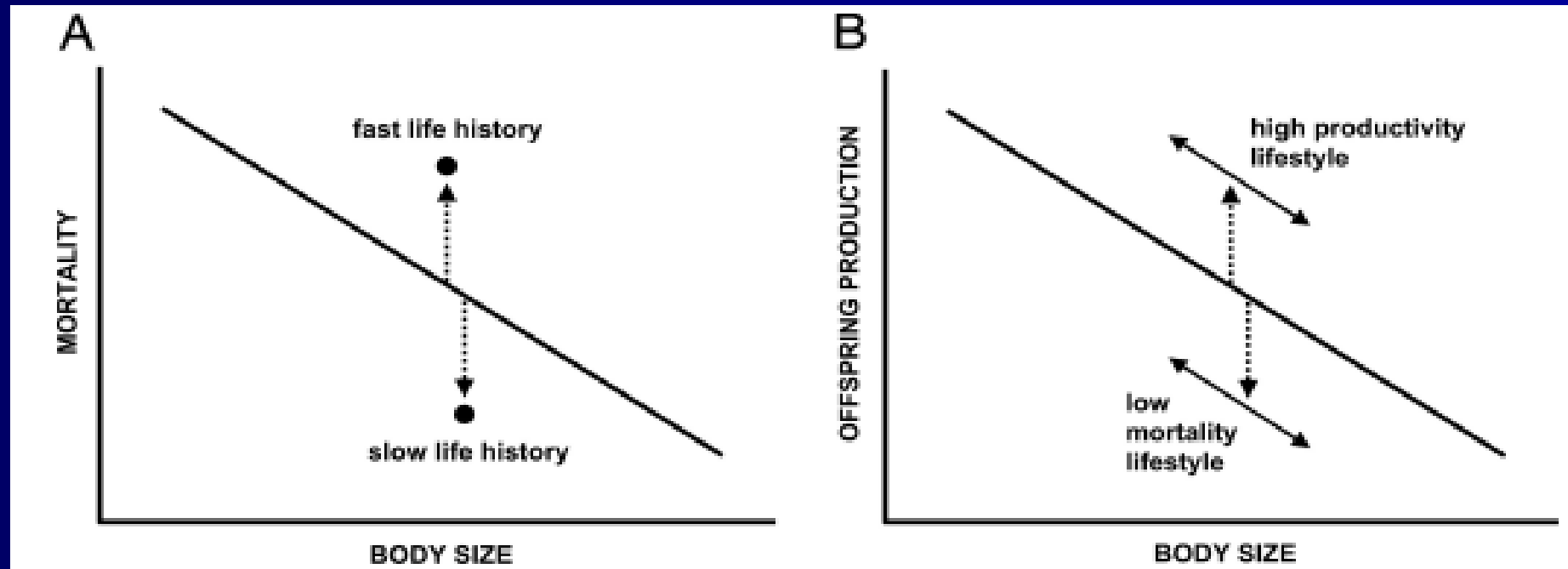


Plant growth rate vs. body mass



(Niklas, 2007)

A lifestyle view of life-history evolution



(Dobson, 2007)

Biological and physical regularities

- constancy of (solar) energy flux per unit (ground) surface area;
- the existence of a minimum value of the volume-specific metabolic rate b_{\min} ensuring the living state of life.

- The crucial feature of organismal energetics is that the energy is consumed from the environment via some part of body *surface* S , while it is spent within body *volume* V .
- If the flux of energy through unit body surface area, f , is constant, then the metabolic rate per unit volume, $b \equiv fS/V$, decreases with growing linear body size l as $b \propto l^{\varepsilon_S - \varepsilon_V}$, where $\varepsilon_S \leq \varepsilon_V$ are the scaling exponents for body surface and volume, $S \propto l^{\varepsilon_S}$ and $V \propto l^{\varepsilon_V}$, respectively.
- In the case of geometric similarity $\varepsilon_S = 2$, $\varepsilon_V = 3$, and $b \propto l^{-1}$.

- Since there exists a certain minimum value b_{\min} , at fixed f , the value of b_{\min} determines the maximum size that the organism can attain.
- Plants exist due to consumption of solar energy, the mean annual flux of which, I (W m^{-2}), is determined by latitude. At a fixed value of efficiency η of assimilation of solar energy by the plant, the flux of energy f_p assimilated by the plant per unit ground area is constant:

$$f_p = \eta I \quad (1)$$

- We now introduce the effective vertical size l_e equal to the thickness of the layer which forms if all the metabolically active mass of the plant is flattened on the area of projection of the plant on the ground surface;
- Effective size l_e corresponds to the commonly used value of leaf area index, d (dimensionless) and can be estimated as $l_e = d h$, where h is the leaf's metabolic thickness.

- As the effective size l_e grows, the metabolic rate per unit metabolically active volume, b , decreases inversely and proportionally to l_e . This is because the amount of solar energy available per unit ground area does not change, while it is spent within a larger metabolically active volume. As soon as the minimum possible value b_{\min} is reached, the vertical growth is stopped at

$$l_{e \max} = f_p / b_{\min} = \eta I / b_{\min} \quad (2)$$

Table 1

Predicted scaling exponents and observed scaling exponents of different allometric relationships for two species under three soil water treatments

	Predicted exponent	Fm	Pa	Fm100	Pa100	Fm50	Pa50	Fm30	Pa30
$\text{Log}_{10} P \propto \text{Log}_{10} M$	$\frac{1}{4}$	<i>1.8302*</i>	0.8314	1.3938**	<i>0.0869</i>	<i>2.6316**</i>	<i>1.7769**</i>	<i>2.3397**</i>	<i>1.4527</i>
		(± 0.6114)	(± 0.4660)	(± 0.6794)	(± 0.0146)	(± 0.9785)	(± 0.2762)	(± 0.8912)	(± 0.2641)
$\text{Log}_{10} P \propto \text{Log}_{10} M_l$	$\frac{1}{4}$	<i>1.3407*</i>	<i>0.4633</i>	<i>1.5505**</i>	<i>0.4570</i>	<i>1.9328**</i>	0.8977	<i>3.3959</i>	<i>-0.1576</i>
		(± 0.2297)	(± 0.0973)	(± 0.6528)	(± 0.1024)	(± 0.5493)	(± 0.2403)	(± 1.015)	(± 0.1003)
$\text{Log}_{10} M_p \propto \text{Log}_{10} M_n$	$\frac{1}{4}$	0.7520	<i>0.2537</i>	<i>0.2653</i>	<i>3.4856</i>	<i>0.7334**</i>	<i>1.1543</i>	<i>0.6019**</i>	<i>1.1612**</i>
		(± 0.1350)	(± 0.0324)	(± 0.0694)	(± 0.0862)	(± 0.0941)	(± 0.0942)	(± 0.1121)	(± 0.8941)
$\text{Log}_{10} M_p \propto \text{Log}_{10} M_s$	$\frac{1}{4}$	0.5545	<i>0.1773</i>	<i>0.0613</i>	<i>2.1020</i>	<i>0.1249**</i>	0.9917	<i>3.4121</i>	<i>2.9194**</i>
		(± 0.1024)	(± 0.0432)	(± 0.0241)	(± 0.1023)	(± 0.0872)	(± 0.1623)	(± 1.0764)	(± 1.422)
$\text{Log}_{10} M_p \propto \text{Log}_{10} D$	2	<i>1.1822</i>	2.3316	2.1015	<i>4.1400</i>	<i>-0.6408</i>	<i>3.5212</i>	<i>1.1704</i>	<i>0.1077</i>
		(± 0.3250)	(± 0.1921)	(± 0.4231)	(± 0.2821)	(± 0.1203)	(± 0.1976)	(± 0.1042)	(± 0.0674)
$\text{Log}_{10} M_s \propto \text{Log}_{10} D$	$\frac{8}{3}$	<i>1.5776</i>	<i>1.7086</i>	<i>4.6373**</i>	<i>1.8017</i>	<i>2.1424</i>	<i>2.0604</i>	<i>2.5339**</i>	<i>0.3537**</i>
		(± 0.1431)	(± 0.1023)	(± 1.024)	(± 0.5132)	(± 0.1520)	(± 0.1675)	(± 1.1420)	(± 0.1165)
$\text{Log}_{10} H \propto \text{Log}_{10} M$	$\frac{1}{4}$	<i>1.0932**</i>	<i>-0.2446</i>	<i>3.9014</i>	<i>0.3345**</i>	<i>-0.5999</i>	<i>-0.2856</i>	<i>1.0167*</i>	0.1846
		(± 0.0976)	(± 0.0561)	(± 1.221)	(± 0.0984)	(± 0.1147)	(± 0.0892)	(± 0.1134)	(± 0.1564)

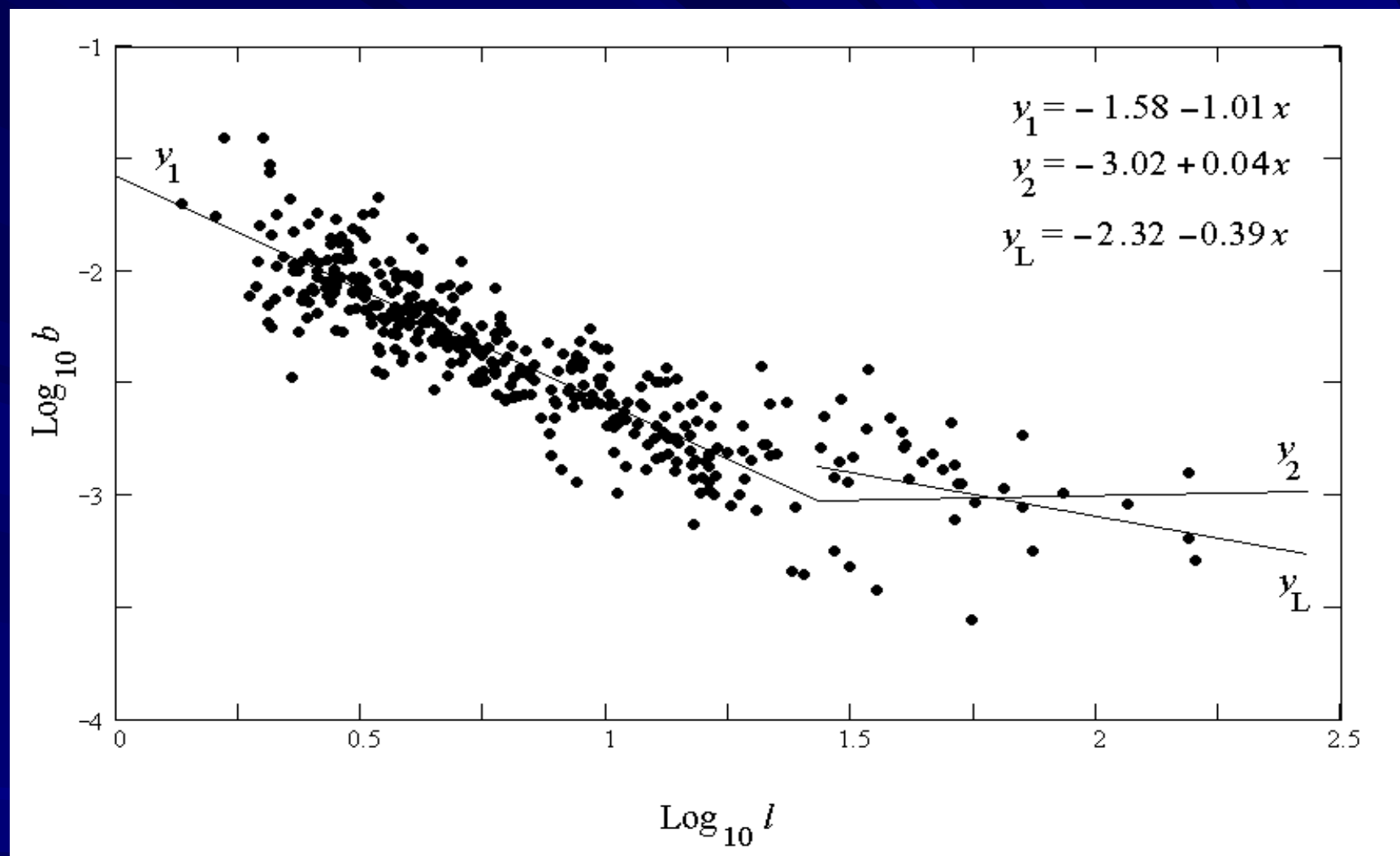
P : photosynthetic rate; M : total biomass; M_p : photosynthetic biomass; M_l : biomass of leaf; M_n : non-photosynthetic biomass; M_s : biomass of stem; D : diameter of stem; H : above ground height of seedling. Fm: *F. mandshurica* at all kinds of soil water contents; Pa: *P. amurense* at all kinds of soil water contents. Fm100, Fm50, Fm30, Pa100, Pa50 and Pa30: *F. mandshurica* and *P. amurense* at relative soil water contents of 100, 50 and 30%, respectively. Values in parentheses are at 95% confidence interval. For each species, the sample number of seedlings at each soil water treatment was 20. Scaling exponents in italics were significantly different from the predicated values.

* Significant at $P < 0.01$.

** Significant at $P < 0.05$.

For example, the plant productivity per unit area does not depend on plant size (Enquist *et al.*, 1998).

- This pattern is immediately retrieved from Eq. (1). The flux of solar radiation I being determined by latitude and the efficiency η of solar energy assimilation being determined by temperature and biochemical properties of the plant tissues directly interacting with light, the energy uptake f_p by the plants per unit ground area is constant, which ensures constant, size-independent productivity.



(Makarieva, Gorshkov & Li, 2003. *J. Theor. Biol.*, 221(3))

Ecology, 85(7), 2004, pp. 1811–1813
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ENERGY PARTITIONING BETWEEN DIFFERENT-SIZED ORGANISMS AND ECOSYSTEM STABILITY

BAI-LIAN LI,^{1,3} VICTOR G. GORSHKOV,² AND ANASTASSIA M. MAKARIEVA²



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Ecological Complexity 1 (2004) 139–175

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

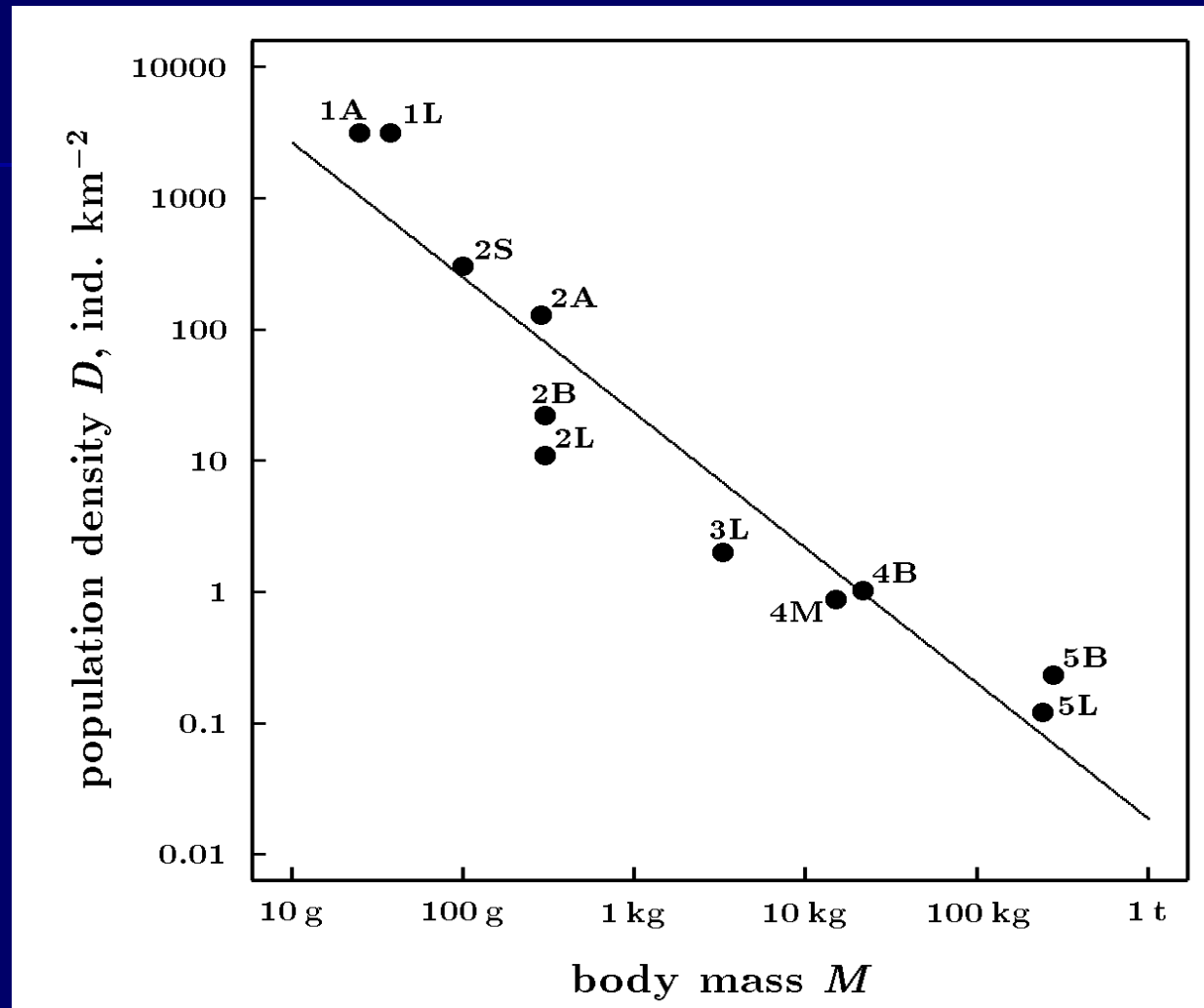
Anastassia M. Makarieva^{a,b,*}, Victor G. Gorshkov^a, Bai-Lian Li^b

- We propose 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.

Example: *Stable ecological communities of boreal forests*

- Our derived biophysical equation predicts that population density D of animals from each size class should decline as $D \propto 1/(IR) \propto M^{-1.06}$, where M is the mean mass for size class and $I \propto M^{1/3}$.

Population density of plant-feeding animals versus size-class body mass in boreal forest communities

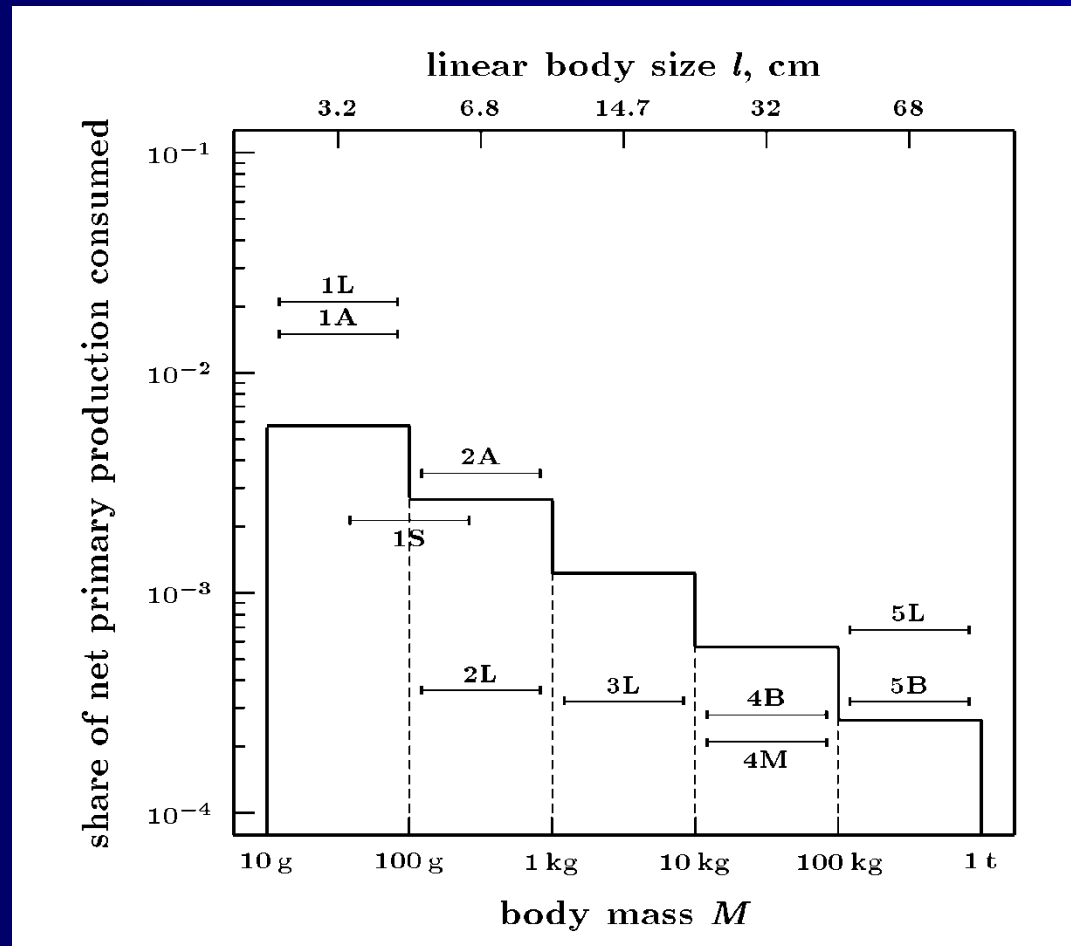


$b = -1.03$
 $SD = 0.11$
 $R^2 = 0.9$

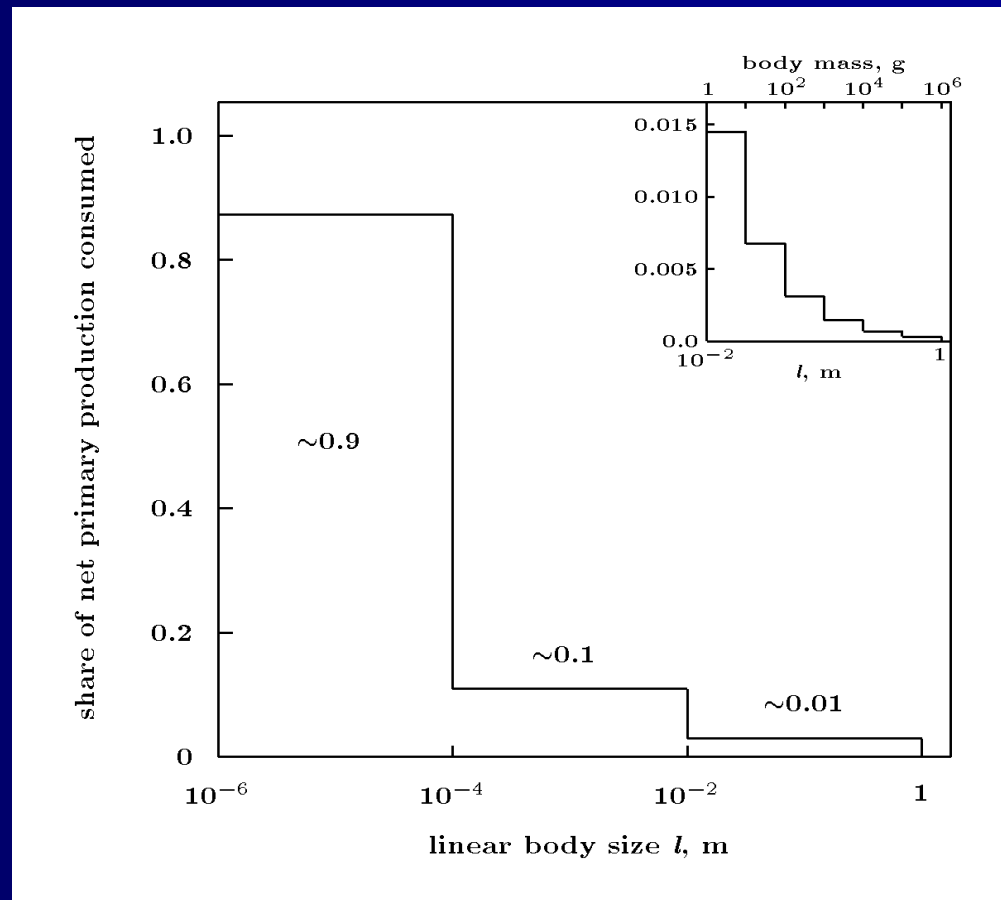
$b_L = -1.06$
 $SD = 0.3$
 $R^2 = 0.86$

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

Relative share $\beta(\lambda)$ 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)



These analyses suggest that the potential of the R — M scaling as an informative indicator of ecosystem stability is tangible and calls for a serious scrutiny (Makarieva et al. 2004*b*). There are straightforward arguments justifying the direct relevance of the energy use patterns to ecosystem stability and opening the way for theoretical research (Gorshkov et al. 2000). In accordance with the statistical law of large numbers, several small organisms consume the same energy flux in a more balanced manner than does one large organism, thus lowering the risk of both underexploitation or overexploitation of the available resources and reducing fluctuations of a community's biomass and nutrient-cycling processes. This is like dividing your money among several investments; return will be stabilized and loss minimized. Ecosystems where energy use is dominated by smaller organisms (but not for terrestrial plants, as we will discuss) are therefore expected to be more stable than ecosystems where large organisms consume considerable portions of a community's energy flux.

The large apparent size of many plants (e.g., trees) is due to a large amount of metabolically inactive tissues (wood) that do not participate in energy conversion processes (Makarieva et al. 2003). Instead, the photosynthetic power in terrestrial plants is exerted by units of relatively small size: leaves and needles. In contrast to rigidly correlated organs within an animal body, different photosynthesizing units of the same plant are correlated only very weakly. This allows plants to make use of the law of large numbers and to stabilize the flux of primary productivity, in the same manner as numerous small heterotrophs are able to stabilize the flux of decomposition. Our prediction is therefore that, similar to the way in which the smallest phytoplankton (unicellular photosynthesizing units)

dominate energy flux in stable aquatic ecosystems (Li 2002), the major flux of solar energy in stable terrestrial ecosystems should also be claimed by plants having the smallest photosynthesizing units. For example, stable late-successional stages in boreal forests are dominated by conifers that have much smaller photosynthesizing units (needles) than grasses and deciduous trees of early-successional stages (Whittaker 1975). We believe that studying the nature and size of photosynthesizing units (rather than the currently emphasized apparent plant size) will yield important insights into how terrestrial ecosystems are organized.



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Ecological Complexity 2 (2005) 259–271

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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,*}

$$\beta_l \equiv \frac{1}{\Delta l} \sum_l^{l+\Delta l} \beta$$

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):

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

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:

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

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, $m(Q_h) = m(Q_c) \equiv m(Q)$:

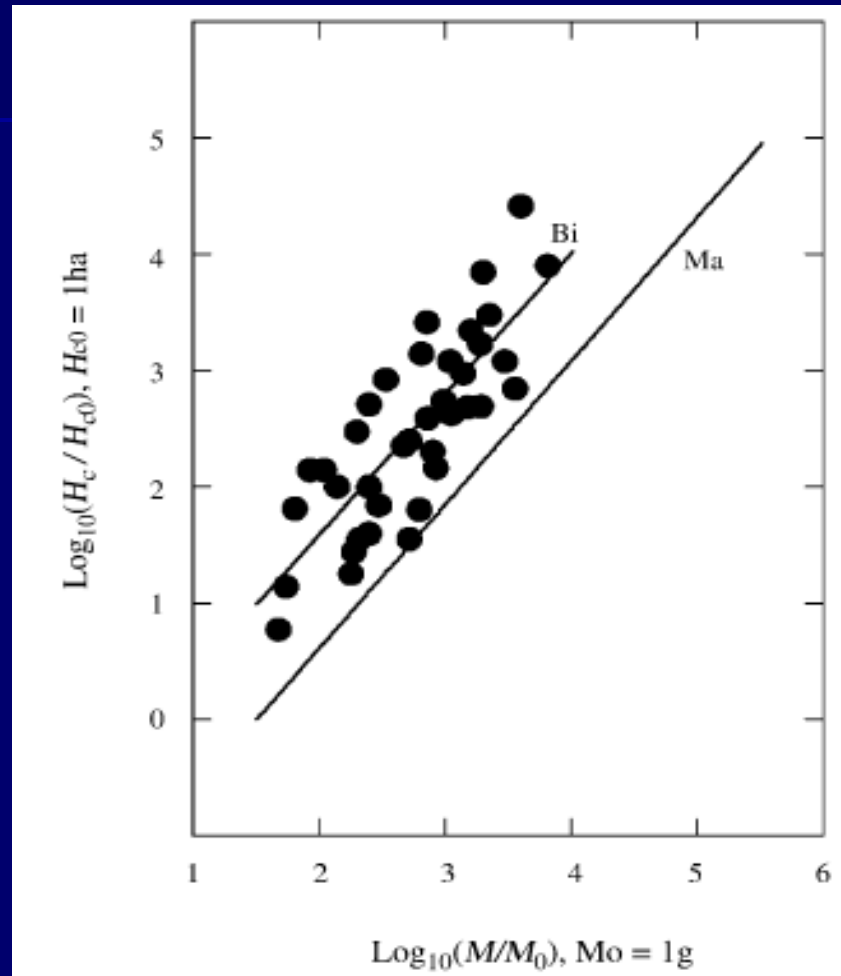
$$N_c \propto N_h \left(\frac{M_h^{m(Q)}}{M_c^{m(Q)}} \right). \quad (3)$$

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):

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

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.

Gigantism, temperature and metabolic rate in terrestrial poikilotherms

Anastassia M. Makarieva^{1,2}, Victor G. Gorshkov¹ and Bai-Lian Li^{2,*}

OIKOS 111: 425–436, 2005

Temperature-associated upper limits to body size in terrestrial poikilotherms

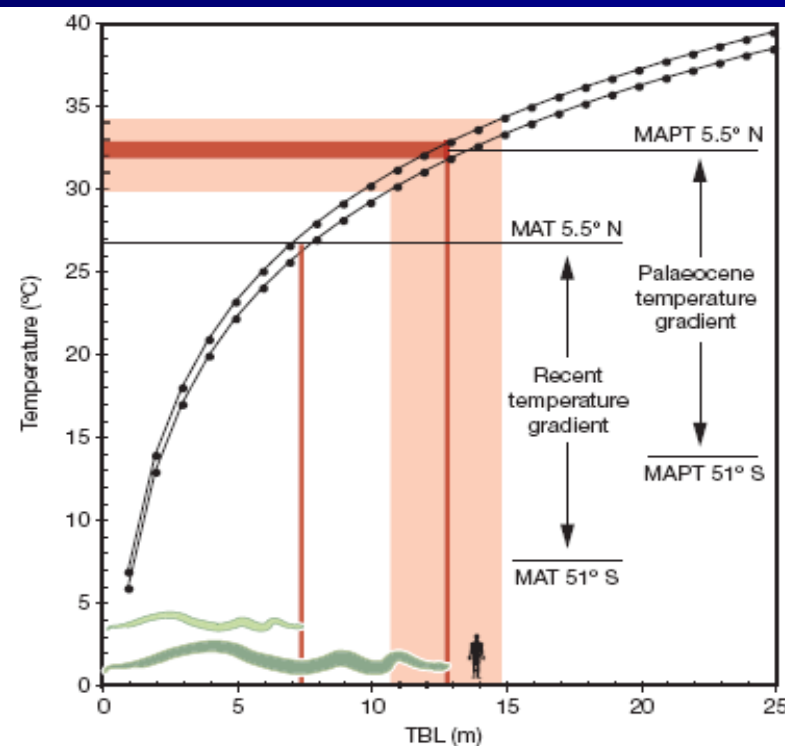
Anastassia M. Makarieva, Victor G. Gorshkov and Bai-Lian Li

- We develop a theoretical approach which quantitatively explains the observed body size patterns and relates them to ambient temperature under the assumption that there exists a temperature-independent critical minimum value of mass-specific metabolic rate b_{\min} , a fall below which is incompatible with successful biological performance.
- This value sets an upper limit to linear body size within a taxon. Mass-specific metabolic rate decreases with increasing body size but, in poikilotherms, grows exponentially with ambient temperature.
- Such compensation of the size-related drop in mass-specific metabolic rate b by higher ambient temperature extends the permitted range of body sizes for which $b \geq b_{\min}$.
- As a result, the maximum linear body size grows approximately twofold per each ten degrees of increase in ambient temperature.

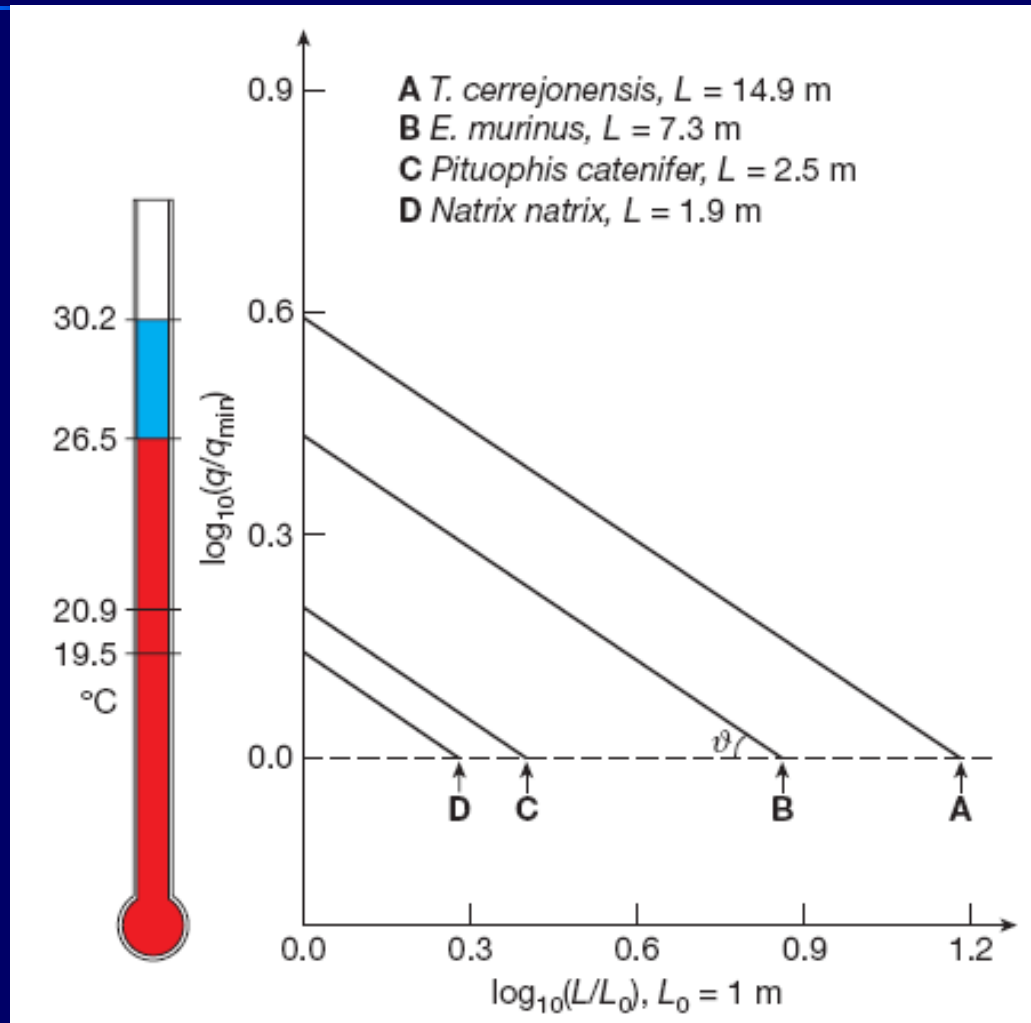
LETTERS

Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures

Jason J. Head¹, Jonathan I. Bloch², Alexander K. Hastings², Jason R. Bourque², Edwin A. Cadena^{2,3}, Fabiany A. Herrera^{2,3}, P. David Polly⁴ & Carlos A. Jaramillo³



MGL, Nature, July 30, 2009, doi10.1038/nature08223



A: Palaeocene neotropics
B: South America
C: Colorado
D: UK

Self-Sustained Optimality: A Novel Concept of Life's Supply/Demand Scaling

Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum

Anastassia M. Makarieva^{a,b,1}, Victor G. Gorshkov^{a,b}, Bai-Lian Li^b, Steven L. Chown^c, Peter B. Reich^d, and Valery M. Gavrilov^{*}

16094–16099 | PNAS | November 4, 2008 | vol. 105 | no. 44

Self-sustained *metabolic* optimality

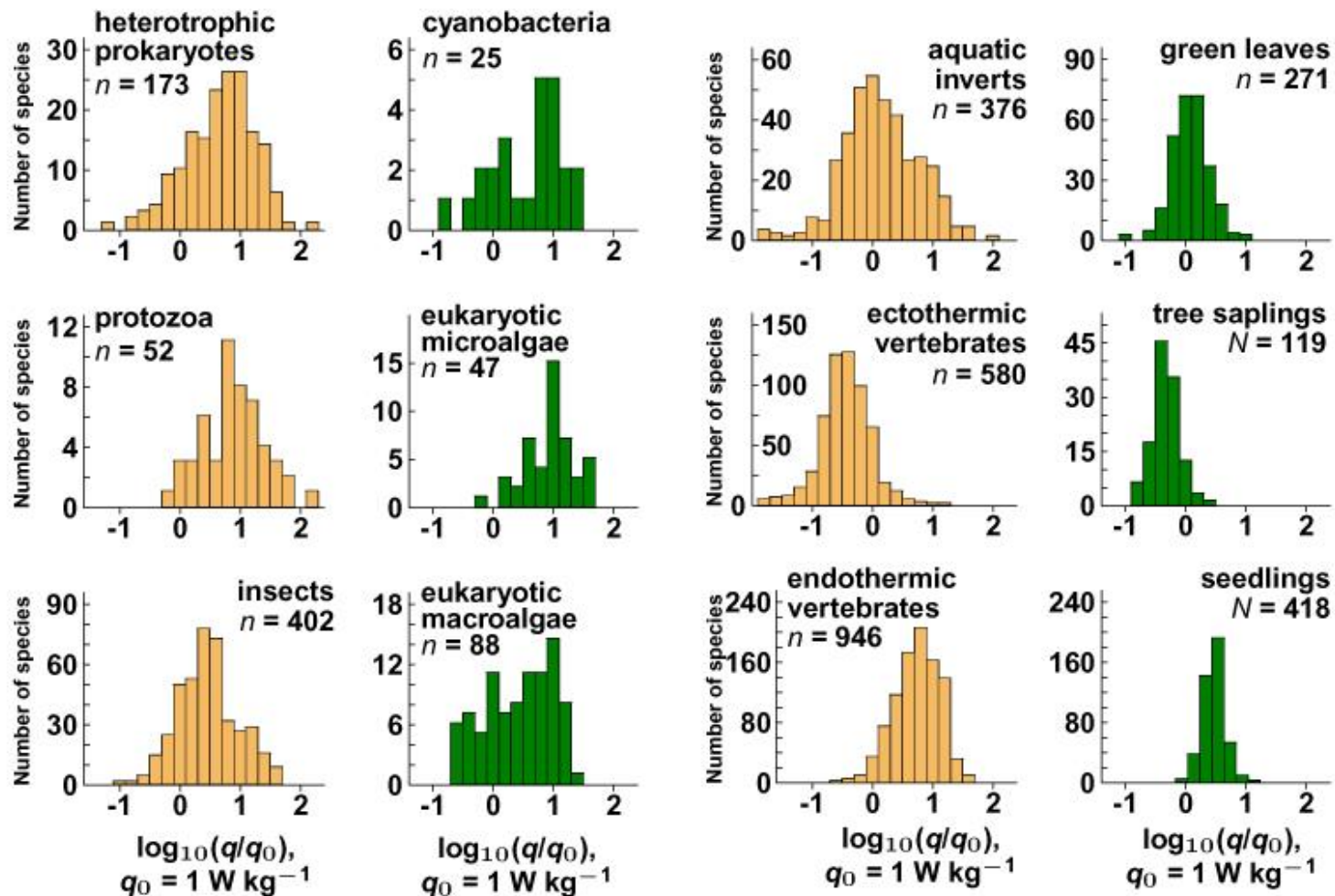
- the ability of living organisms to keep their mass-specific metabolic rates within an optimal limit, which is independent of body size and is the same for minute as well as huge organisms

- Using the largest database to date, for **3,006 species** that includes most of the range of biological diversity on the planet – from bacteria to elephants, and algae to sapling trees, **we show that metabolism displays a striking degree of homeostasis across all of life.**
- Despite the enormous biochemical, physiological, ecological, and size differences between the surveyed species, mean metabolic rates of major taxonomic groups displayed at physiological rest converge on a narrow range from **0.3 to 9 W kg⁻¹**; a difference of only 30-fold for organisms that vary 100,000,000,000,000,000,000,000-fold in body mass.

- The observed broad convergence on a narrow range of basal metabolic rates suggests that organismal designs that fit in the narrow physiological window have been favored by natural selection across all of life's major kingdoms, and that **this rate can therefore be considered as optimal for living matter as a whole.**

- The self-sustained optimality predicts that living matter should feature its own optimum rate of energy consumption per unit mass, which it should be able to maintain irrespective of body size of the organisms, i.e. irrespective of physical constraints imposed on the process of energy consumption by the decreasing S/M ratio with growing body size.

Frequency distribution of log-transformed values of mass-specific metabolic rates q in species differing greatly in size, taxonomy and trophic status. Yellow histograms: heterotrophs, green histograms: photoautotrophs.



- This means that living organisms were able to evolve these rates, apparently favored by natural selection, overcome the various physical limitations imposed by environmental physics.

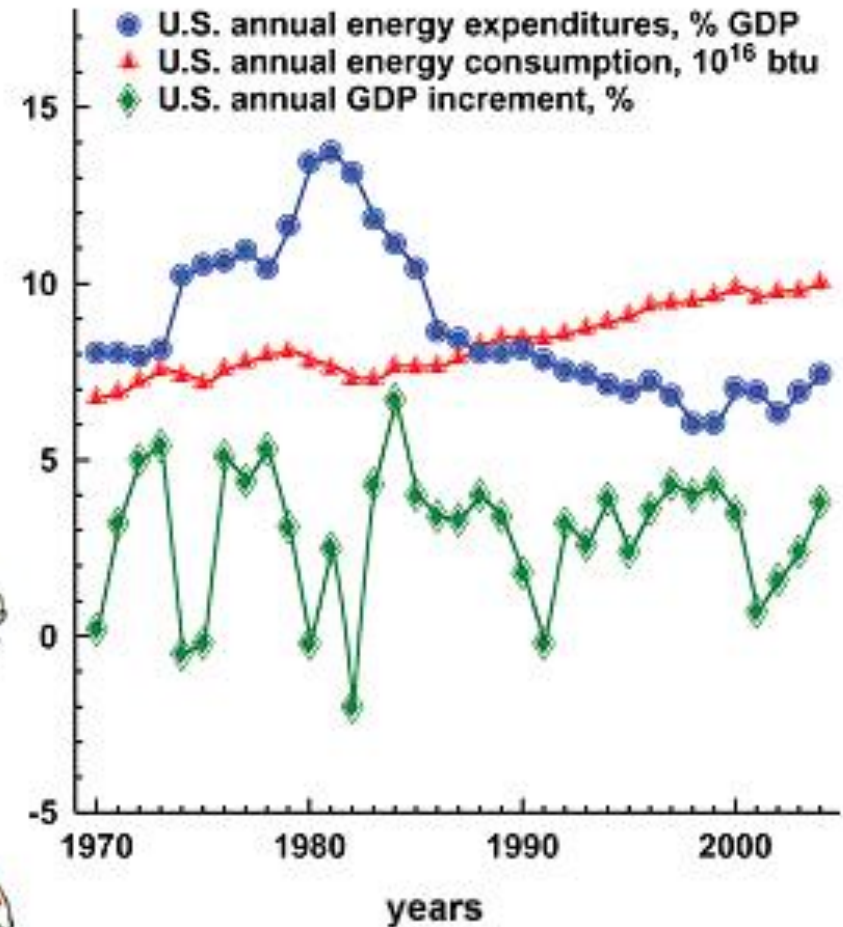
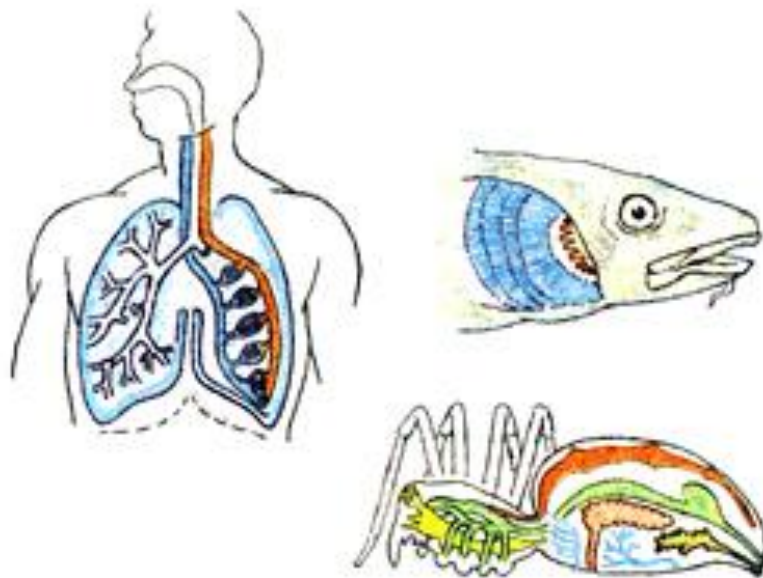
Breathing Efficiency

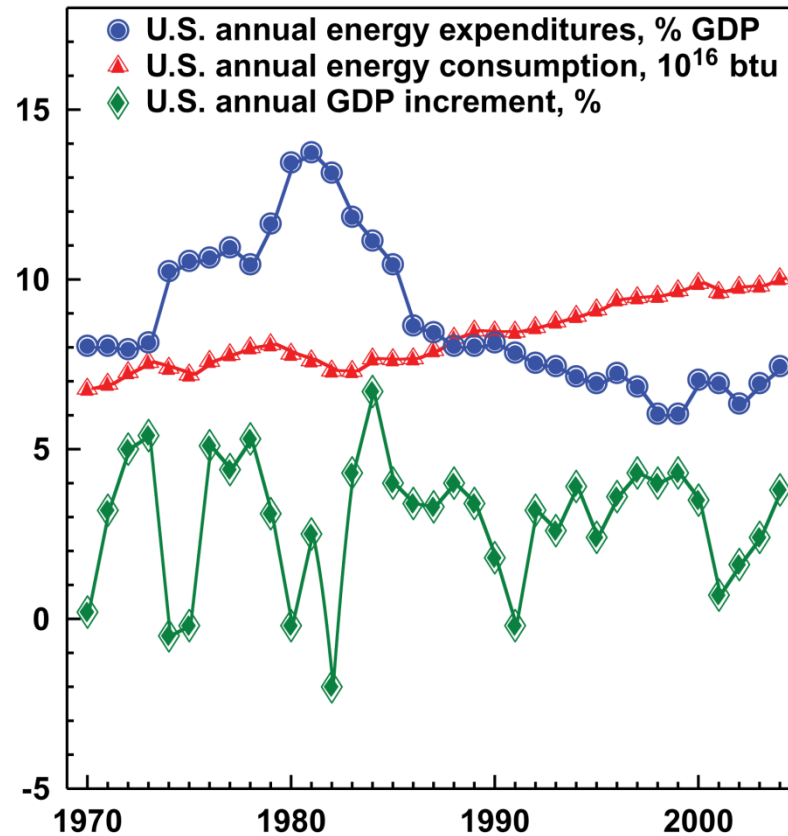
Constraints on Animal Design

- In order to sustain metabolic optimality, i.e. the size-independent value of mass-(volume-)specific metabolic rate q , the organisms must increase flux f of energy via unit body surface area S , as far as $qV = fS$, $S/V \propto M^{-1/3}$, so for q to remain constant, f must grow as $M^{1/3}$, where M is mean taxonomic body mass. Flux f_o of oxygen needed to oxidize the energy consumed should grow accordingly.

- With body size changing from micro- to macro-organisms, flux f_o has to grow by hundreds and thousands of times. While the smallest organisms meet their oxygen needs with passive diffusion of oxygen at low f_o , the larger organisms had to invent active breathing pumps to mechanically push oxygen into their bodies at highly increased rates.
- Therefore, self-sustained metabolic optimality predicts that large organisms must breathe.

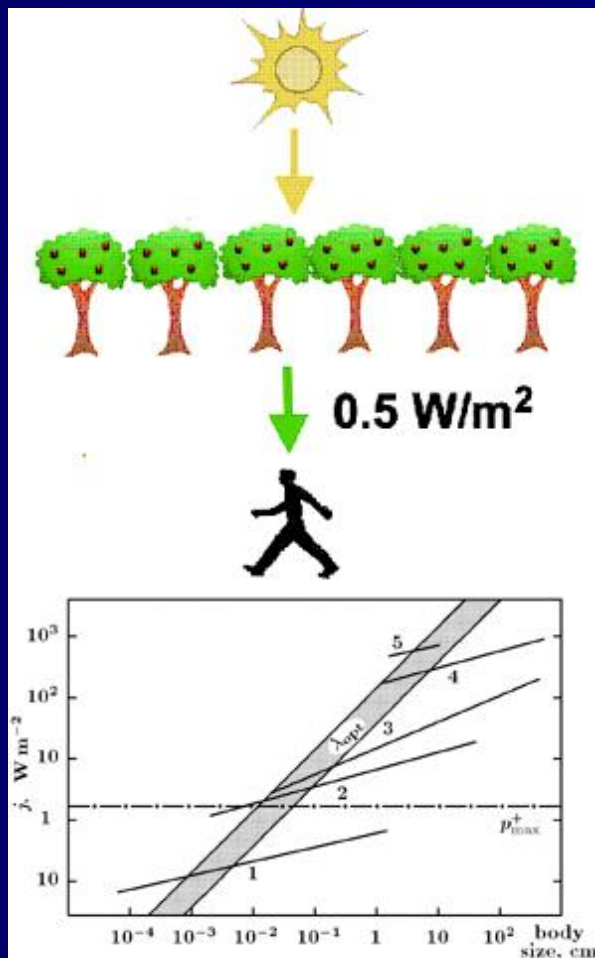
Supply becomes too costly, functionality of the system is compromised.





Annual energy expenditures, energy consumption and GDP increment in U.S.A. in 1970-2004. Mean energy expenditures are 7% GDP. During the energy crisis of the 1980s, the twofold rise of energy expenditures resulted in economic instability when annual GDP increment dropped to the lowest negative values recorded during the entire period. When the energy expenditures returned to mean values, annual GDP increment and economics as a whole stabilized. This indicates that current energy expenditures (7% GDP in U.S.A., ~10% GDP on a global scale) represent the permissible threshold, beyond which economics starts to disintegrate.

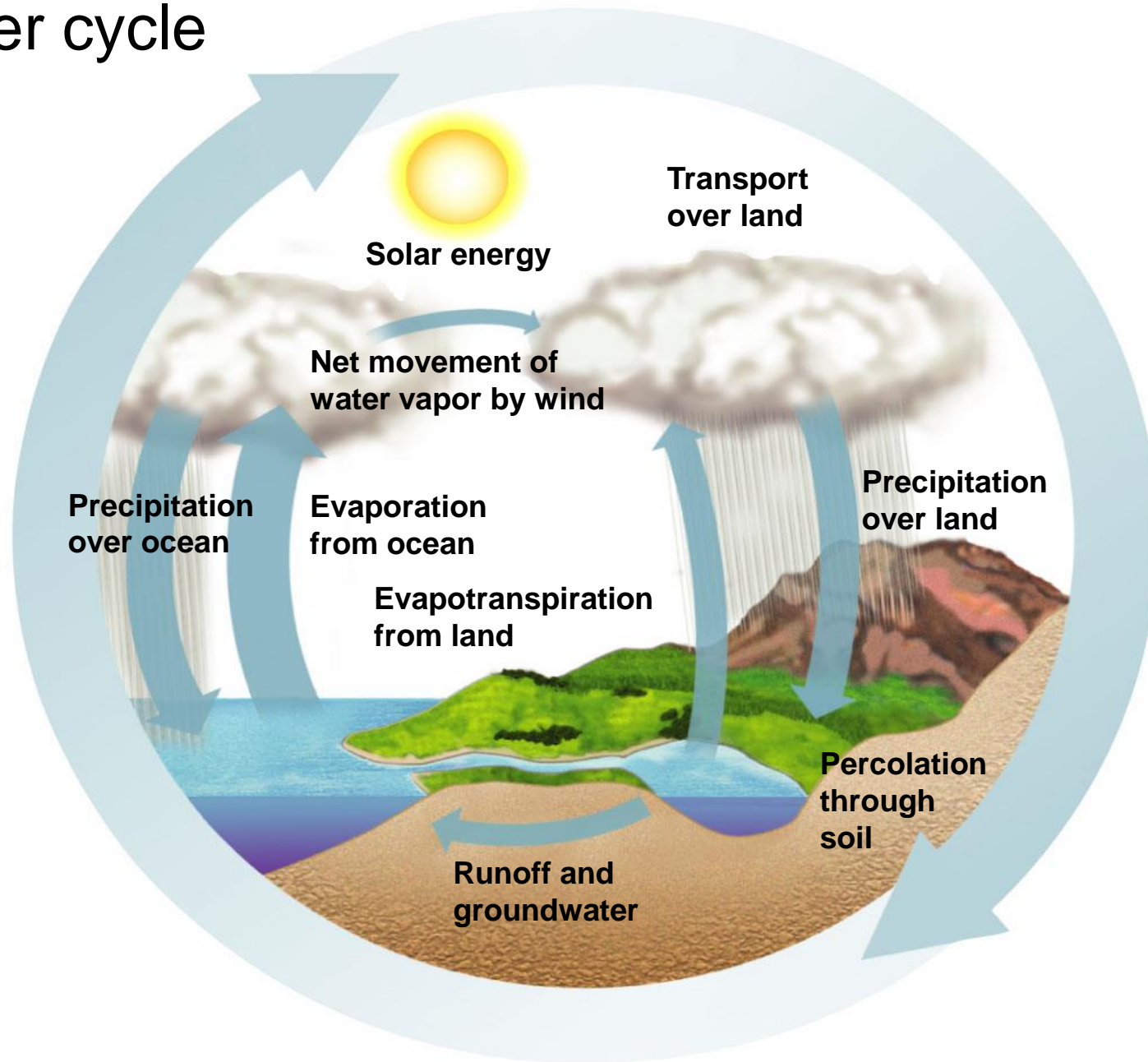
Self-sustained metabolic optimality explains the ubiquitous feature of ecosystem organization:

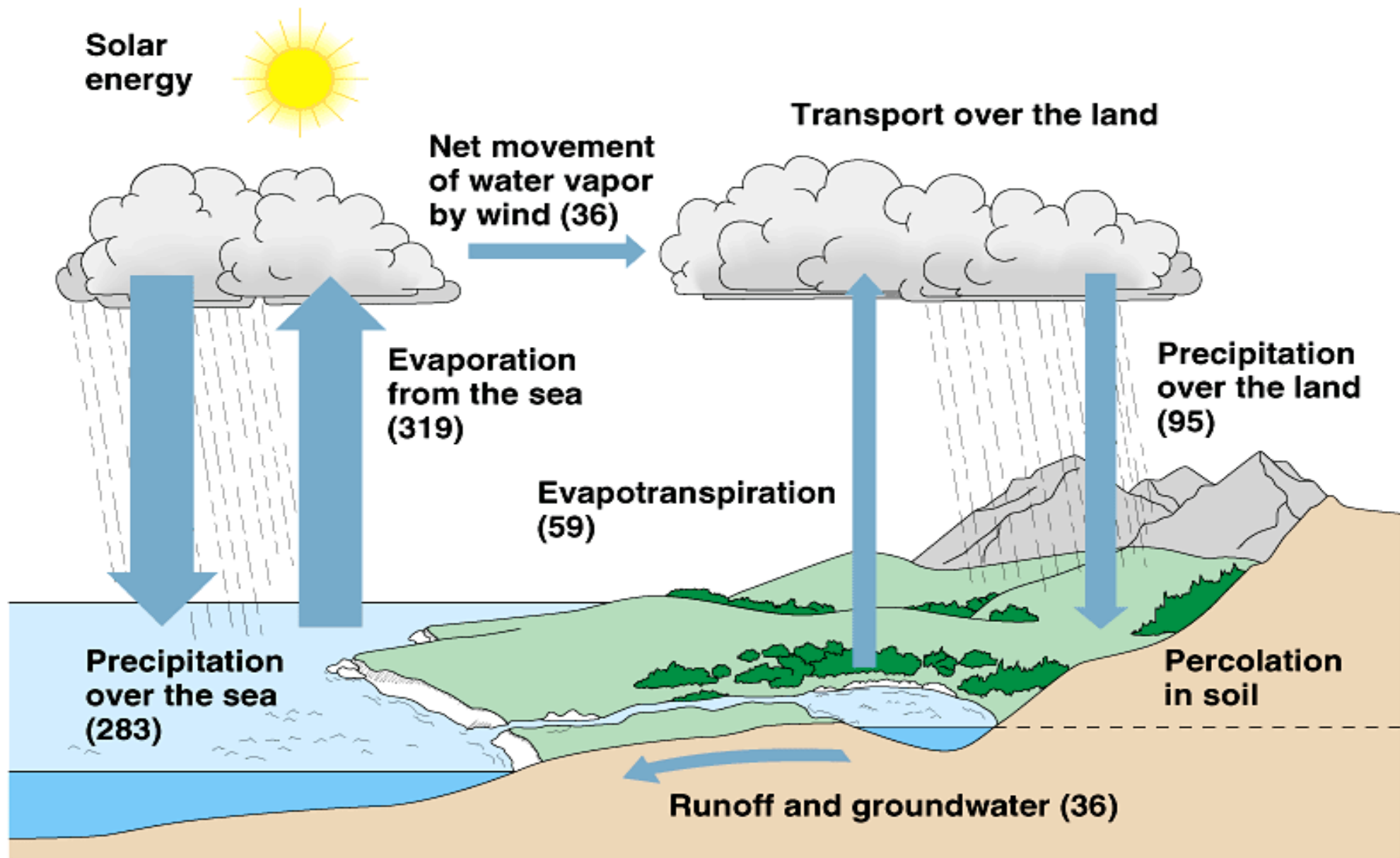


plant immobility and animal locomotion. Solar power converted to energy-rich biomass by immobile plants provides no more than $p_{\text{max}}^+ = 0.5 \text{ W}$ per square meter on the global average .

All organisms consuming more than this (human bodies, for example, consume about 2000 times more) must move and collect biomass.

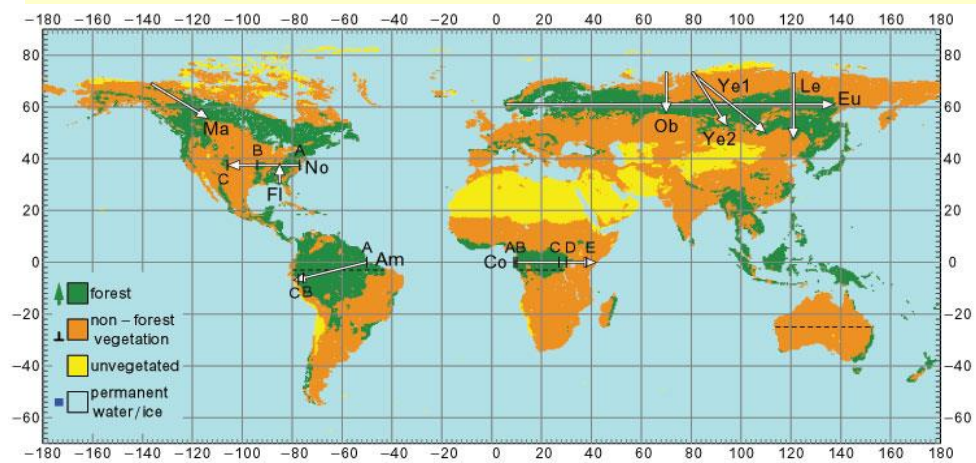
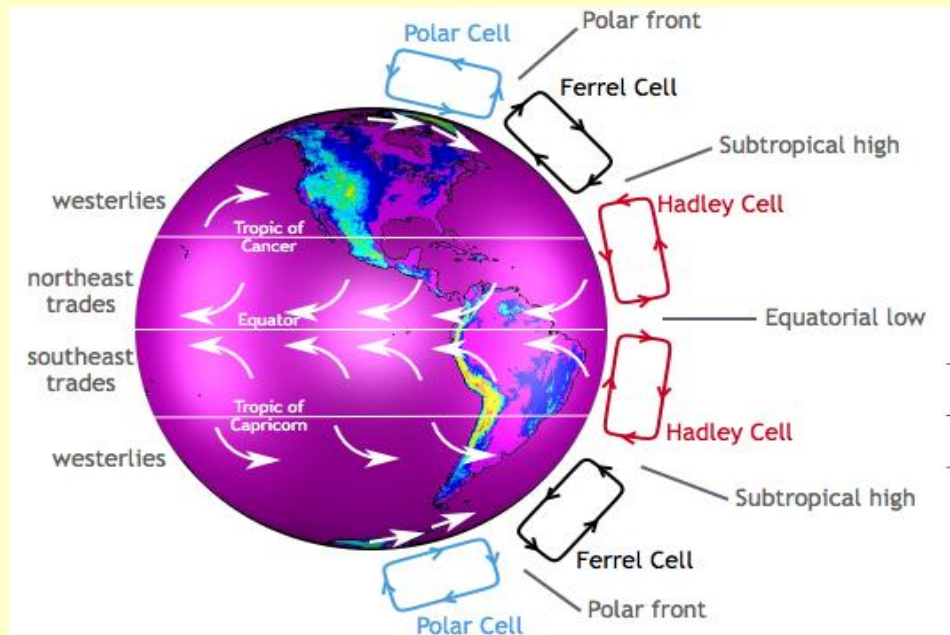
The water cycle





How extensive forest cover
controls the inflow of
atmospheric moisture to the
continental interiors
(the so-called biotic pump
concept/theory)

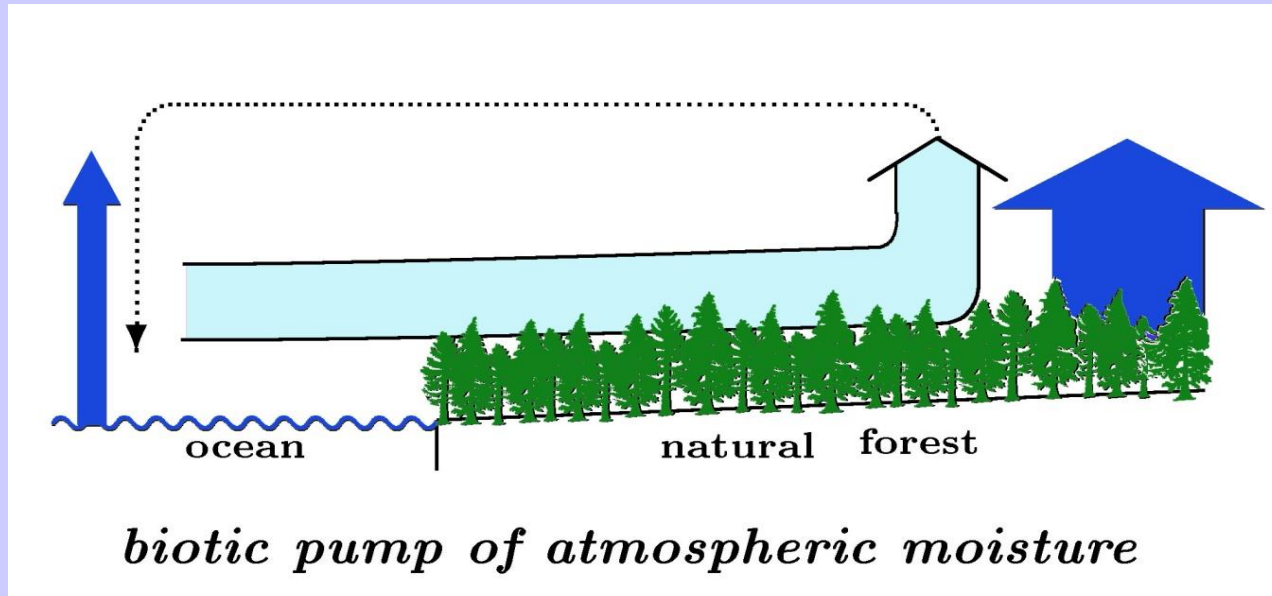
General circulation and biotic pump



Circulation cells would occur in the absence of land: no explanation for the Ocean/land difference in precipitation
No explanation for the persistence of rich vegetation in modern deserts (Sahara, Australia)
The regions of ascending air are the least vulnerable areas with respect to the terrestrial water cycle: this explains why forests first perished elsewhere.

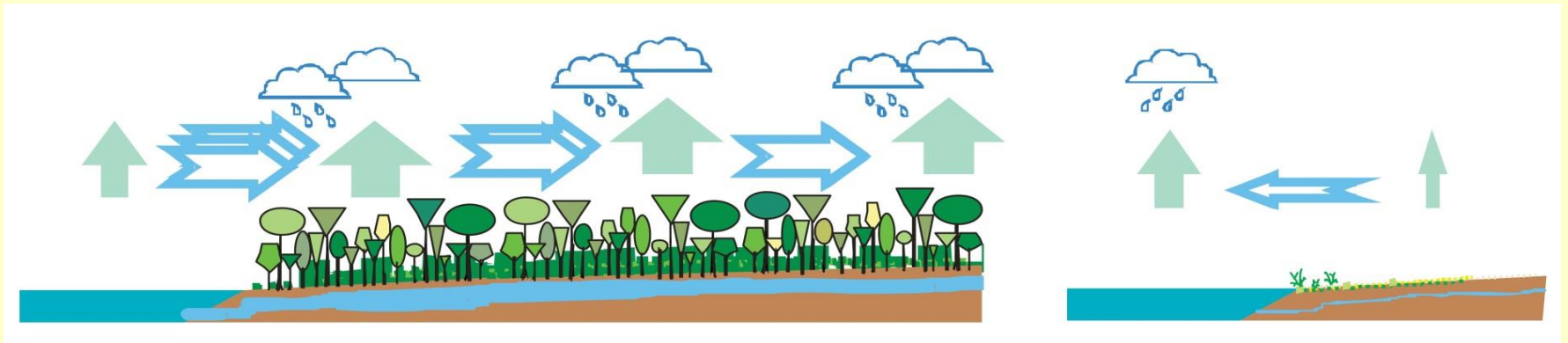
- Water cycle on land owes itself to the atmospheric moisture transport from the ocean. Properties of the **aerial rivers** that ensure the "**run-in**" of water vapor inland to compensate for the gravitational "**run-off**" of liquid water from land to the ocean are of direct relevance for the regional water availability. The biotic pump concept clarifies why the moist aerial rivers flow readily from ocean to land when the latter gives home to a large forest -- and why they are reluctant to do so when the forest is absent.

Forests drive mild moist winds and sustain rivers

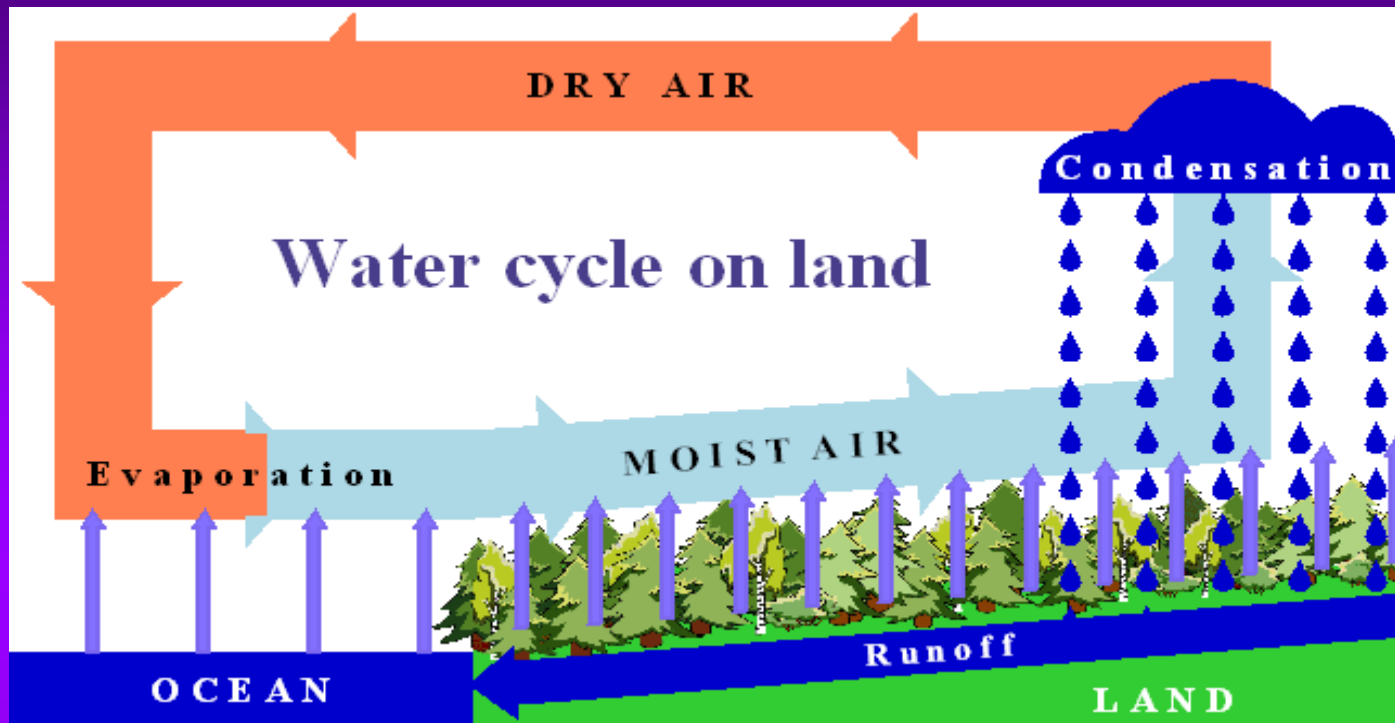


Due to their high leaf area index, natural forests maintain high transpiration fluxes (thick dark blue arrow), which exceed the evaporation fluxes over the ocean (thin dark blue arrow). The evaporated moisture undergoes condensation and disappears from the gas phase. Air in the atmospheric column above the forest rarifies. In the result, there appears ascending air motion over the forest canopy, which, in its turn, "sucks in" moist air from the ocean (light blue arrow). It then returns to the ocean in the upper atmosphere (dotted arrow) after precipitation of moisture over the continent.

Forests drive mild moist winds and sustain rivers (cont.)



High evaporation from the forest canopy maintains an intense water vapor condensation over land such that low pressure zones are formed on land causing the moisture-rich oceanic air to flow inland. A deforestation-induced drop in land evaporation results in erosion of the low pressure zones and weakening of the coast-to-interior moisture transport.

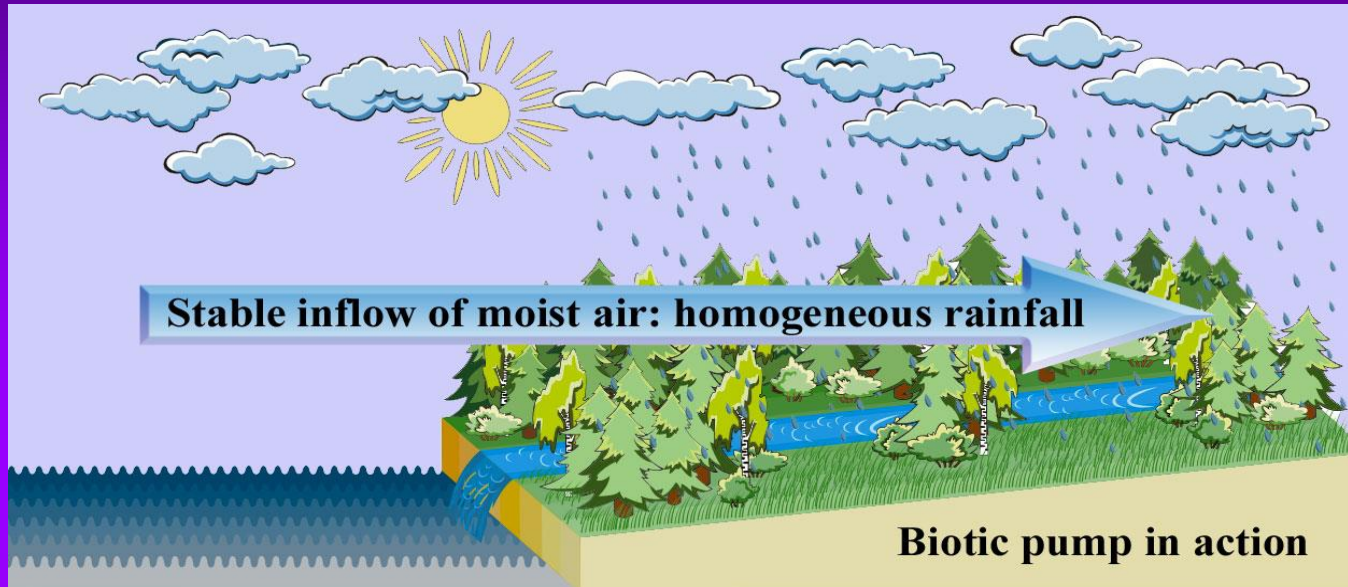


Key features

- Land is elevated over the ocean. Because of gravity, land continuously loses liquid water
- There is little water on land: global runoff could deplete it in just a few years
- **Water on land is replenished by ocean-to-land winds in the lower troposphere**
- Winds bring moisture evaporated from the ocean (as water vapor)
- As moist air ascends over land, it cools. Water vapor condenses to form rainfall

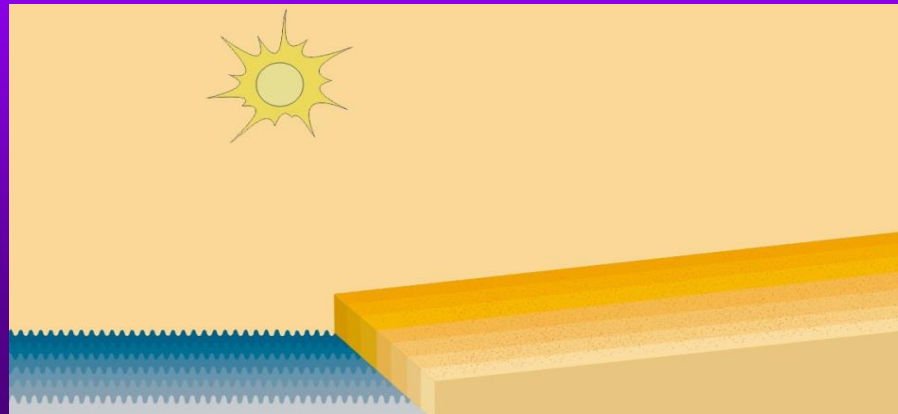
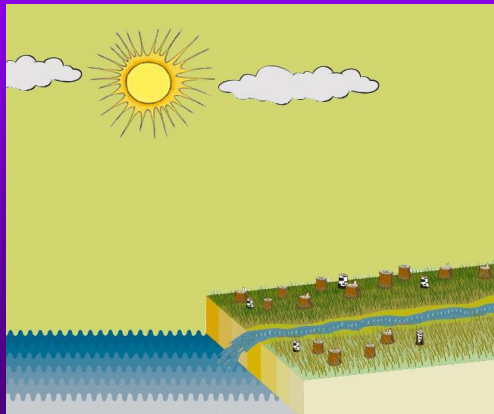
Biotic pump of atmospheric moisture

Natural forests control the ocean-to-land atmospheric moisture inflow

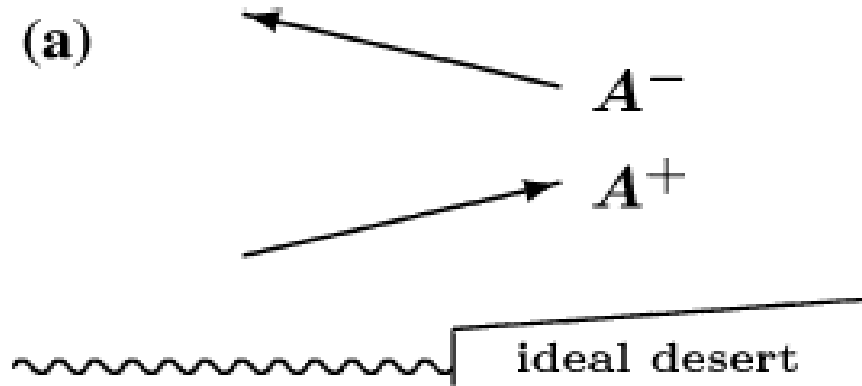


Moist air penetrates far from the ocean deep into the continental interior. Rainfall is spatially and temporarily uniform

Unforested land: (a) water extremes (floods, droughts) closer to the ocean
(b) scarce continental precipitation

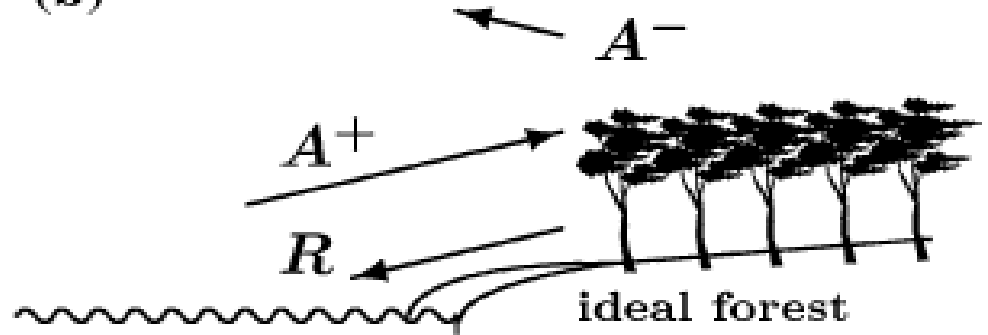


(a)



$$A^- = A^+, R = 0$$

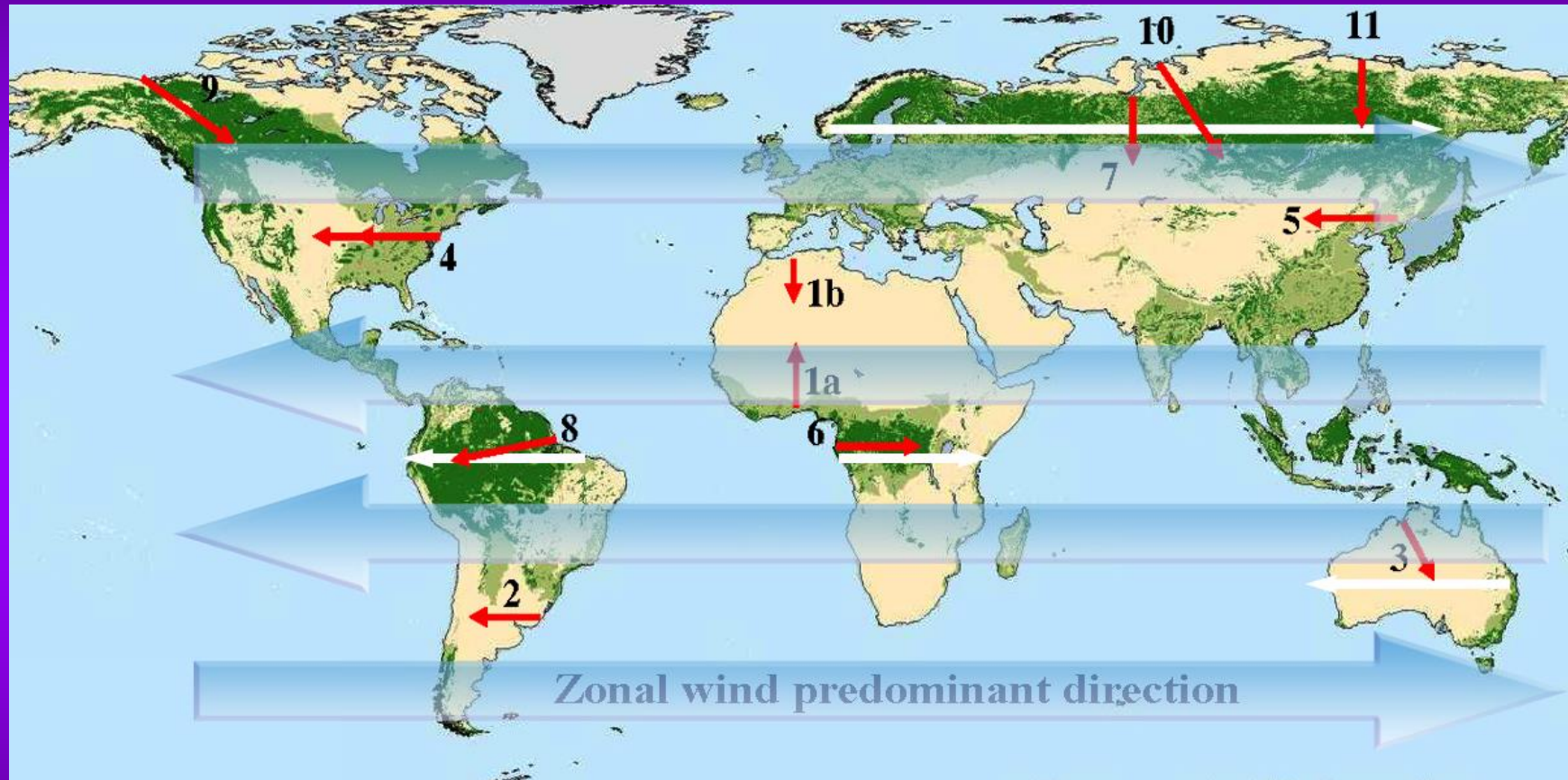
(b)



$$A^- \ll A^+, R \approx A^+$$

Schematic representation of the influence of the vegetation cover on the water cycle budget. A^+ and A^- represent the inflow and outflow of atmospheric water vapor to and from the ecosystem, respectively; $R = A^+ - A^-$ is the runoff.

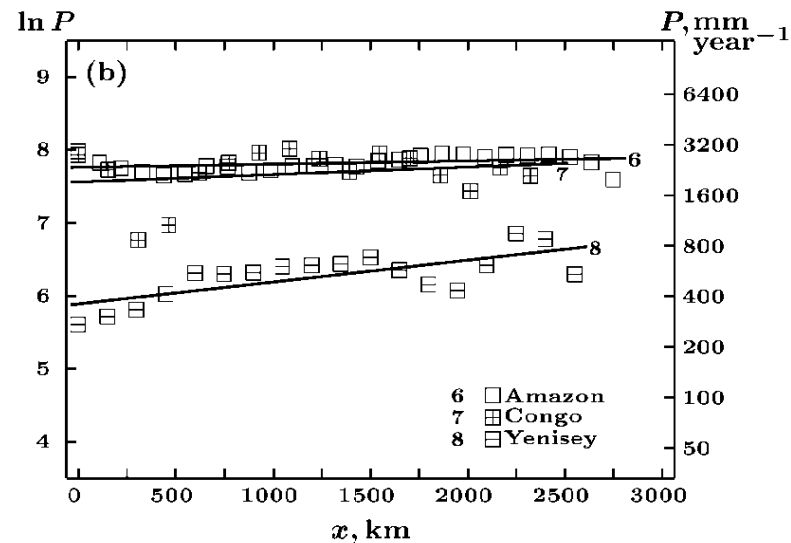
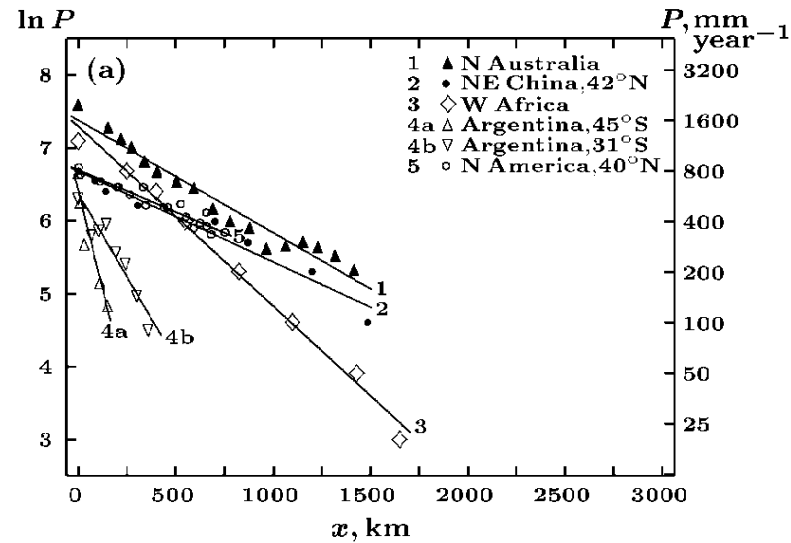
How does precipitation vary in space and time in world's forested versus unforested regions?



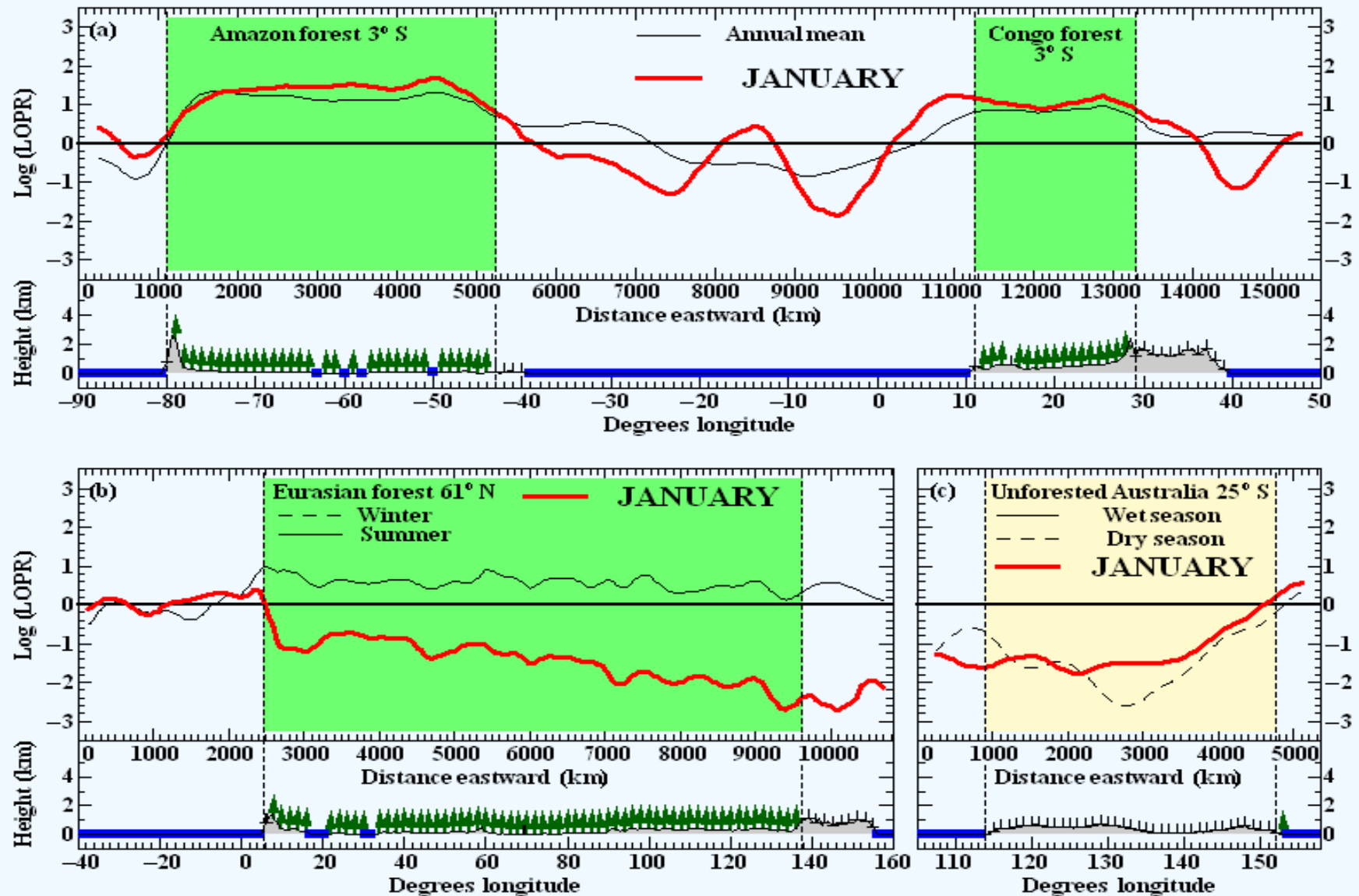
Red numbered arrows: transects from Fig. 2 of Makarieva, Gorshkov, Li (2009) Ecol. Complexity 6: 302

White arrows: transects from Fig. 6 of Makarieva, Gorshkov, Li (2013) Theor. Appl. Climatol. 111: 79

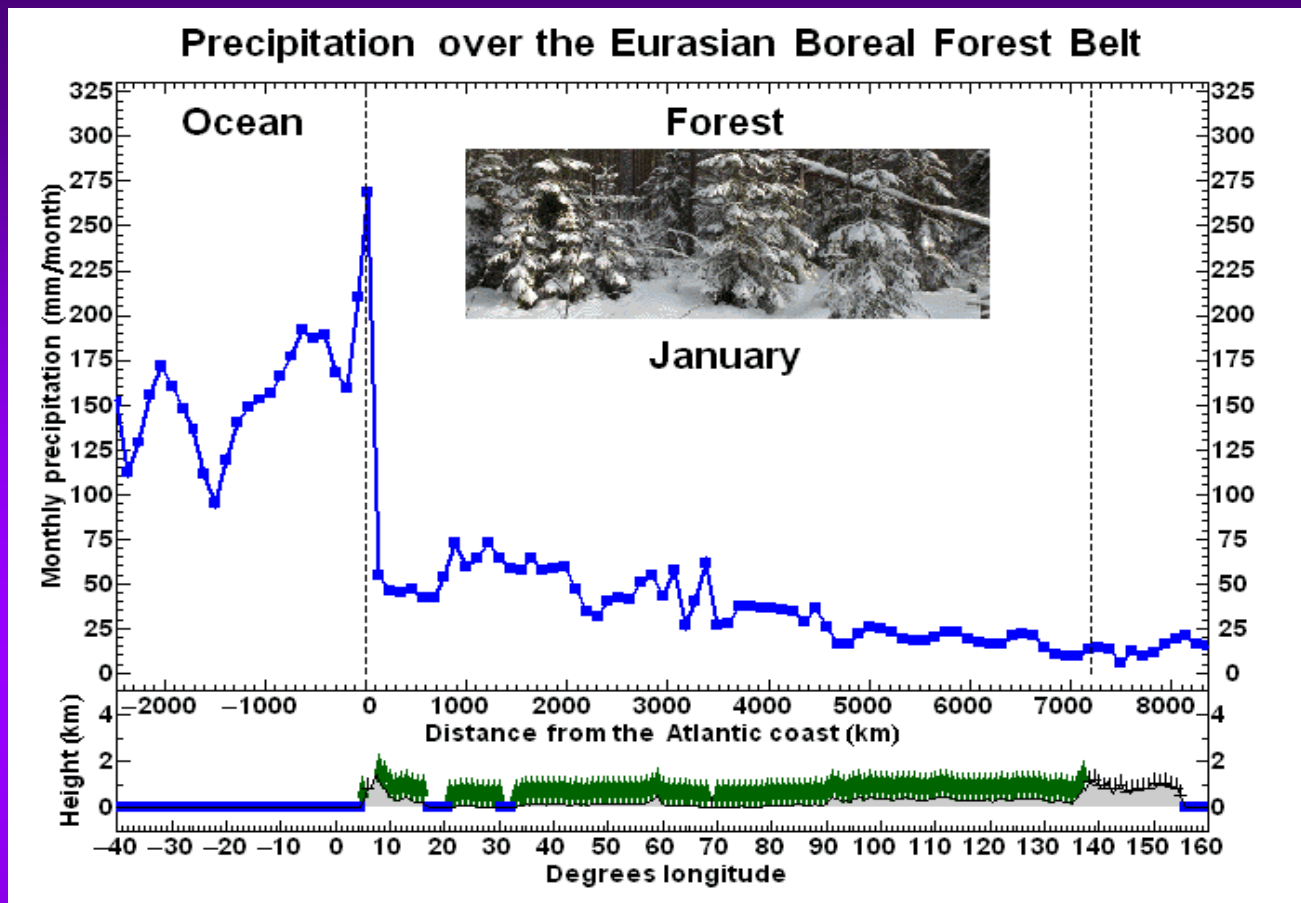
Dependence of precipitation P (mm year^{-1}) on distance x (km) from the source of atmospheric moisture on unforested territories (a) and on territories covered by natural forests (b).



LAND / OCEAN PRECIPITATION RATIO (LOPR) : SEASONAL CHANGES



Source: Makarieva, Gorshkov, Li (2013) Theor. Appl. Clim. 111: 79 (white arrows from the map)



- In summer, when forest is active, precipitation on land is higher than over the ocean: biotic pump works at its most
- Summer rainfall is spatially uniform over several thousand kilometers
- Oceanic precipitation is small in summer and rises sharply in winter despite lower temperature. The biotic pump is less intense in winter, so moisture remains over the ocean

- The data describe how the active **summer** forest wins the water "tug-of-war" with the Atlantic Ocean. Indeed, in summer the forest steals most moisture inland and depletes the oceanic precipitation.
- The dormant **winter** forest loses this war to the ocean, such that precipitation over the Atlantic Ocean in winter, despite the oceanic evaporation is minimal, rises threefold compared to summer months.
- Analyzed for comparison, the unforested Australia is unable to draw moisture far inland in either wet or dry season, i.e., irrespective of moisture availability over the neighboring ocean.

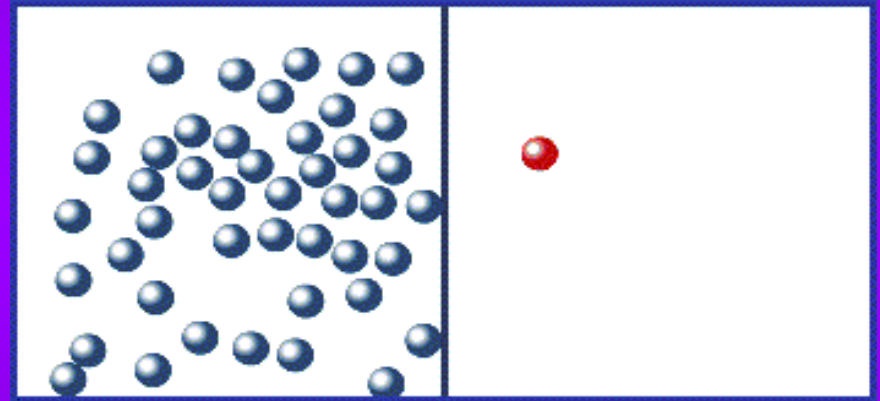
Moist air cannot penetrate into the interior of an unforested continent

It is not the absolute availability of moisture that distinguishes forested regions from unforested ones, but the presence/absence of an efficient ocean-to-land moisture transport. Unforested land regions are locked to oceanic moisture all year round even when moisture is abundant over the adjacent ocean.

How it works: biotic pump physics

Three fundamental laws combine to drive winds:

1) The ideal gas law: air pressure is proportional to temperature and concentration of gas molecules (their number per unit volume).

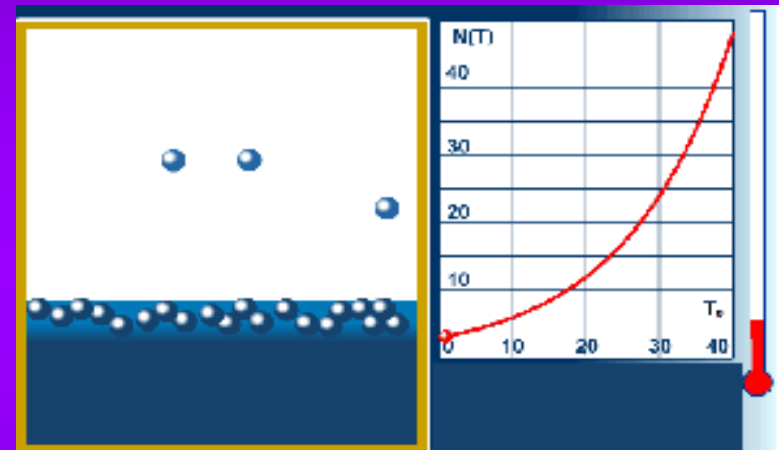


Where the number of molecules decreases, air pressure drops. The pressure difference induces winds directed towards the area of low pressure.

How it works: biotic pump physics

Three fundamental laws combine to drive winds:

2) Clausius-Clapeyron law: pressure of saturated water vapor increases (decreases) approximately twofold per each ten degrees Celsius of temperature rise (fall).



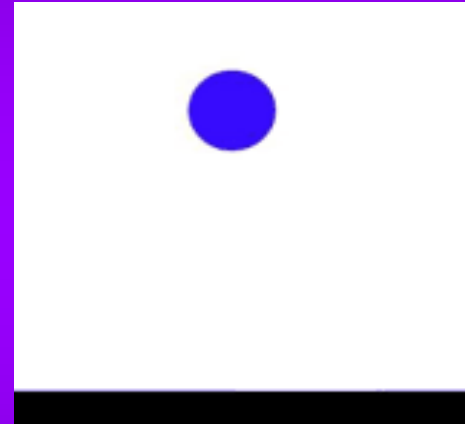
With rising temperature more and more water molecules become able to overcome the intermolecular attraction forces in liquid water and evaporate. Hence, the water vapor concentration rises as well.

How it works: biotic pump physics

Three fundamental laws combine to drive winds:

3) Gravity law: gas ascending in the gravitational field of Earth loses internal energy and cools.

Temperature of the rising air declines.

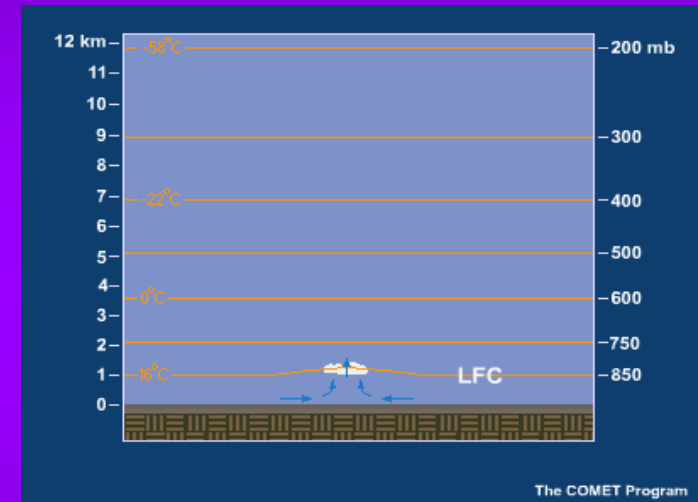


A physical analogy: bouncing ball loses kinetic energy as it rises in the gravitational field of Earth. Likewise the ascending gas loses internal energy (energy of molecular motion) and its temperature drops.

How it works: biotic pump physics

Condensation-induced atmospheric dynamics

1. When the atmosphere contains a lot of water vapor, it is unstable to condensation.
2. Vertical displacement of moist air leads to its cooling.
3. Water vapor condenses forming clouds. Local concentration of gas molecules is reduced.
4. Local pressure drops. Air starts flowing towards the condensation area.
5. The incoming air ascends. If it contains enough water vapor, condensation continues as well as the associated air circulation.

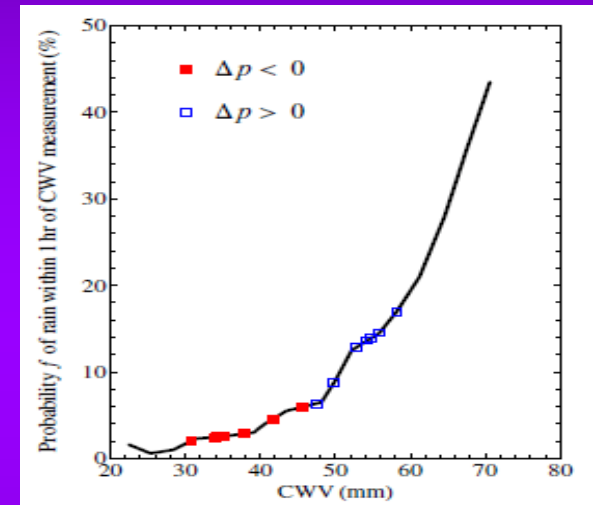


Stages of cloud formation.
Condensation starts where
water vapor reaches saturation.

How it works: biotic pump physics

! Three important things to remember about condensation !

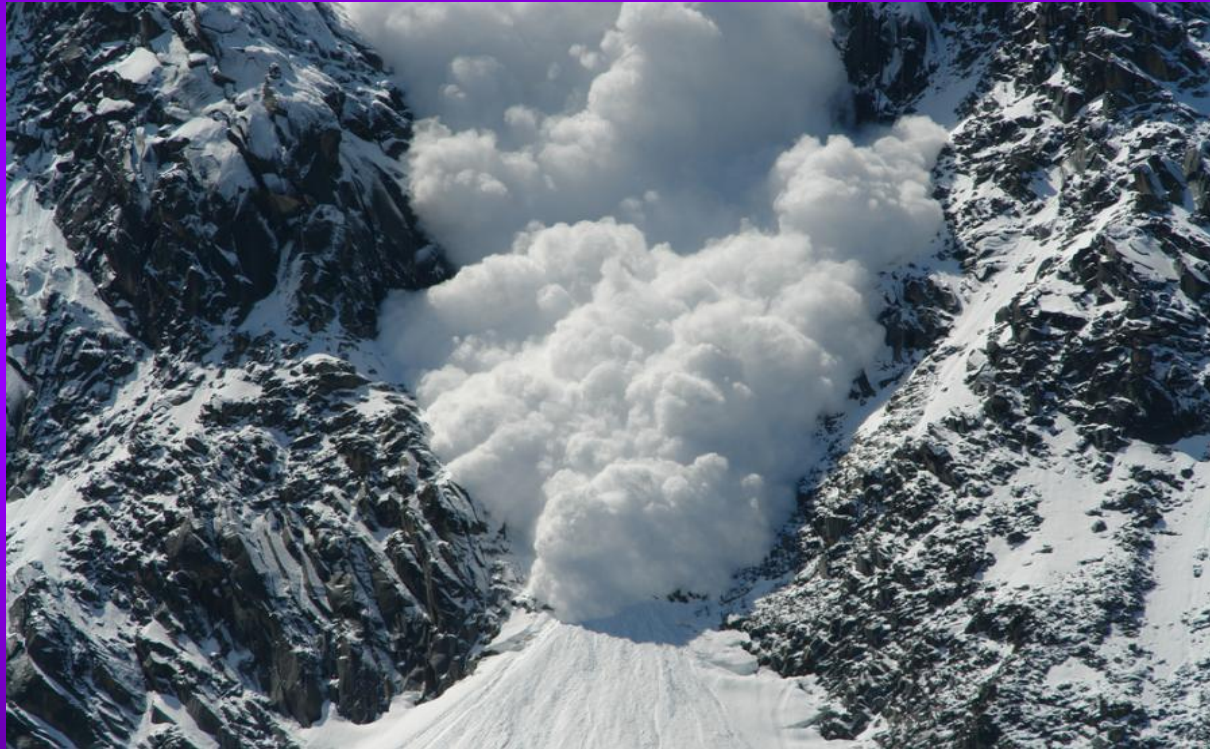
- Moist atmosphere is unstable to condensation: the more water vapor it contains, the higher the probability of condensation.
- Condensation may occur at an **arbitrarily high rate** determined by vertical velocity of the ascending air.
- **Evaporation** that replenishes the atmospheric water vapor store is a **much slower gradual process** determined by solar energy flux.



Probability of rain as a function of atmospheric water vapor content.

Sources: Holloway and Neelin (2010) J. Atm. Sci. 67: 1091; Makarieva et al. (2013) J. Hydrometeorol. doi: 10.1175/JHM-D-12-0190.1

We thus can compare atmospheric condensation to an **avalanche** – a severe outburst of potential energy that suddenly occurs after a long period of gradual accumulation. Partial pressure of water vapor is a store of potential energy.



How does the forest play in?

How it works: biotic pump ecology

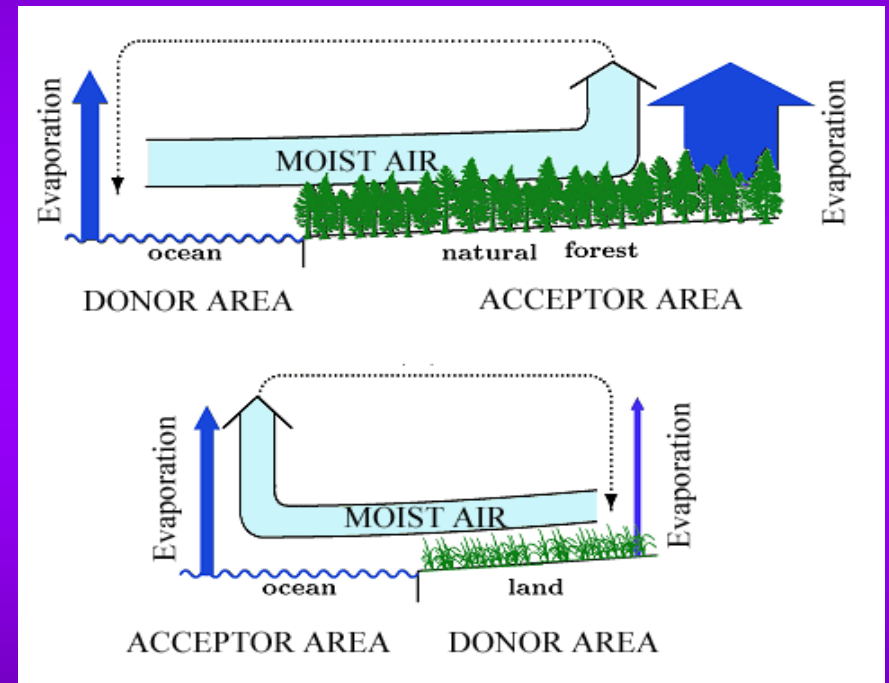
Forest: winning the tug-of-war with the ocean

The air flows towards the low pressure area where condensation occurs.

For there to be a stable ocean-to-land inflow of moist air, condensation should predominantly occur over the forest.

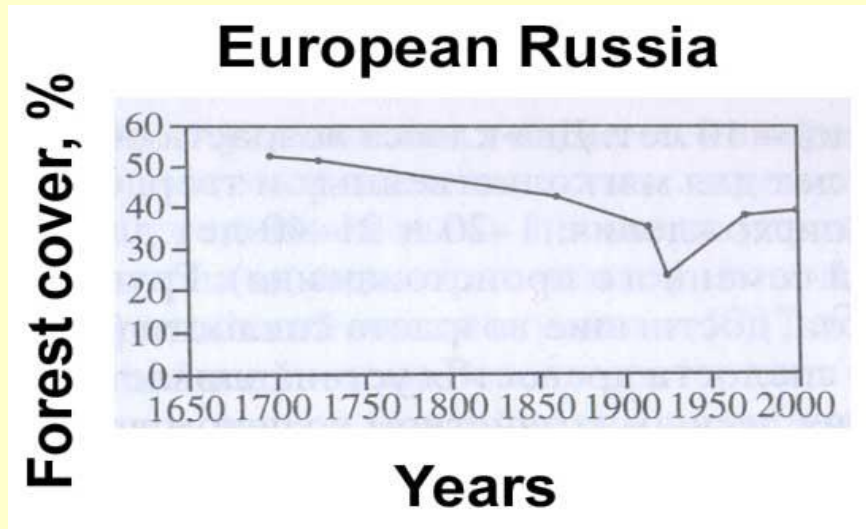
In this case the forest is the **acceptor area** (receiving moist air) and the ocean is the **donor area** (supplying moist air).

If condensation predominantly occurs over the ocean, then the ocean steals moisture from the continent.

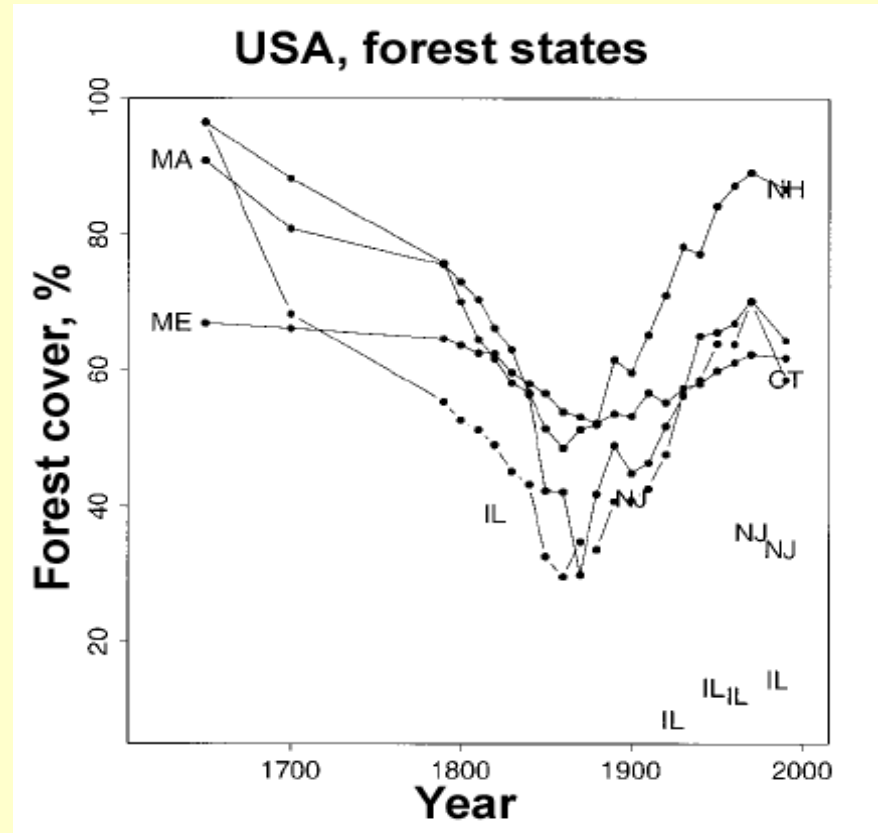


High evaporation from the forest cover allows the forest to win the moisture “tug-of-war” with the ocean.

Temperate and boreal forests had been regrowing
in the 20th century from a minimum



**This trend has recently
reversed.**

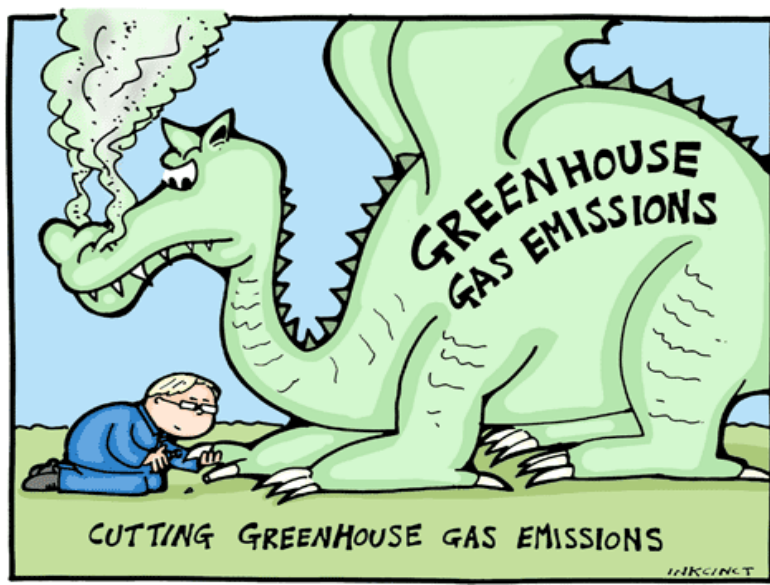


A conflict (rarely appreciated or discussed) exists between the modern commercial value of a forest and the forest's ability to regulate the regional water cycle and to be self-sustainable: these parameters cannot be maximized simultaneously.

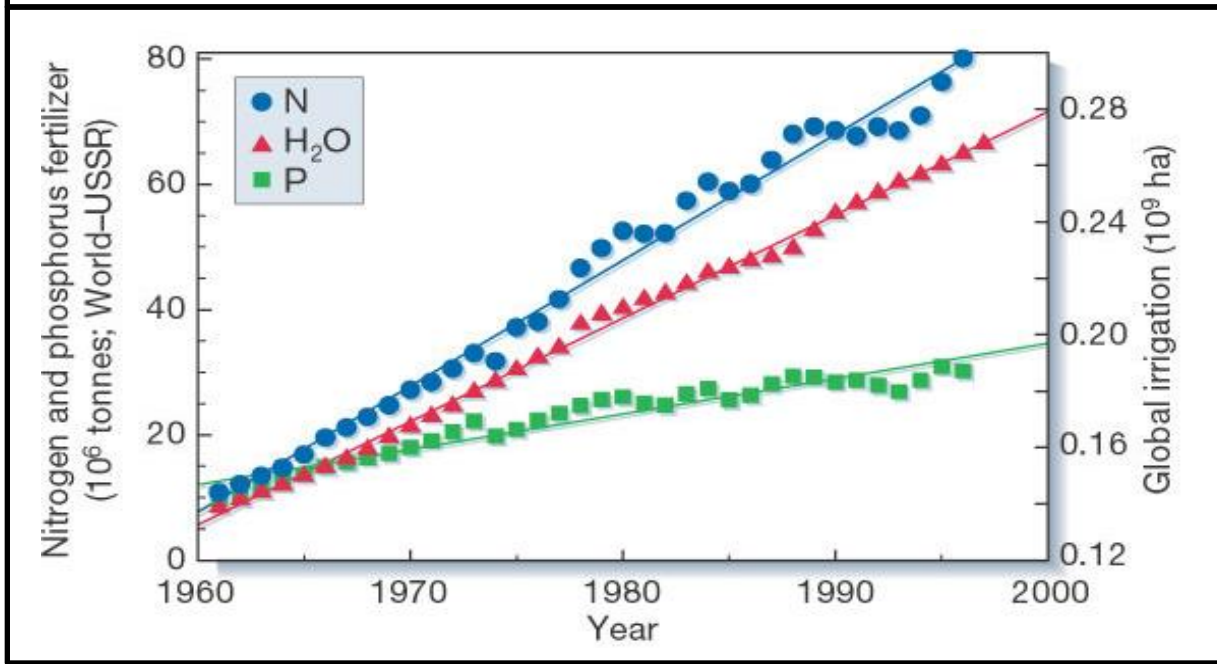
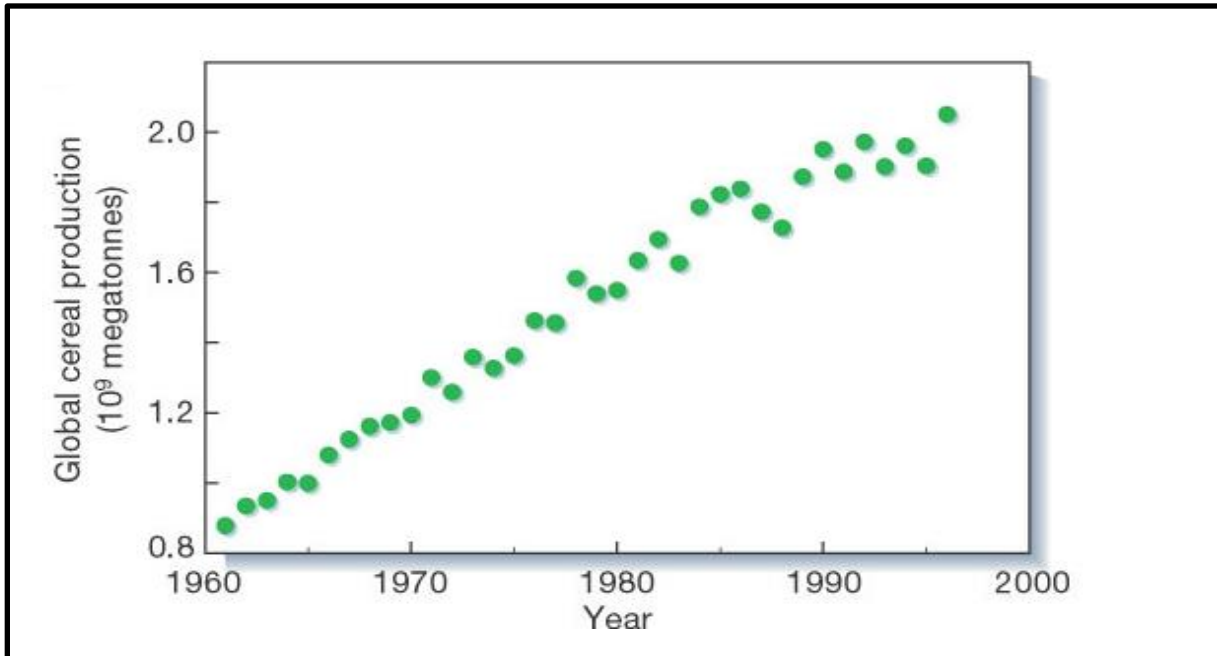
- **The regional water security is not about keeping the live forest biomass stationary; It is about keeping it stationary in an environmentally competent condition.**

The challenge of modern agriculture:

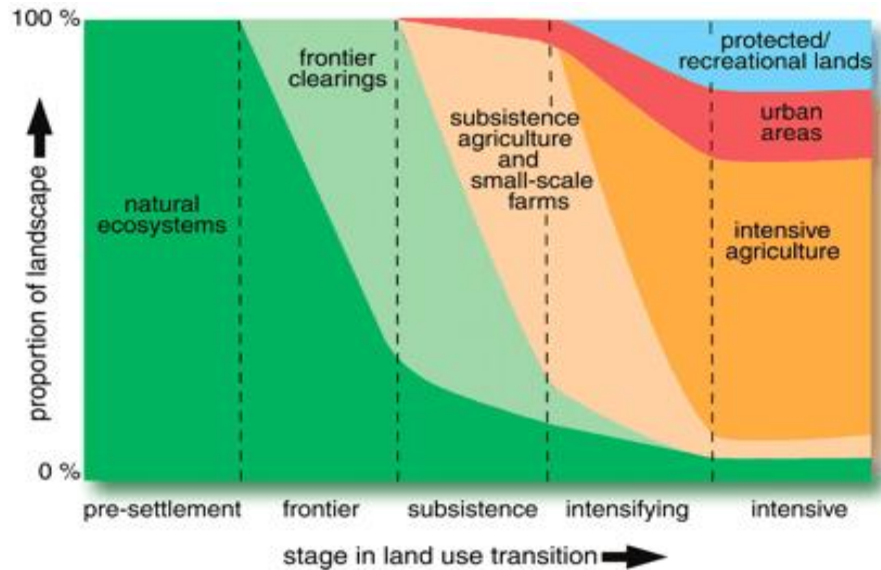
How do we increase productivity while decreasing environmental impacts?



2008-719 © INKCINCT Cartoons www.inkcinct.com.au



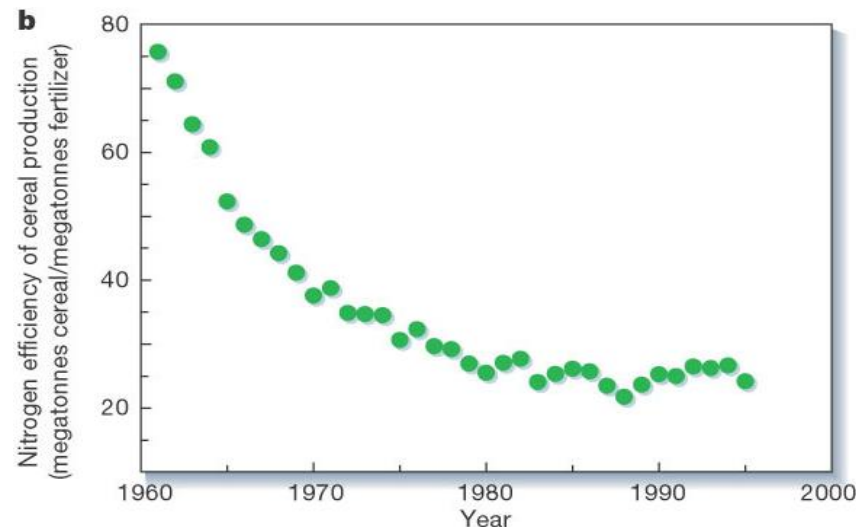
While production has been on the rise, efficiency is on the decline



HERBICIDES
IRRIGATION
PESTICIDES
FERTILIZER
FUNGICIDES



Foley *et al* 2005



Tilman *et al* 2002

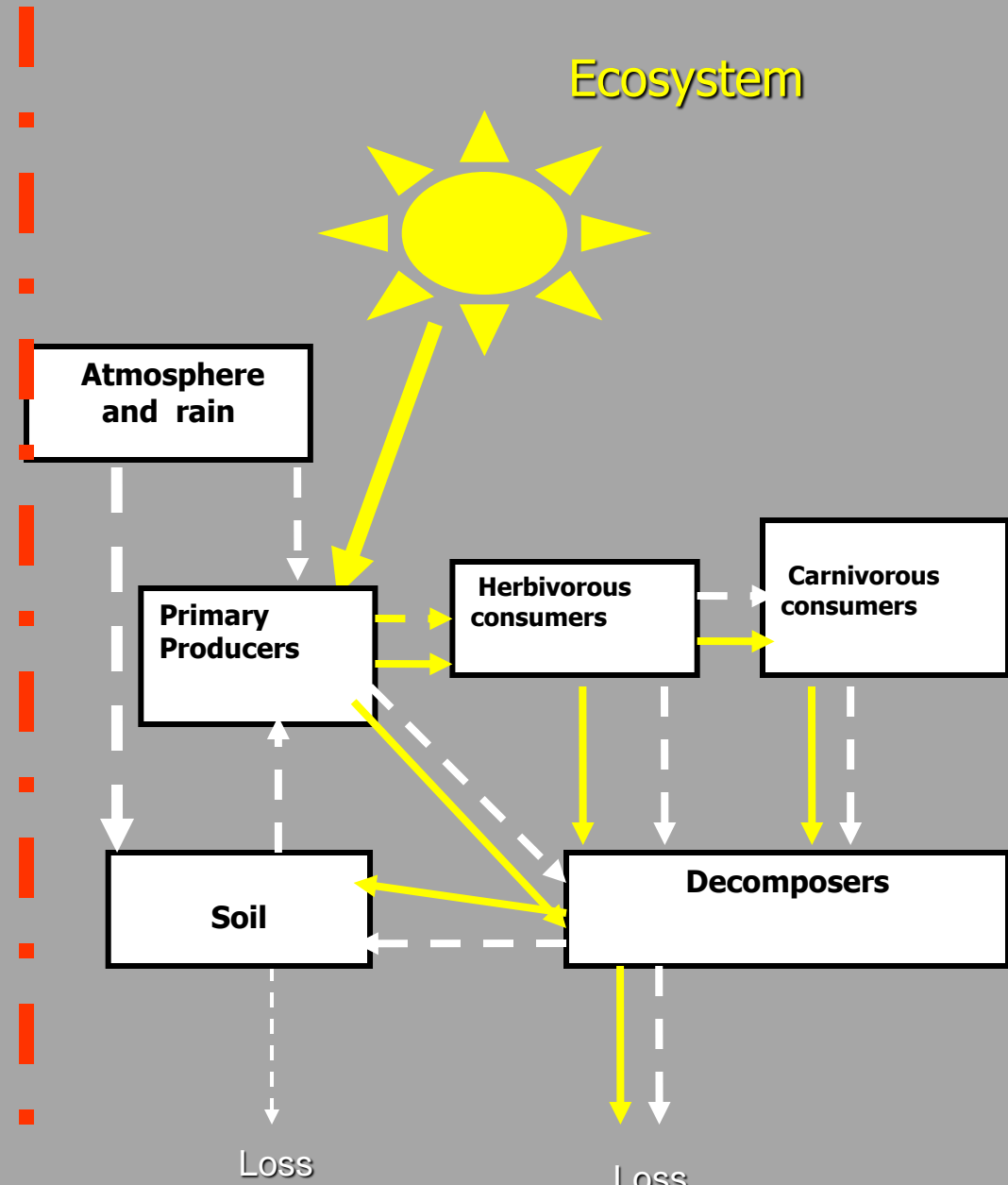
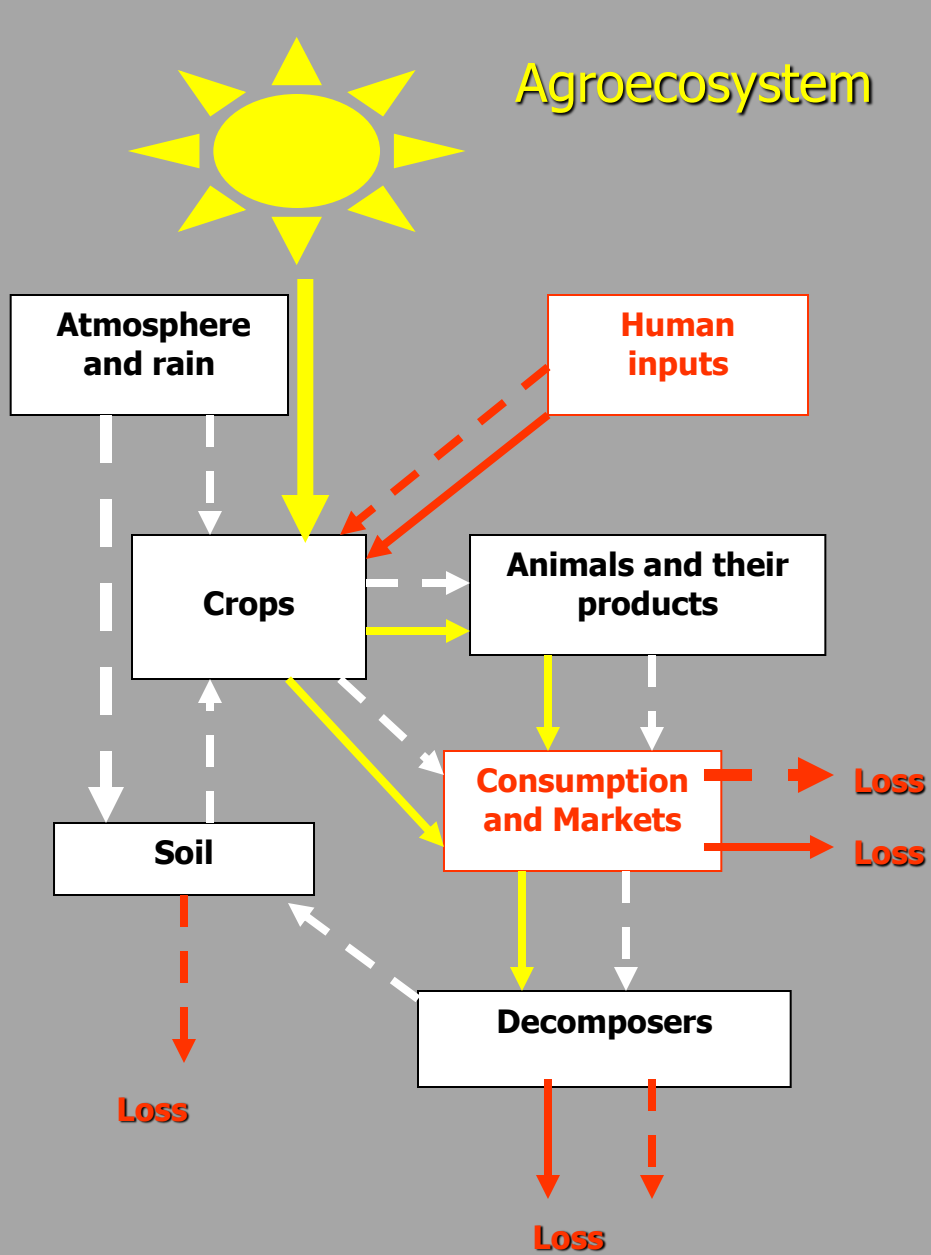
Ecological intensification suggests that we take a tip from nature on improving efficiency



High input, high waste and pollution
low resilience



No input, little to no waste, resilient

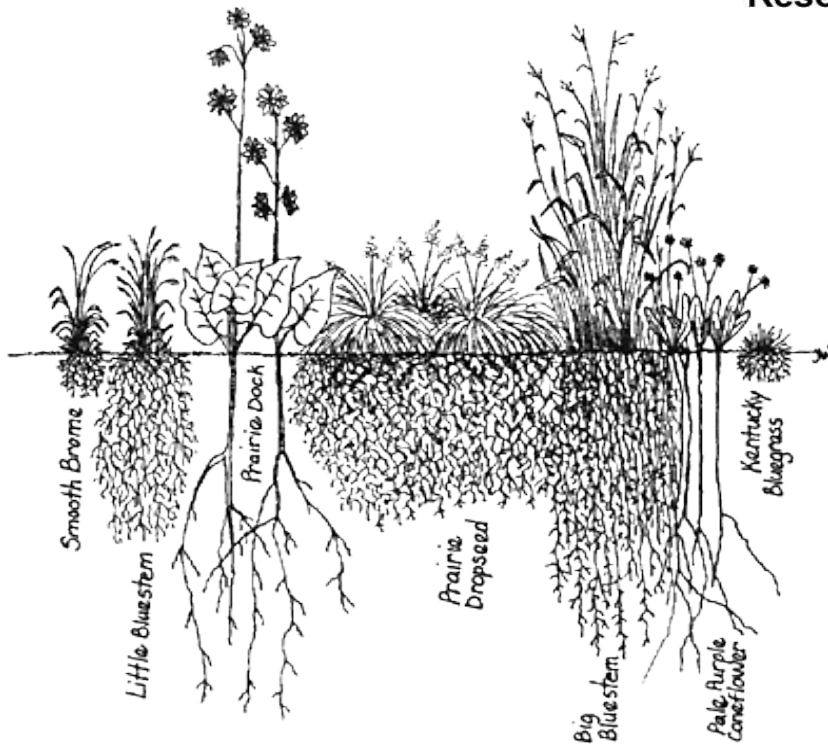
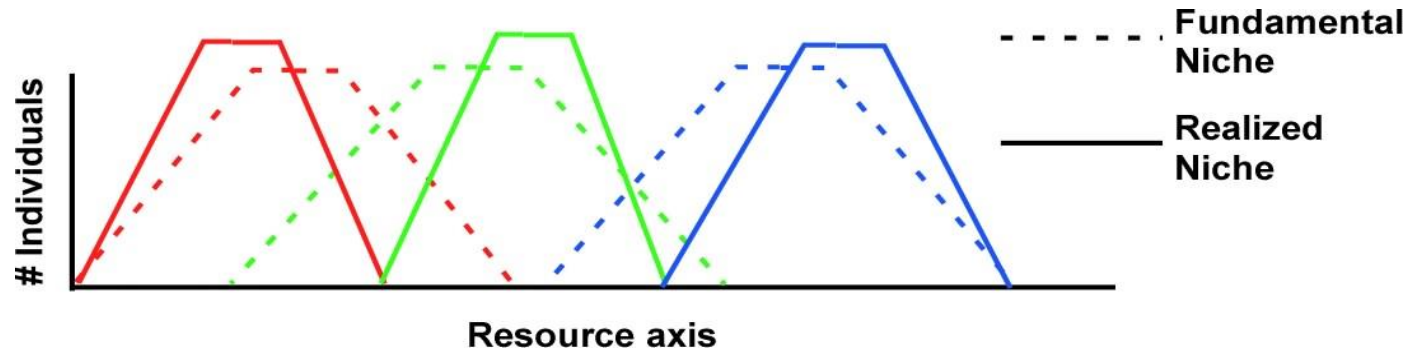


← Energy
← Nutrients

Differences between Ecosystems and Agroecosystems

- **More open energy flow:**
 - More inputs (fuel, organic matter).
 - More outputs (harvest).
- **More open nutrient cycles.**
- **Reduction of capacity for self-regulation:**
 - Less diversity
 - Simplification of structure and trophic levels.
 - Control of populations of organisms.

Diversity confers efficiency and productivity in natural systems

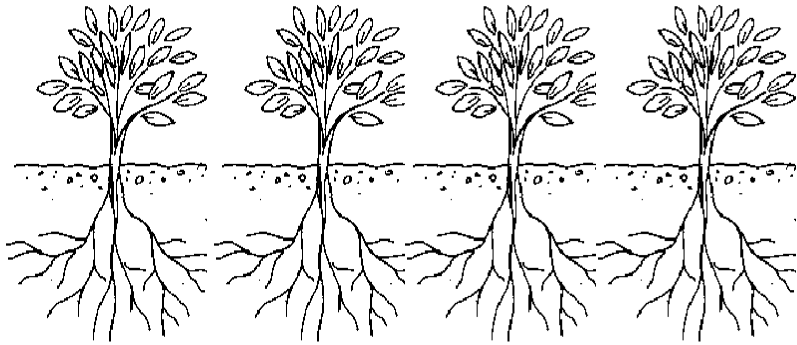


Diversity → Complementarity

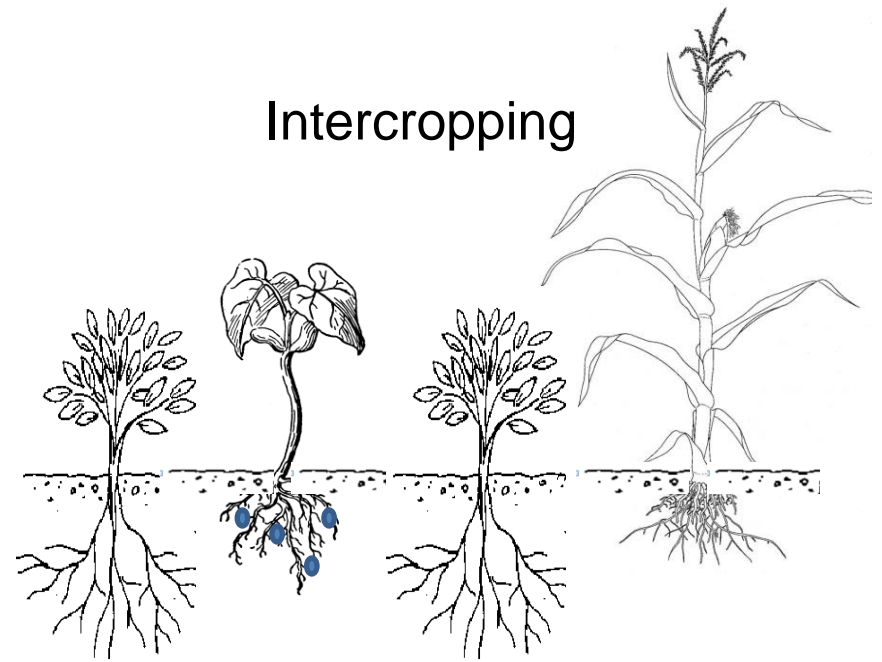
Complementarity → Efficiency

Efficiency → Productivity

Conventional monoculture cropping system



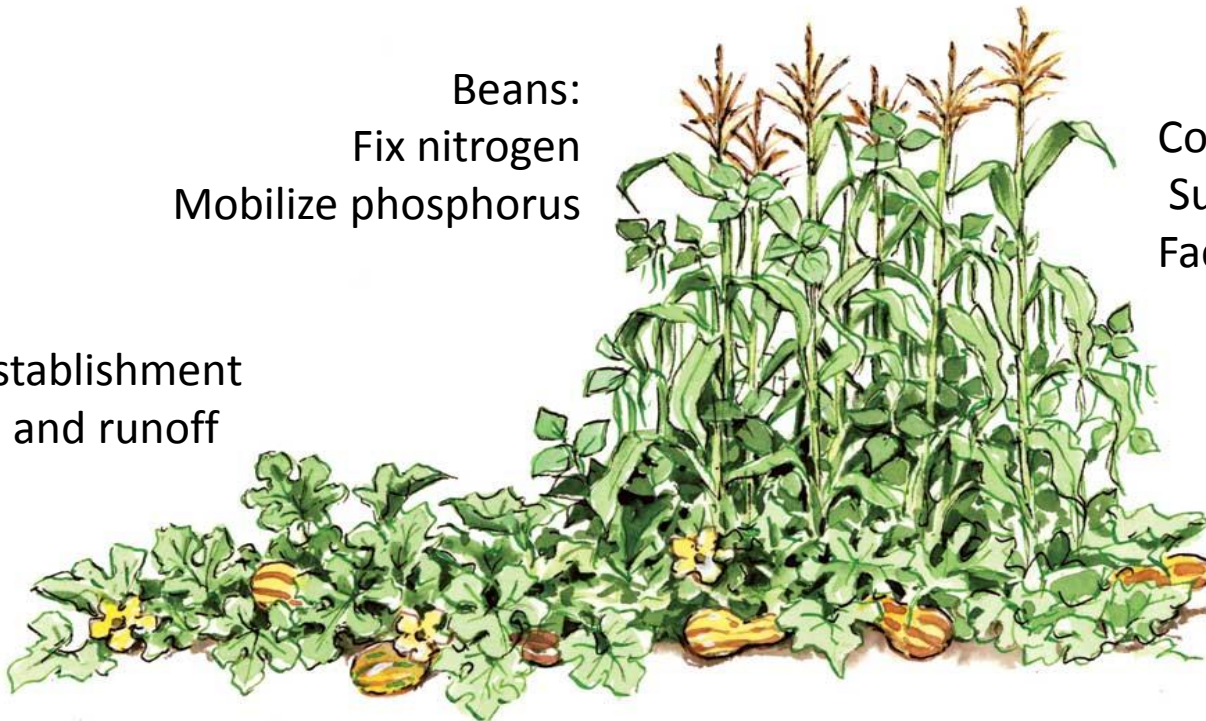
Intercropping



Beans:
Fix nitrogen
Mobilize phosphorus

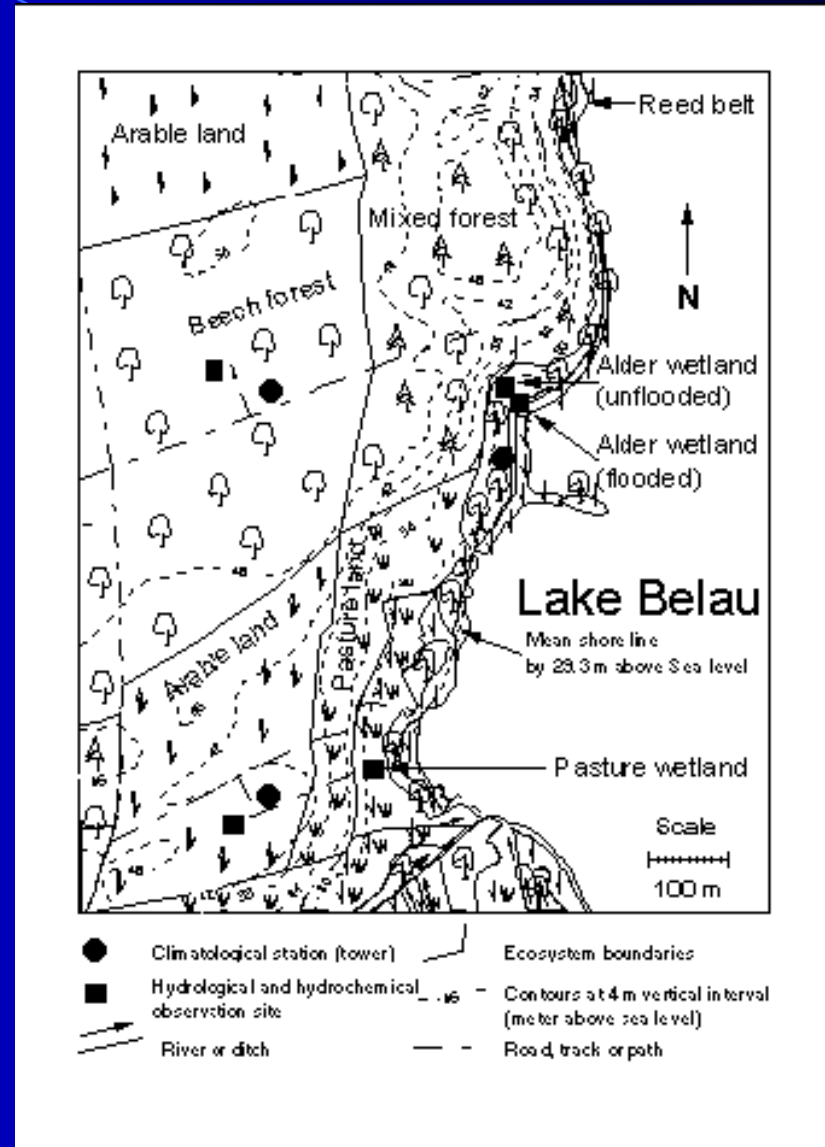
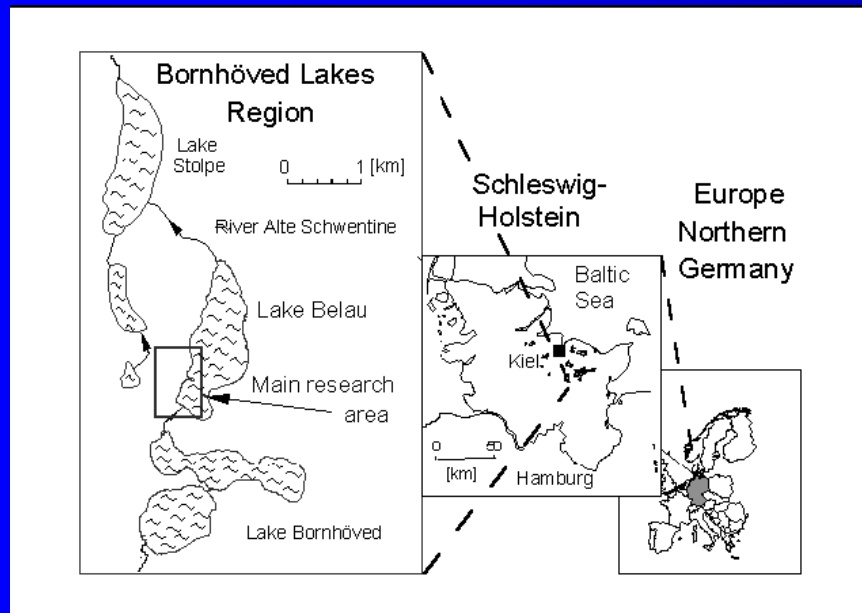
Corn:
Supports beans
Facilitate iron uptake

Squash:
Inhibit weed establishment
Reduce erosion and runoff



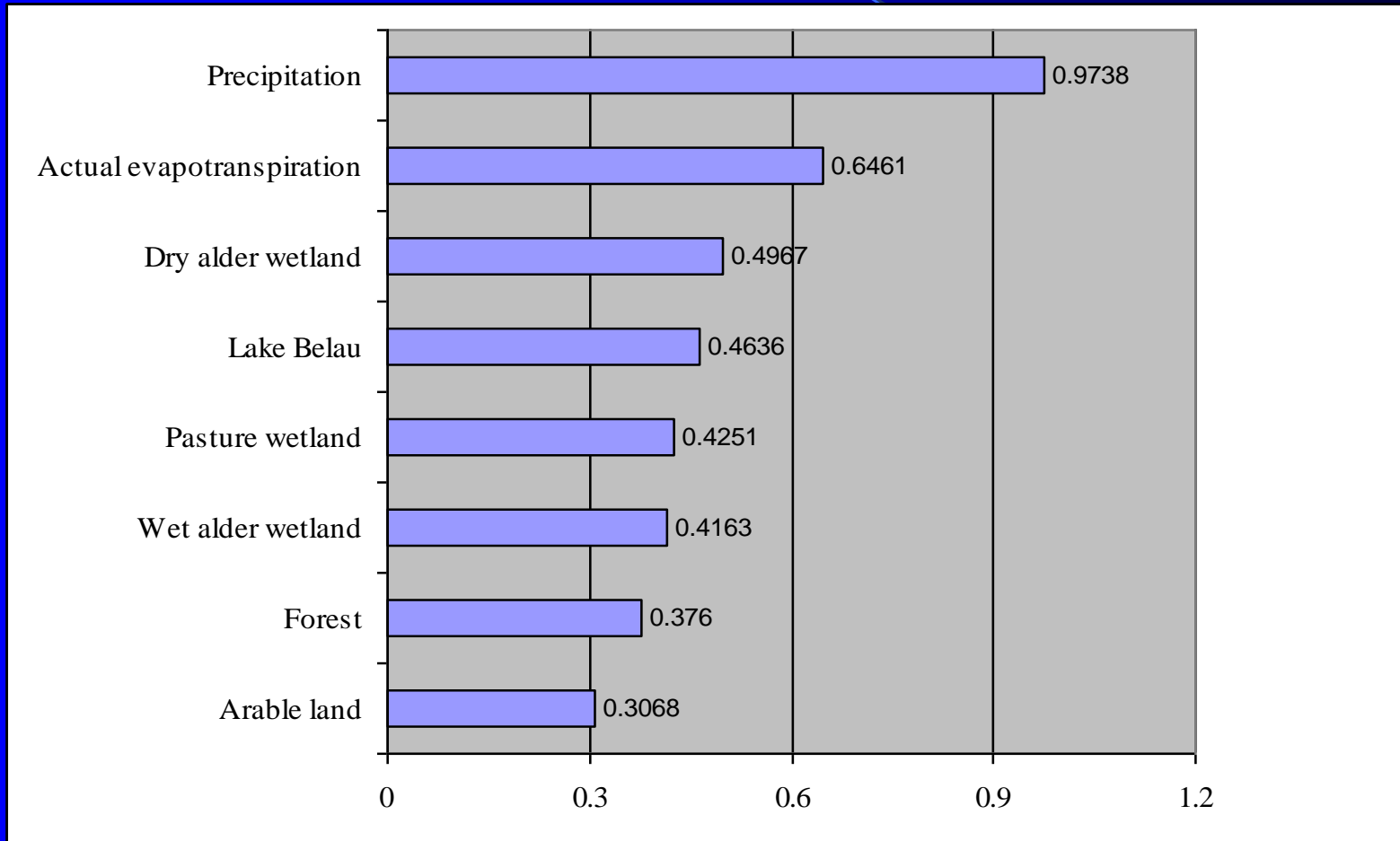
WHOLE:
Higher yields ha^{-1}
Reduce pest presence
Mitigate disease spread

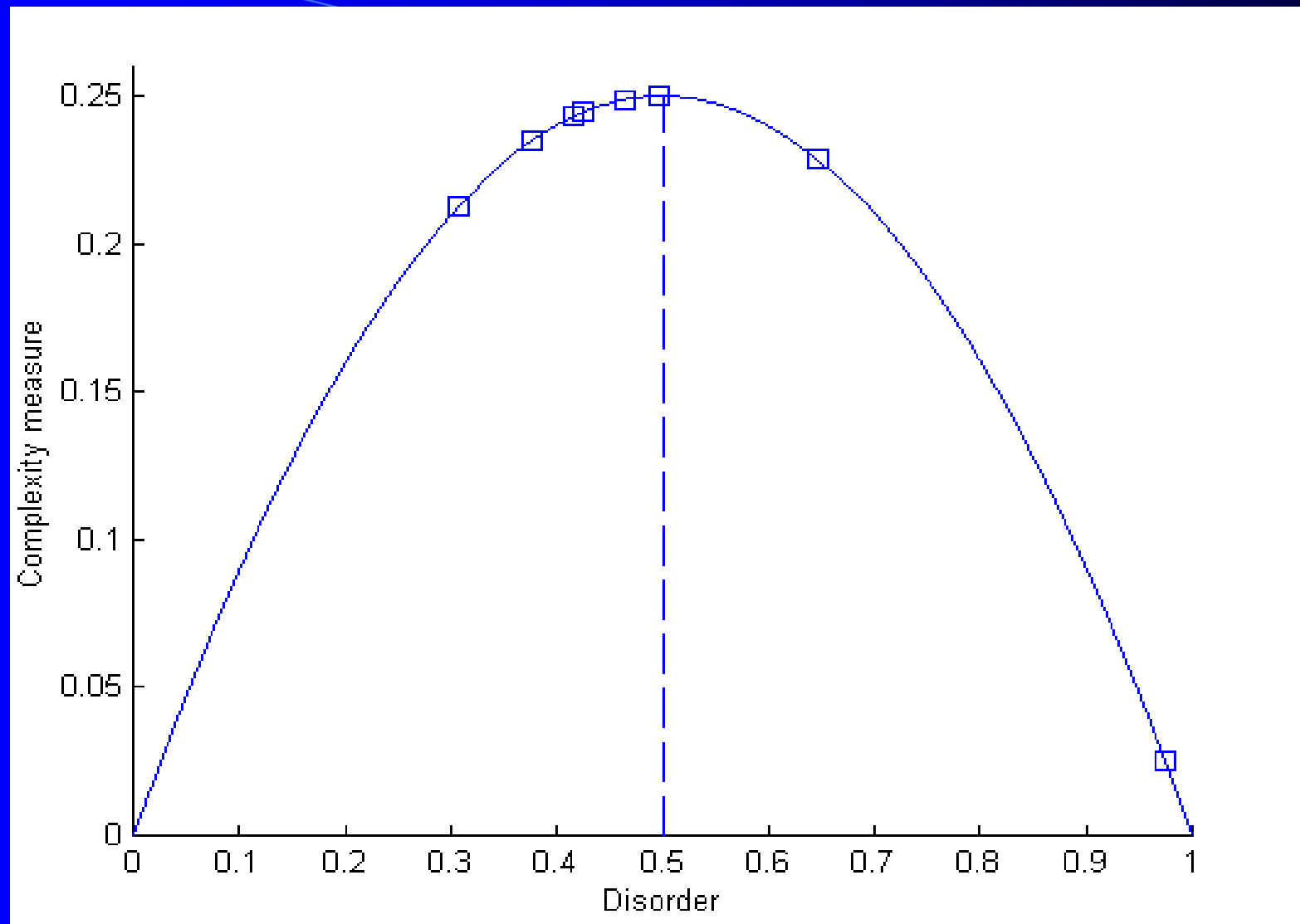
German Long-Term Ecological Monitoring Site



Self-organization, entropy, order and complexity

The normalized spectral entropy measure





Biotic

Abiotic



Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Order and disorder in ecological time-series: Introducing normalized spectral entropy

Nicola Zaccarelli^{a,*}, Bai-Lian Li^b, Irene Petrosillo^a, Giovanni Zurlini^a

Global Change Biology

celebrating 20 years

Global Change Biology (2014), doi: 10.1111/gcb.12707

LETTER

Spectral entropy, ecological resilience, and adaptive capacity for understanding, evaluating, and managing ecosystem stability and change

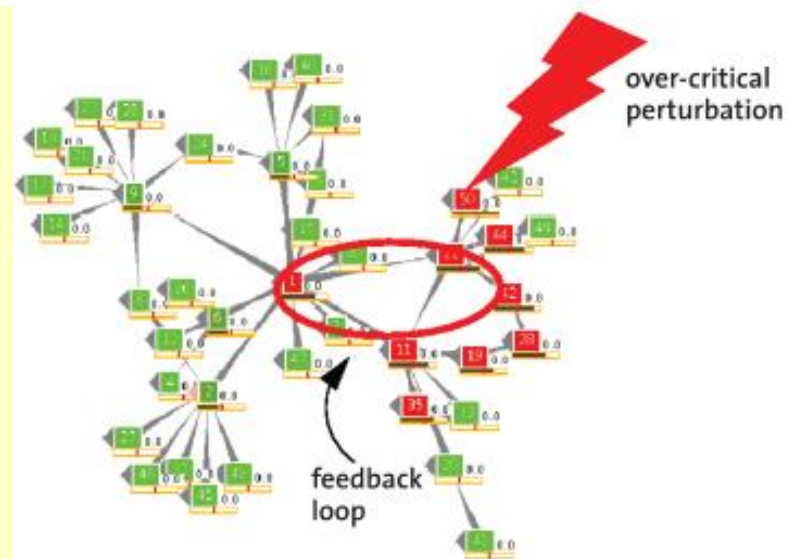
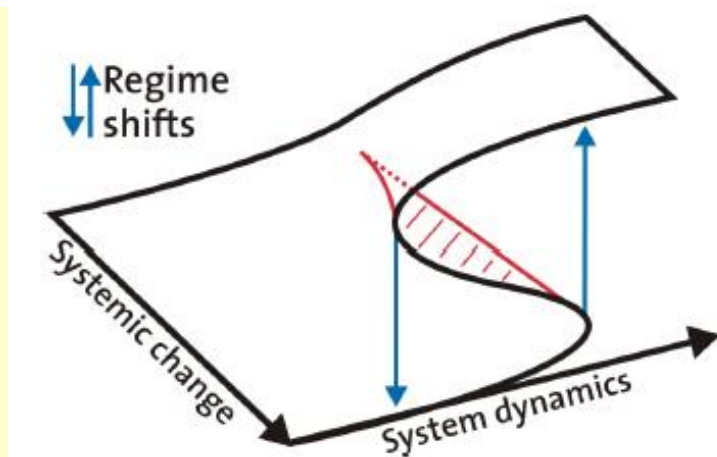
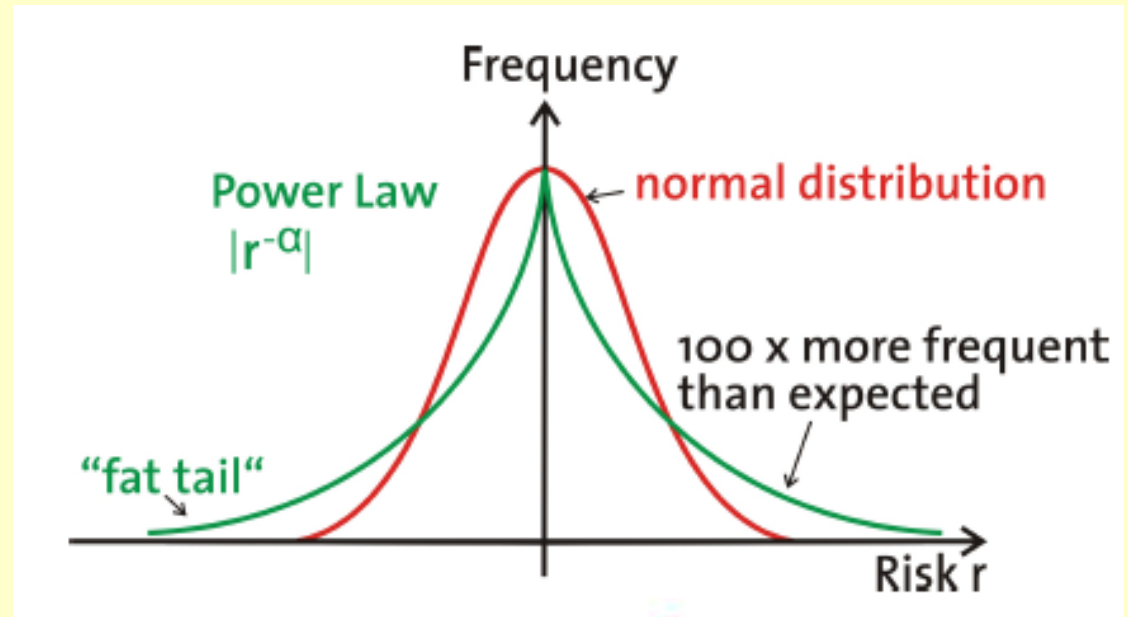
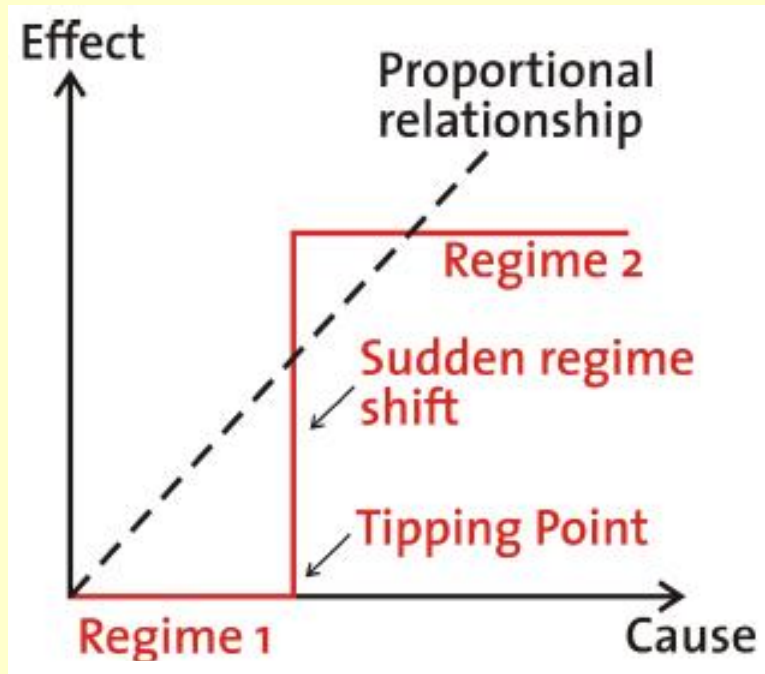
GIOVANNIZURLINI¹, BAI-LIAN LI², NICOLA ZACCARELLI¹ and IRENE PETROSILLO¹

Contribution of biodiversity to ecosystem functioning: a non-equilibrium thermodynamic perspective

Amit CHAKRABORTY^{1,2}, B Larry LI^{1,2*}

- We propose here that at a homeostatic state of ecosystem, biodiversity which includes both phenotypic and functional diversity, attains optimal values.
- As long as biodiversity remains within its optimal range, the corresponding homeostatic state is maintained.
- However, while embedded environmental conditions fluctuate along the gradient of accelerating changes, phenotypic diversity and functional diversity contribute inversely to the associated self-organizing processes.
- Furthermore, an increase or decrease in biodiversity outside of its optimal range makes the ecosystem vulnerable to transition into a different state.

Typical behaviors of complex systems



Theoretical and methodological aspect:

- Ordinary Gaussian distribution
→ equilibrium thermodynamics
- Lévy statistics → Strange
kinetics and far from
equilibrium phase transition



Spatial Scaling and Ecotone Transition: Diffusion Entropy Analysis

(Larry Li and Andrew Morozov, UCR)

Diffusion Entropy Analysis (DEA)

(Scafetta, et al. 2001. Fractals 9, 193)

- the Shannon entropy of the diffusion process

$$S(t) = - \int_{-\infty}^{\infty} dx p(x, t) \ln[p(x, t)]$$

- Let's suppose that $p(x, t)$ fits the scaling condition:

$$p(x, t) = \frac{1}{t^{\delta}} F\left(\frac{x}{t^{\delta}}\right)$$

DEA (cont.)

- Let's plug the above scaling condition into Shannon entropy, Based on changing the integration variable from x to $y=x/t^\delta$, we obtain

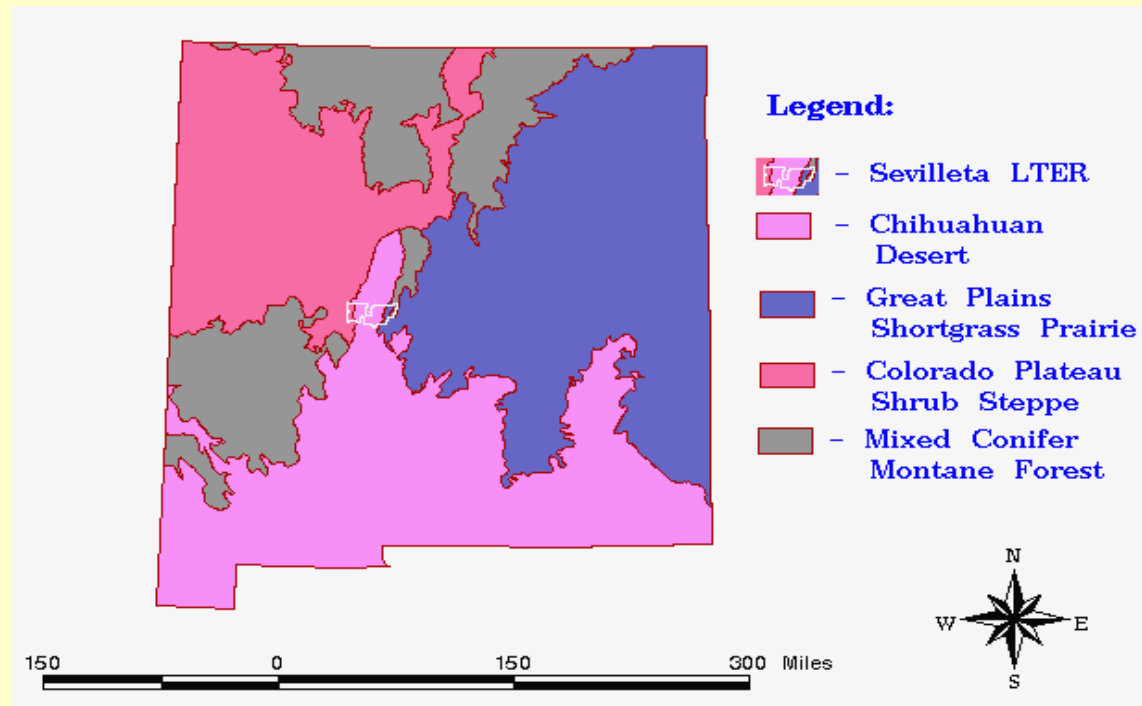
$$S(t) = A + \delta \ln t$$

- where

$$A \equiv -\int_{-\infty}^{\infty} dy F(y) \ln[F(y)]$$

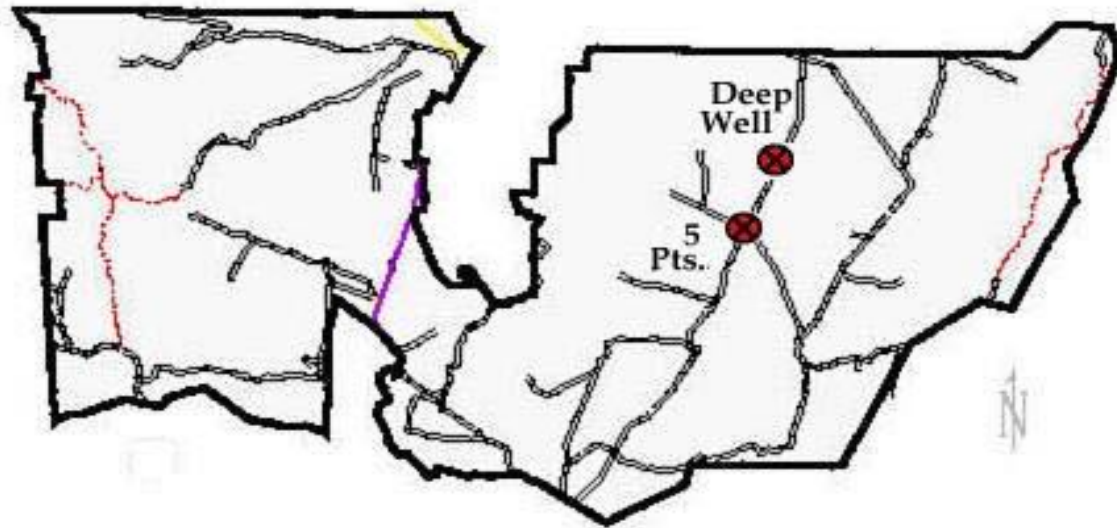
Great Plains – Chihuahuan Desert Transition Zone

Topography, geology, soil nutrients, and hydrology interact with major air mass dynamics. They provide a spatial and temporal template that has resulted in the Sevilleta being an important biome transition zone.



There are four major biomes in New Mexico, Three of them – Great Plains grassland, Great Basin shrub steppe, and Chihuahuan Desert – intersect at the lower elevations of the Sevilleta. And all of the three have transitions to conifer woodland at higher elevations.

Site Description: Deep Well and Five Points



Deep Well and Five Points are located in biome transition zone between Chihuahuan Desert and Great Plain that make these two sites inherently advantageous to evaluate temporal and spatial dynamics of vegetation transitions.

Deep Well and Five Points are two major research sites on the Sevilleta NWR. They are both located on the east side of the Sevilleta.

Great Plains Steppe

Black Grama



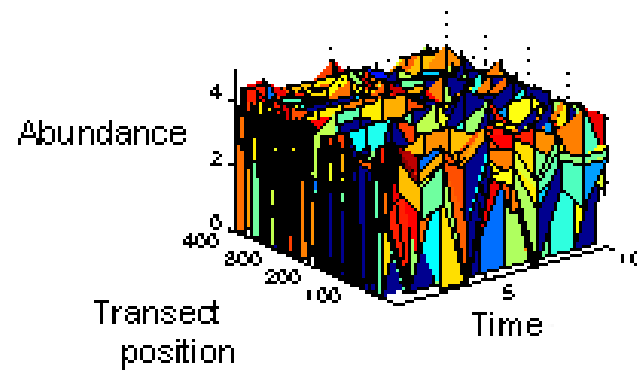
Blue Grama

Chihuahuan Desert

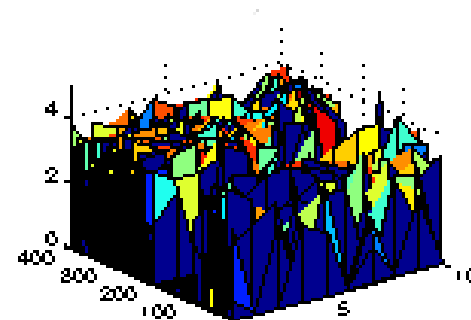
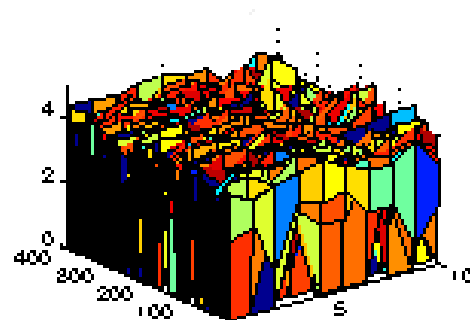
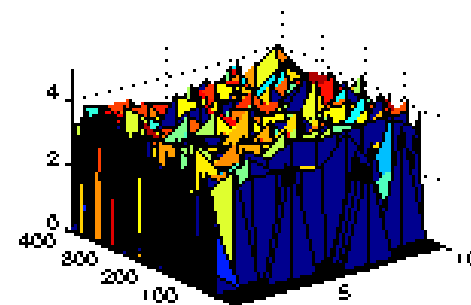
Deep Well

Five Points

B. eripoda



B. gracilis



(Anand and Li, 2001. *Community Ecology*, 2: 161-169.)

Summary Table of estimated values

The Great Plains short-grass
Steppe site, central New Mexico

BOER: black grama

BOGR: blue grama

Year	species	DEA	SDA	DFA	$\bar{\delta}_H$
		$\bar{\delta}$	H	H	
89	BOER	0.7666	0.8082	0.7920	0.7144
	BOGR	0.7844	0.7592	0.7770	0.6832
90	BOER	0.8104	0.7667	0.7390	0.6292
	BOGR	0.8041	0.7288	0.7190	0.6442
91	BOER	0.7376	0.7592	0.7621	0.6763
	BOGR	0.8078	0.7531	0.7693	0.6768
92	BOER	0.7735	0.7369	0.7816	0.6750
	BOGR	0.8292	0.7219	0.7317	0.6467
93	BOER	0.7638	0.7897	0.8094	0.7138
	BOGR	0.7793	0.7125	0.7049	0.6319
94	BOER	0.7554	0.7418	0.7517	0.6638
	BOGR	0.8299	0.7382	0.7117	0.6451
95	BOER	0.6740	0.7072	0.7544	0.6500
	BOGR	0.7989	0.7073	0.7108	0.6322
96	BOER	0.7440	0.7033	0.6912	0.6229
	BOGR	0.8375	0.7687	0.7463	0.6734
97	BOER	0.6763	0.7175	0.7672	0.6599
	BOGR	0.7714	0.7305	0.7568	0.6611
98	BOER	0.7488	0.7024	0.7672	0.6534
	BOGR	0.8428	0.7446	0.7431	0.6612

Summary Table of estimated values

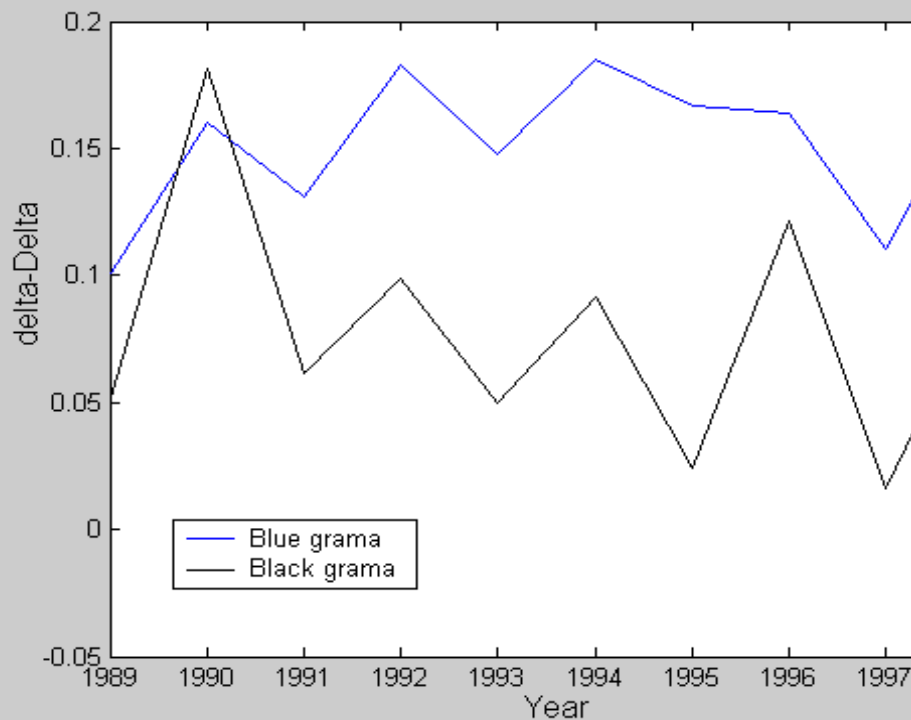
Chihuahuan desert grassland site,
central New Mexico

BOER: black grama

BOGR: blue grama

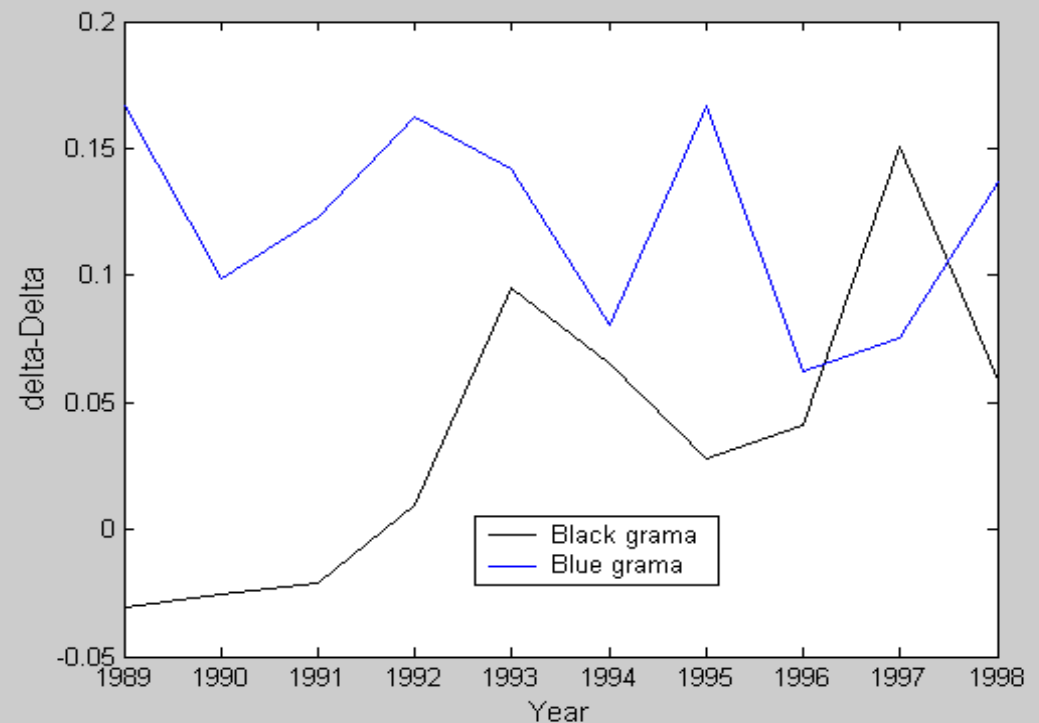
Year	species	DEA	SDA	DFA	$\bar{\delta}_H$
		$\bar{\delta}$	H	H	
89	BOER	0.6057	0.6893	0.7383	0.6363
	BOGR	0.7882	0.7190	0.6719	0.6211
90	BOER	0.6410	0.7294	0.7700	0.6667
	BOGR	0.7249	0.7141	0.6872	0.6258
91	BOER	0.6235	0.7102	0.7380	0.6444
	BOGR	0.7504	0.7196	0.6859	0.6272
92	BOER	0.6364	0.7063	0.6981	0.6267
	BOGR	0.7848	0.7248	0.6848	0.6228
93	BOER	0.7331	0.7232	0.7096	0.6381
	BOGR	0.7627	0.6991	0.6892	0.6205
94	BOER	0.6957	0.7058	0.7084	0.6306
	BOGR	0.7155	0.7245	0.7000	0.6347
95	BOER	0.6408	0.6741	0.6935	0.6126
	BOGR	0.7912	0.6902	0.7094	0.6248
96	BOER	0.6470	0.6709	0.6783	0.6058
	BOGR	0.7637	0.8078	0.7668	0.7016
97	BOER	0.7784	0.7237	0.6831	0.6277
	BOGR	0.7379	0.7397	0.7510	0.6626
98	BOER	0.7657	0.7831	0.8026	0.7071
	BOGR	0.7762	0.7109	0.7246	0.6392

Change of $\Delta\delta=\delta-\delta_H$



Great Plains shortgrass steppe

Mean_Blue=0.153, SD=0.03
Mean_Black=0.079, SD=0.05



Chihuahuan desert grassland

Mean_Blue=0.122, SD=0.04
Mean_Black=0.037, SD=0.06

Ecosystem services

subject to valuation for environmental markets

Clean water

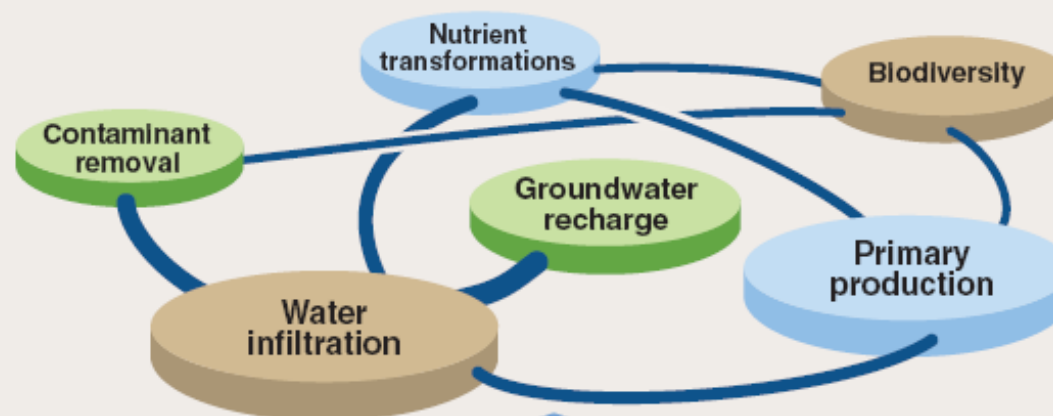
Natural areas for recreation and aesthetics

Flood and erosion control

Food

Ecosystem functions

biophysical processes that generate ecosystem services



Restoration toolbox

actions that may enhance or restore biophysical processes

- Remove invasive species
- Replant riparian vegetation
- Reconnect floodplain
- Reforest surrounding areas
- Add step-pools and wetland islands
- Improve stormwater infrastructure

Synergetic Theory of Ecological Landscape Systems

(4 fundamental principles governing landscape dynamics and evolution from a phenomenological viewpoint)

- *Landscape wholeness and hierarchy (or holarchy) principle*
- *Landscape antagonism principle*
- *Landscape instability or multistability principle*
- *Landscape selection principle*

(Li, 2000. *Landscape and Urban Planning*, 50, 27-41.)



ELSEVIER

Landscape and Urban Planning 50 (2000) 27–41

LANDSCAPE
AND
URBAN PLANNING

www.elsevier.com/locate/landurbplan

Why is the holistic approach becoming so important in landscape ecology?

Bai-Lian Li*

**Ecological
restoration by
learning how nature
works**

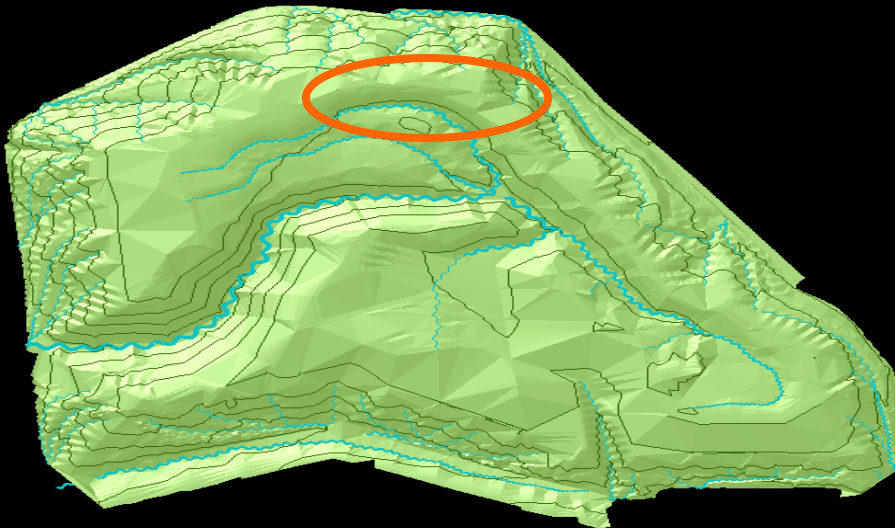
How vegetation would respond?



**moisture variation resulting from complex topography
will likely play a larger role in creating community
diversity**

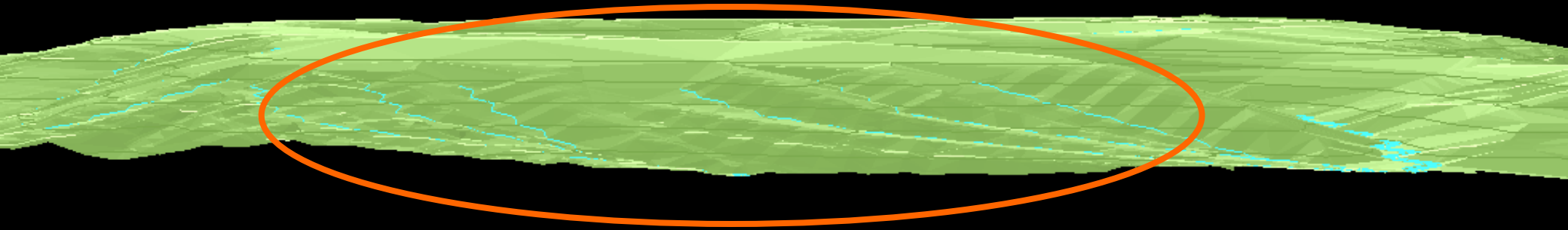
- Clark, 2008

satisfy desires for natural appearance?
Low-gradient channel, buses for scale



**a constructed example
with very similar
dimensions to circled
area**

**satisfy desires for natural appearance? GeoFluv
steep slope channels**



**constructed example with a design very similar to
circled area**

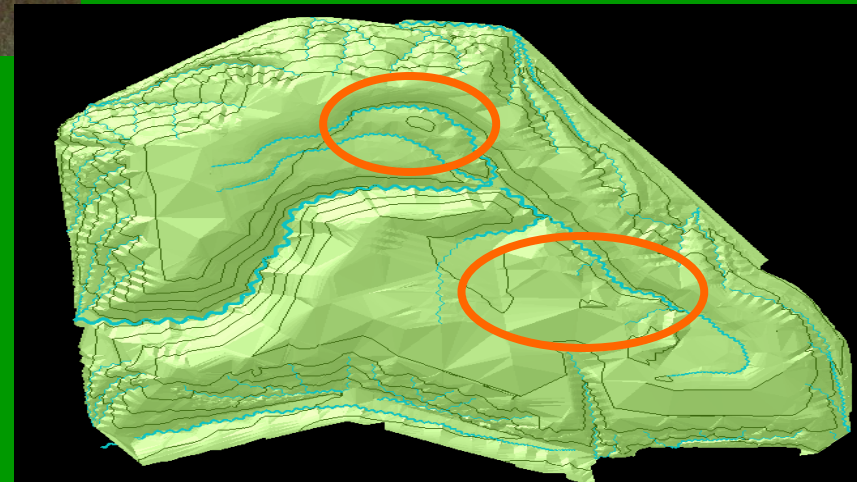


satisfy desires for natural appearance?



**constructed
example with a
design very
similar to circled
areas**

**Ridgeline with steep
tributary channel**



Conclusions





your planet needs **YOU!**
UNite to combat
climate change
WORLD ENVIRONMENT DAY, 5 JUNE 2009

**ACT
MORE**
www.unep.org

PHOTOS: THEBIGGERPICTURE

你的地球需要**你!**



环境署

联合国国际力量应对气候变化

世界环境日，2009年6月5日

C 100%
M 0%
Y 0%
K 100%
Warm Red
C 0% Y 100%
K 100%



Thank you!