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NATURAL SELECTION OF COMMUNITIES AND THE STABILITY OF BIOGEOCHEMICAL CYCLES

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The closed matter cycles should be maintained by natural selection of local ecosystems of finite size. The existence of local ecosystems is possible provided that (1) the physical diffusion of biogenic fluxes do not exceed bioproductivity and (2) there is a definite distribution of biodestructivity over the body sizes of heterotrophic organisms.

Key words: cycles, biocenose, fluctuation, distribution

The resources of biogenic elements being limited, the long existence of life is possible only if biochemical matter cycles are closed ones. This is provided for by correlation of organisms of various species and trophic levels in the biocenoses. Every kind of internal correlation in biological systems, from cells in a multicellular organism to different species in community, should be maintained by natural selection inside of an uncorrelated set (or population) of corresponding competitively interacting biosystems. Therefore the internally correlated biocenoses must interact competitively, have a finite size and form local ecosystems in their environment. The simplest example of a local ecosystem is lichens (Farrar 1976). Let us call by (i) *physical stability* the stability of an isolated biosystem which is maintained be the correlative ("altruistic") interaction of its different parts, and by (ii) *biological stability* the stability of a set of different biosystems capable of replication, which is maintained by their competitive interactions.

A local ecosystem, like any single organism, is physically stable and has a finite lifetime. On the contrary, like any animal or plant population, the uncorrelated set of competitively interacting local ecosystems is biologically stable and should have practically an infinite time of existence.

The stability of the environmental chemical composition may be characterized by a disbalance

$$\kappa \equiv (P_X^+ - P_X^-)/P_X^+ \tag{1}$$

where P_X^+ and P_X^- are the total biota productivity and destructivity (biogen X = C, N, P ... flux in the organic synthesis and disintegration processes), respectively. The consumption and ejection of various biogenes takes place at fixed stoichiometric ratios $P_C^\pm : P_N^\pm : P_P^\pm$ (Ivanov 1972). So, approximately, κ does not depend on X. The mean biospheric net productivity in carbon units is $P_C^+ = 1.5 \cdot 10^2$ g C $m^{-2}yr^{-1}$ (Whittaker and Likens 1975). The mean global rate of carbon accumulation in the sedimentary rocks is $P_C^+ - P_C^- = 3.1 \cdot 10^{-2}$ g C $m^{-2}yr^{-1}$ (Ronov 1976). Therefore the mean disbalance is $\bar{\kappa} = 2 \cdot 10^{-4}$. The annually average disbalance probably does not exceed 10^{-3} in most natural regions (Ivanov 1975, Kempe 1979).

The existence of local ecosystems means that there is a difference $\Delta[X] > \Delta[X]_{min}$ of the concentration [X] inside and outside of a local ecosystem, where $\Delta[X]_{min}/[X] \equiv \varepsilon$ is the relative sensitivity limit (resolution) of the biota. The biotic resolution ε should be of the order of the disbalance κ, $\varepsilon \sim \kappa$, in the case of biologically stable matter cycles . The diffusion flux F_X is approximately equal to $(D \cdot \Delta[X])/L$ and tends to decrease the concentration difference $\Delta[X]$, where D is the eddy or molecular diffusivity, L is the size of the local ecosystem. The biota is capable of maintaining concentration difference provided that the diffusion flux F_X may be compensated by the flux of biochemical transport that equals to the productivity (or destructivity), i.e. if

$$F_X \leqslant P_X^+ \simeq P_X^- \quad \text{for} \quad \Delta[X] > \Delta[X]_{min} \tag{2}$$

In the case of $\Delta[X] \sim [X]$, the biota is capable of maintaining the local concentration inside of the ecosystem. Such biologically locally accumulated biogenes are C, N, P in soil. In the case of $\Delta[X]_{min} < \Delta[X] << [X]$ the biota is capable of maintaining the global concentration by means of redistribution of biogen X content in organic M^+ and inorganic M^- active global reserves provided that $M^+ \sim M^-$. Such biologically globally accumulated matter are CO_2 in the atmosphere, and fresh water in forest regions. In the case of $\Delta[X] < \Delta[X]_{min}$, or $M^- >> M^+$, the biologically regulation of the concentration X is impossible. Such biologically unaccumulated biogens are O_2 and N_2 in the atmosphere. Only biologically unaccumulated biogenes and physically unaccumulated sun light may constitute a limiting factor for ecosystem productivity.

The relations (2) are not valid in running waters (in their rest systems) and surface water of open ocean due to the large value of diffusivity D in these locations (Ivanov 1975, Kempe 1979). The existence of local ecosystems in such biotopes should be maintained by biota that is located in the regions with low diffusivity, i.e. by bentic fauna and flora in the running waters and by heterotrophes inside and below the main thermoclean in the open ocean.

The total destructivity P^- is the sum of destructivities P_i of all heterotrophic species i, which changes proportionally to the net productivity P^+ at small κ, see (1): $P^- \equiv \sum_i P_i$. The variable that does not depend on productivity is the relative destructivity β_i of i-th species: $\beta_i \equiv P_i/P^+$. Let us define the body size l as $l = (m/\rho)^{1/3}$, where m and ρ are the body mass and density, respectively. Let us introduce then the densities per unit of relative size $dx = 0.43\, dl\, l^{-1}$, $x = \lg(l/l_o)$, of (i) the number of species n and (ii) the relative destructivity of community β by the following equations:

$$n = \left(\sum_x^{x+dx} i\right)/dx, \quad \beta = \left(\sum_x^{x+dx} \beta_i\right)/dx$$

where the sumation is understood over species whose body sizes are in the interval (x,x+dx). Then the average relative destructivity β_l of a species of definite size l is

$$\beta_l = \beta\, n^{-1}; \quad P_l \equiv \beta_l\, P^+ \qquad (3)$$

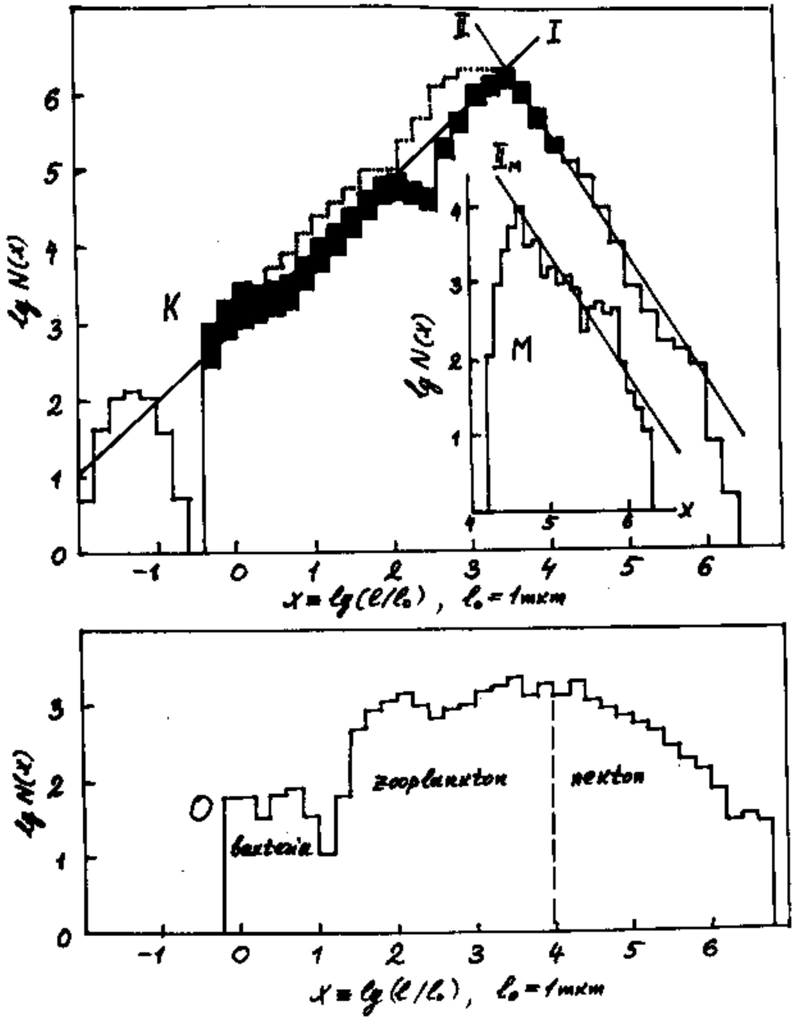

Fig. 1. The density ($N_{(x)}$) of the number of herbivore species (including reductors) per unit of the relative body size interval (dx) in the World fauna and flora as the function of body size (l); $l = (m/\rho)^{1/3}$; l, m and ρ are the body size, the mass and the density, respectively; $x = lg(l/l_o)$;

[continued on the next page]

The destructivity of a given species does not correlate over regions that have linear size r of the order of body size l (Gorškov 1981). The number of these regions in the area of the local ecosystem (in the case of a two dimensional feeding territory (Gorškov 1982) is of the order of $N_l = L^2 \cdot l^{-2}$. Therefore the annually averaged fluctuation $\Delta_l = \sqrt{\overline{(\beta_l - \bar{\beta}_l)^2}}$ of mean relative destructivity, $\beta_l = \sum_{k=1}^{N_l} \beta_{lk} \cdot r_k^2/L^2$, $r_k \sim 1$, of the entire local ecosystem is

$$\Delta_l \approx \beta_l \cdot N_l^{-\frac{1}{2}} \approx \beta_l \cdot L^{-1} \tag{4}$$

The annually averaged square of fluctuation $\Delta_t^2 = \overline{(P^- - \bar{P}^-)^2}/P^{+2}$ of total destructivity according to eqn. (1) is $\overline{(\kappa - \bar{\kappa})^2}$ and should be of order to $\bar{\kappa}^2$ for the entire local ecosystem. The relative destructivities β_i of various herbivore species (including reducers) do not correlate. Therefore their squares of fluctuations $\Delta_i^2 \equiv \overline{(\beta_i - \bar{\beta}_i)^2}$ are summed and then we have

$$\Delta_t^2 = \sum_i \Delta_i^2 = \int_{x_{min}}^{x_{max}} \Delta^2 dx, \quad \Delta^2 \equiv \Delta_l^2 n \tag{5}$$

$dx = 0.43\ dl/l$; $N(x) = (\sum_x^{x+dx} i)/dx$, where the sum is taken over those species i which body size are in the interval (x,x+dx).

The histogram K is the distribution of land biota. The following taxonomic groups (k) give the main contribution (Čislenko 1981): Ribonucleoproteinealee (1.9),(-1.4); Actinomycetes, Bacteria (3.0–3.4),(0.20); Protozoa (4.4–4.6),(1.7); Nematoda (4.3–4.5),(2.0); Oligochaeta (3.6),(3.2, 3.9); Diplopoda (3.9),(3.6); Acari (4.0),(2.2); Insecta (5.9–6.2),(3.4); Gastropoda (4.9),(4.2); Chelonia (2.3),(5.0); Mammalia (3.5),(4.6), where the first brackets are ($lg\ N_{k\ min} - lg\ N_{k\ max}$), where $N_k = \int_{x_{k\ min}}^{x_{k\ max}} N_k(x)\ dx$ is the total number of species in the taxonomic group k, $N_{k\ min}$ and $N_{k\ max}$ are their minimal and maximal data as quoted in literature; the second brackets are the logarithms of sizes (x_k), at which the distribution $N_k(x)$ have maxima (Čislenko 1981). The black region includes uncertainties due to the differences between $N_{k\ min}$ and $N_{k\ max}$. The dashed part of the histogram approximately takes into account the Fungi (4.9),(1.0) and the insect larvae. It is assumed that the distribution of thickness of hyphae of Fungi is Gaussian in the x scale with $\sigma = 0.5$ [x_{min} = o(mucor), x_{max} = 2.3 (Achlia) (Bilaj 1976)] and that the larvae sizes at $x < 3.4$ change from 1/3 to 1, where l is the size of adult insects (Cobben 1968). The histogram M is the distribution of mammals (Čislenko 1981). The histogram 0 is the distribution of pelagic ocean biota (the main part of necton are the carnivore species). Lines I, II, II_m are the scaling approximation. The slopes of lines are $N' = 0.96$ for I, $N' = -1.6$ for II and II_m.

It would be natural to assume that all sizes give comparable contributions to the total fluctuation Δ_t of the entire local ecosystem and density of the fluctuation Δ does not depend on the size and according to (5) is of order of $\kappa \cdot x_m^{-\frac{1}{2}}$, where $x_m = x_{max} - x_{min} \sim 6$. Thus we obtain from eqn. (3) - (5)

$$\beta_l \equiv \frac{\Delta L}{l\sqrt{n}}, \quad \beta \equiv \frac{\Delta L}{l}\sqrt{n} \tag{6}$$

In the scaling approximation

$$\lg(z/z_o) = z'\lg(l/l_o), \quad z \equiv \beta, \beta_l, n \tag{7}$$

we obtain from (6) for $\Delta' = 0$ the following connections between the slopes β', β_l' and n':

$$\beta_l' = -1 - n'/2, \quad \beta' = -1 + n'/2 \tag{8}$$

According to biogeographic data, the areas of various species do not depend on the body sizes (Čislenko 1981). Therefore the distribution n of species in an average local ecosystem should be similar to the distribution N of species in the World fauna and flora (Čislenko 1981) (Fig. 1), and hence $n' = N'$.

The relations (8) agree with empirical data. In the size interval $0 < x < 3.4$ the slope $N' = 0.96$, (Fig. 1), and, hence, $\beta' = -0.52$, which agrees with the empirical $\beta' = -0.5$ (Giljarov 1944, Gorškov 1981). For $3.4 < x < 6.2$ (including mammals) the slope $N' = -1.6$, (Fig. 1), and, hence, $\beta_l' = -0.2$. According to Damuth (1981) the slope $P_l' = 0$ for mammals of the World But his data do not take into account possible changes of productivity P^+. The maximum P^+_{max} and mean P^+ land productivity relates as $P^+_{max}/P^+ = 4$ (Whittaker and Likens 1975). So in the mammalian sizes range $4.2 < x < 6.2$ we have $0 < P^{+'} < 0.3$, and therefore $0 < \beta_l' = P_l' - P^{+'} <$ < -0.3, which agree with the prediction $\beta_l' = -0.2$. In the open ocean $N' = 0$, and hence $\beta' = \beta_l' = -1$, inside the sizes range $1.5 < x < 4.0$, (Fig. 1), which agree with empirical data (Cejtlin 1981).

The relation (6) may be used to estimate the size L of local ecosystems. For lichens we have: $l \sim 10^{-5}$ m, $n = 1$, $\beta = 1$, $\Delta \sim \kappa / x_m \sim 10^{-4}$, and therefore $L \sim 0.1$ m. In all local ecosystems we have (Whittaker and Likens 1975, Gorškov 1981) $\beta \sim 1$, $n \sim 10$ at $1 < 10^{-5} - 10^{-4}$ m, and hence $L \sim (0.1\text{-}1)$ m. For large mammals at $P^{+} = P^{+}_{max}$ the values are $\beta_l = 3\cdot 10^{-4}$, $n = 1$ (Damuth 1981) and from (6) we have that $L \sim 10$ m. Thus the local ecosystems size do not exceed the size of large plants and are much smaller then the size of feeding territories of large animals, which must have according to (6) a very small relative destructivity.

The fluctuation Δ_l of the total primary productivity of entire ecosystem also should be limited by the value of order of κ. The higher plant has a maximal radius of correlation between leafs and roots of order of plant size $L_l \sim L \sim 1$ m. But the mean radius of correlation between different parts of plant may be of the order of leaf thickness $l_l \sim 10^{-4}$ m. Therefore the fluctuation Δ_l of higher plant may be of order of $N_l^{-\frac{1}{2}} \sim$ $\sim L/l_l \sim \kappa$, where $N_l = L^2 l_l^{-2}$.

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