

Functional–Ecological Role of Biological Diversity in Populations and Communities

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Abstract—The functional role of differentiation with respect to local population density, expression of responses to the presence of other individuals, and body weight has been analyzed from an ecoenergetic standpoint with consideration of known mathematical laws. The results indicate that increased variation in these parameters (i.e., their higher diversity) improves the efficiency of energy flow through the animal population: the input of energy increases, while its expenditures decrease. The greatest effect is achieved when the population is divided into alternative modal groups.

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At the United Nations Conference on the Environment and Development (Rio de Janeiro, 1992), representatives of 179 countries adopted the concept regarding the study and conservation of biological diversity as a scientific, political, and economic priority both for individual countries and on a global scale. In relevant research, attention is usually focused on the genetic–taxonomic aspect of the biological diversity. The reasons for this are mainly utilitarian. First of all, there is the hazard of irreversibly losing genetic material that may find potential applications in medicine (e.g., for creating new, efficient drugs) and in various genetic engineering projects, including production of genetically modified organisms.

Meanwhile, biological diversity has many other aspects. Among them, the functional–ecological aspect is of special interest. There is a growing body of evidence confirming the significance of living matter in all its diversity (see Vernadsky, 1978) for global geochemical processes determining the general image of the Earth, including its physicochemical characteristics. Increasingly popular has become the idea that it is *the whole diversity of life* that makes the biosphere a highly complex self-sustaining system and maintains the Earth in the hardly probable state that distinguishes it from all other planets of the Solar System (Lovelock, 1979; Gorshkov, 1988; Gorshkov and Kondrat'ev, 1990). Ecological systems are the systems in which a living (active) component interacts with other such components and with nonliving nature, and the biosphere is the ecological system of the highest order (Bolshakov and Kryazhimskii, 2001). The most important, func-

tional role of diversity must somehow manifest itself at different levels of biological organization, from the intrapopulation to the biosphere level. The principal function of the biological components (subsystems) of ecosystems is regulation of energy flows and, hence, of biogeochemical cycles.

In this study we consider the functional–ecological role of biological diversity at the lower structural levels of ecological systems, mainly at the intrapopulation level, although many ideas and schemes presented below concern also the communities of systematically and ecologically related species. As a methodological basis for formulating and evaluating the problem, we use the ecoenergetic approach that deals with integrated characteristics of ecological systems and has a solid natural scientific foundation.

METHODOLOGICAL PREREQUISITES FOR ESTIMATING THE FUNCTIONAL ROLE OF BIOLOGICAL DIVERSITY

It has been proved in mathematics that when a certain function is nonlinear (has a nonzero second derivative), an increase in the variation of its argument leads to change in the mean value of the function, compared to that observed at the same mean value of the argument in the absence of its variation: if the function is convex (the second derivative is positive), its mean value increases; if the function is concave, it decreases. This approach was used, e.g., by Houston and McNamara (1990) in theoretical analysis of the effect of variation in environmental conditions on the growth of animals.

The curves best approximating various relationships of some biological objects with other objects, biotic or abiotic, rarely approach a straight line. In most cases, relationships between different biological phenomena and processes are nonlinear. For example, such curves often tend to a certain limit, despite the increase in the argument. This is usually related to the fact that the objects whose characteristics are taken as the argument do not exert their full effect on the objects whose state is taken as an independent variable. A good example is the well-known equation of enzymatic reaction kinetics: the form of the kinetic curve is accounted for by the fact that part of the enzyme at a given moment does not function as a catalyst, being bound within the enzyme–substrate complex. Another example is the equation describing the functional response of the consumer to resource density (Holling, 1965), which provided a basis for the ecological theory of optimum foraging (Pyke, 1979; Stephens and Krebs, 1986): the consumer (predator) expends part of the response time for “processing” the resource (prey).

Such relationships are described by concave curves. In some cases (*S*-shaped curves), the concave and convex parts are separated by the inflection point at which the second derivative is zero; i.e., an increase in the variation of the argument within two different intervals of its possible values should lead to a decrease in the mean value of the function in one case and to its increase in the other case.

The relationship of different characteristics is often described as an autonomous process: the rate of change in the dependent variable (e.g., of abundance) versus the independent variable (e.g., time) is represented as a function of the dependent variable itself. The best known example is the equation of exponential population growth proposed long ago by Malthus (1798). Such functions are used most frequently when the rates of change in dimensional characteristics of biological processes are parameterized.

Huxley showed (1936) that, if changes of two characteristics in time (growth) are described by exponential curves (are autonomous processes), then the dependence of one on the other will have the form of the so-called allometric dependence: $Y = aX^b$. When the “allometric exponent” b is less than 1, the relationship is termed hypometric (the function is concave), when $b = 1$, isometric (direct proportionality, the second derivative is zero); and when $b > 1$, hypermetric (the function is convex). Such relationships, being very widespread, gave rise to the actively discussed problem of scaling (Peters, 1983; Schmidt-Nielsen, 1987).

In the 1980s, the ideas of Mandelbrot (2002) concerning the fractal geometry of nature became very popular and subsequently found practical applications, e.g., in economics and computer science. The term “fractal” is derived from the Latin participle *fractum* originating from the verb *frangere*, which means to

break or divide. Thus, it has a double meaning: a piece (part) or an irregularly shaped fragment. In the light of notions concerning the fractal organization of nature, it has become possible to interpret the allometric exponent as a fractal dimensionality reflecting self-similarity of two allometrically related objects.

FUNCTIONAL ROLE OF SPATIAL DISTRIBUTION AND BEHAVIORAL HETEROGENEITY OF A POPULATION

In nature, population density is a major environmental factor influencing all aspects of animal life activities. In one of the most actively developing branches of population ecology dealing with various aspects of self-regulation of animal abundance and density, attention is focused on the dependence of production processes (growth and reproduction) on population density. In this study, we consider only one specific and readily apparent aspect of this complex problem: the potential influence of density on the structure of the energy budget via changes in the structure of the time budget, which are explained by the necessity to pay attention to the presence of other individuals (Kryazhinskii, 1988). To describe such changes, we relied on the logic applied by Holling (1965) in constructing his well-known model of the functional response of a consumer to resource density, following the time-energy approach accepted, e.g., in the aforementioned theory of optimum foraging.

It is known that population ecologists distinguish mean and ecological (local) population densities (Odum, 1986; etc.), with the latter depending on the type of spatial distribution of the population: uniform, random, or aggregated. The results of estimating the distribution type depend on the sampling area (Greig-Smith, 1967). Its decrease may lead to the situation that the distribution classified as aggregated in a greater area should be eventually regarded as random or uniform.

We made an attempt to analyze theoretically possible effects of the spatial distribution of animals on their time and energy budgets. In addition, special attention was also paid to their behavioral characteristics, namely, responses to the presence of other individuals within the detection range. These responses were quantified in units of time expended for them; hence, their nature (antagonistic or friendly) was irrelevant.

If an animal is involved in social (intrapopulation) contacts, the structure of its time budget may be represented in a simplified way as

$$t = t_f + t_c + t_n,$$

where t is the total period of its activity, t_f is the time expended for foraging and “food processing,” t_c is the time expended for interaction with other individuals, and t_n is the time expended for all kinds of activity unrelated to foraging and social contacts (grooming, predation avoidance, etc.). Obviously, the time t_c should be

proportional to the number of contacts with other individuals:

$$t_c = t_e C,$$

where C is the number of contacts and t_e is the mean duration of one contact. This value may be considered the index of “sensitivity” of a given individual to presence of other individuals. In turn, the number of contacts with other individuals C should be proportional to the time during which the animal can meet other individuals (the activity period t minus the time of contacts themselves t_c) and to population density (N):

$$C = aN(t - t_e C),$$

where a is the coefficient of proportionality that may be interpreted as the detection range, or the area in which the animal interacts with all other individuals occurring in it. As a first approximation, a may be taken proportional to the squared “individual distance” (Panov, 1983).

Solving this equation in relation to C , we obtain

$$C = \frac{a \cdot N \cdot t}{1 + t_e \cdot a \cdot N}, \text{ and, therefore, } t_c = \frac{t_e \cdot a \cdot N \cdot t}{1 + t_e \cdot a \cdot N}.$$

If $\eta = \frac{t_n}{t}$ is the fraction of the activity period expended for activities unrelated to foraging and social interactions and $c = at_e$ is a measure of “reactivity” to the presence of other individuals within detection range, then

$$t_f = t \left(\frac{1}{1 + cN} - \eta \right).$$

Thus, the time expended for foraging is inversely proportional to the product of ecological population density N and reactivity index c , which may be defined as the index of actual (local) density (c_N), and, therefore, is a decreasing convex function of c_N (Fig. 1).

It is clear that even when the distribution is uniform (the local density is identical for all individuals), an increase in the variation of reactivity index c (the product of average time expenditure for one contact t_e and detection range a) should lead to an increase in the average amount of time that can be used for foraging. Therefore, the total intensity of food consumption by an animal group of fixed size also increases under such conditions. If the distribution of animals within this group is also aggregated, the effect should be even stronger.

Apparently, the maximum effect (amount over the mean time of foraging in a heterogeneous group of a given size on the condition that all animals in it exist at identical ecological density and do not differ in their behavioral characteristics) should be observed when all animals are divided into two subgroups, the first com-

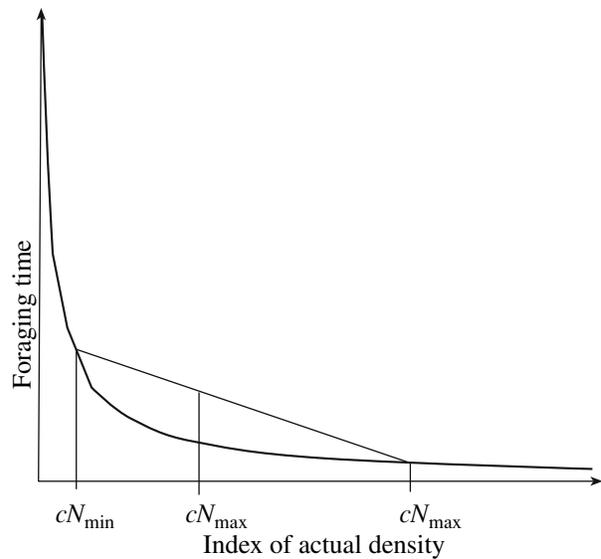


Fig. 1. Dependence of the time expended for foraging on the index of actual local density.

prising tolerant animals (indifferent to other individuals) and the second group comprising reactive animals responding to the presence of neighbors. The former obtain more food and, hence, are more productive than the latter. The effect should be significantly stronger when the first (tolerant) group lives at a low local density, while the second (reactive) group lives at a high density.

Indeed, observations on rodents (Beachem, 1979) showed that animals tolerant to the presence of other individuals had a higher growth rate than aggressive animals. Our data on the growth rate of root voles (Kryazhimskii and Malafeev, 1983) provide evidence that rodents in areas with relatively low local density grow more rapidly than those living under conditions of increased density.

Numerous population-ecological studies have shown that the dependence of fecundity on population density in many animal species is plotted as a decreasing convex function (Fig. 2). Such a curve agrees quite well with the aforementioned expectations following from the concept of positive balance between energy (production) and the time used for foraging. In addition, the conclusions following from this fact apply not only to monospecific populations but also to parts of communities, the groups of population systems belonging to different species but related taxonomically and similar to each other in ecological terms.

This is clearly manifested, for example, when analyzing small mammal communities in different altitudinal zones of mountain regions. Our investigations (Bolshakov, 1972) revealed basic differences between territorial distribution patterns of mountain species and of mountain populations of widely distributed species:

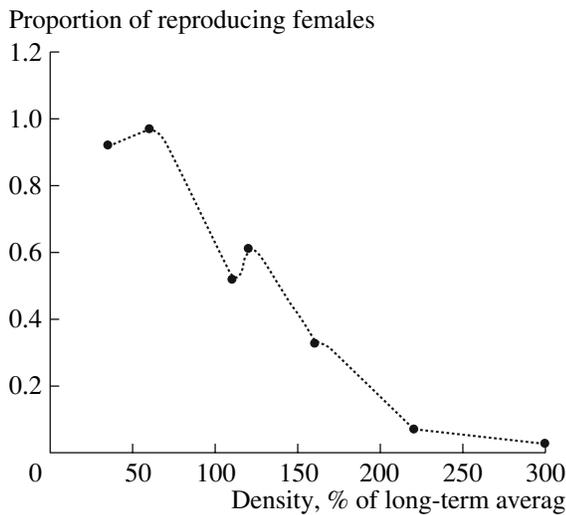


Fig. 2. Dependence of production on actual local density. The curve was plotted for the proportion of reproducing female red foxes in the Cisural region (1983) in the course of constructing an imitation model (Korytin et al., 1989).

the former concentrate in limited areas and occupy specific biotopes (e.g., screes in the upper mountain belts), whereas the latter populate most habitats of the altitudinal belt and are characterized by considerable territorial mobility. No less significant are differences in parameters of fecundity and population dynamics: few litters and small litter size, low mortality, and the absence of sharp fluctuations of abundance are characteristic of specialized mountain species; in the mountain populations of widespread species, conversely, the number of litters and litter size increase with elevation, mortality among different generations is high, and, consequently, abundance fluctuates in a wide range. These groups also differ in activity: the home ranges, where the foraging activity manifests itself, are much smaller in mountain species. From the viewpoint of the general adaptation theory and taking into account ecological adaptive mechanisms of mountain species and populations, it may be concluded that these groups show different energy approaches to adaptation in the environment (its colonization), since adaptation means the maintenance of energy balance with the environment (Kalabukhov, 1946).

Therefore, the growing tendency toward the group pattern of spatial distribution and increasing diversity by tolerance to the presence of other individuals should lead to an increase in the total productivity of a population group at the same mean density (the total number of individuals in a given area).

It should be emphasized that both increasing non-uniformity of spatial distribution and subdivision of animals into two behavioral types can be interpreted as group responses to deterioration of environmental conditions aimed at optimizing the energy flow through the

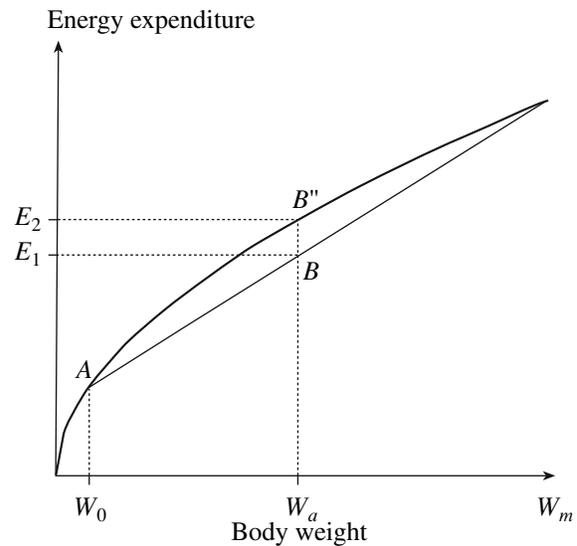


Fig. 3. Dependence of energy parameters on body weight.

population. In other words, the group consisting of animals that respond differently to the presence of other individuals (i.e., to the local population density) and are distributed over the area nonuniformly should have higher productivity than the group of the same total abundance and biomass consisting of identical and uniformly distributed animals.

ENERGY EXPENDITURE AND DIFFERENTIATION BY SIZE

It is known that parameters of energy expenditure for different needs (basal metabolism, muscular work, chemical thermoregulation, etc.) are hypometric to the body weight: the allometric exponent of their dependence on body weight (fractal dimension) is smaller than 1 (Kleiber, 1932; Dol'nik, 1968, 1995; etc.). As was shown fairly long ago (Kleiber, 1961, 1965; Poczopko, 1979), this applies both to representatives of different species related taxonomically and (or) belonging to the same ecological group (e.g., to primary consumers) and to individuals of the same species. The curve of this relationship is concave; the second derivative of energy parameters with respect to body weight is negative. The physical rationales for the fact that coefficient b is always smaller than 1 have been repeatedly discussed beginning from the study by Rubner (1883) (see Dol'nik, 1978). Consequently, an increase in the variation of individual body weight with its group mean value remaining unchanged should lead to the reduction of average individual energy expenditure or, when the group size also remains unchanged, to the reduction of the total energy expenditures of the group.

Let us consider the allometric dependence of the index of energy expenditure E on body weight W :

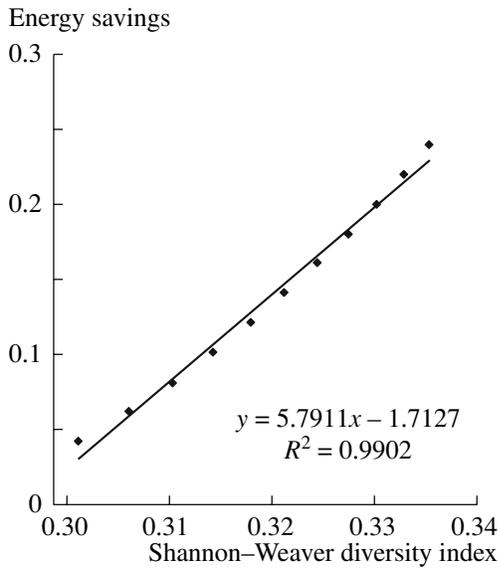


Fig. 4. Calculated values of energy savings as the ratio of energy expenditures in the group consisting of both small-sized (body weight W_0) and large-sized individuals (the body weight W_m) to those in the group of even-sized individuals depending on the Shannon-Weaver diversity index (with the number of animals remaining unchanged).

$$E = aW^b,$$

where W is body weight and a and b are coefficients, and $0 < b < 1$. It was shown previously (Kryazhimskii, 1985; Fig. 3) that if the number of individuals in the group N remains unchanged and individual body weight varies from W_0 to W_m , averaging W_a , then energy expenditures (both average individual and total for the whole group) should increase as the range of variation in body weight broadens. Under these conditions, the minimum expenditure E_1 would be observed in the group consisting of only two groups of individuals: small (body weight W_0) and large (body weight W_m); the maximum energy expenditure E_2 would be observed in the group of individuals with the same body weight W_a .

These considerations may shed light on the functional-ecological significance of the phenomenon of alternative types of animal growth, which clearly manifests itself in rodents of northern and temperate latitudes (Olenev, 1991, 2002): it is interpreted as an adaptive group response providing for the reduction of total energy expenditures, with the maximum effect being achieved when alternative, discrete size groups of animals are formed.

Kryazhimskii (1989) proposed a theoretical scheme according to which the appearance of drastic differences in growth rate and body size among individuals of the same age which may be related to nonlinearity in the behavior of energy parameters. A certain systemic mechanism operating at two levels (individual and pop-

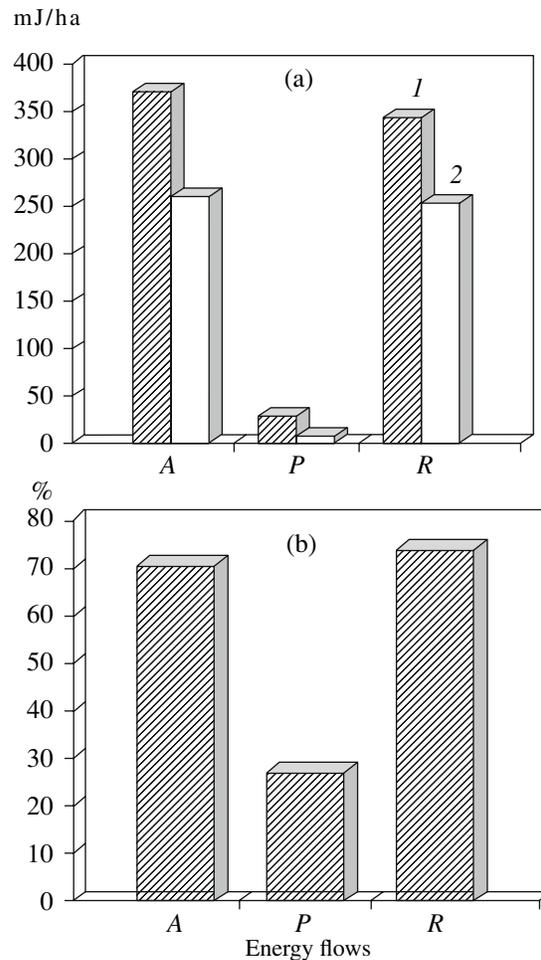


Fig. 5. Annual energy flows through the population of root voles in southern Yamal (1) in 1977, the year of population peak, and (2) in 1978, the year of population decline: (a) absolute values of (A) energy consumption, (P) production, and (R) respiration; (b) the ratios of energy flows in the year of decline to those in the peak year.

ulation) begins to take shape. Deterioration of environmental conditions leads to the situation that the growth rate of some individuals decreases and they remain small, while others grow to a relatively large size. Their coexistence provides for the maintenance of abundance and total production of the rodent population with lower energy expenditures.

It is relevant to note that the phenomenon of differentiation by body size among individuals of the same age is not unique to rodents. It manifests itself in different animal species upon an increase in the density of experimental groups consisting of same-aged individuals (Dobrinskaya and Sled', 1974; Mina and Klevezal, 1976; Shvarts et al., 1976).

It is easy to show that, at a given total abundance and fixed limits of variation in body weight, there is always the abundance ratio of "small" and "large" individuals that provides for the maximum energy efficiency of the

corresponding animal group due to nonlinearity of the relationship between energy expenditures and body weight. The maximum effect should be observed at the maximum diversity of the population (Fig. 4).

There are also reasons to believe that differentiation of animals by size is a factor stabilizing the energy flow through their populations under conditions of considerable fluctuations in their abundance and biomass. For example, consider the data on production parameters estimated for the root vole population in years with contrasting levels of animal abundance.

In the summer season of the year of population peak (June–August 1977), root voles in meadow associations of the southern Yamal Peninsula consumed approximately 674 000 kJ/ha and assimilated 370 000 kJ/ha of energy, with 27 600 kJ (about 7% of the latter amount) and 342 400 kJ (93%) being expended for biomass production and respiration, respectively. During the same period of the next year, at the stage of abrupt population decline, these rodents consumed 478 000 kJ/ha and assimilated approximately 259 400 kJ, with the energy accumulated in new tissues being only 7400 kJ (about 3% of assimilated energy). It is easy to calculate that the values of energy consumption in the years of population peak and decline differed by 30%, energy expenditures for respiration differed by 26%, whereas production in the second year decreased by 73% (Fig. 5). Thus, the energy flow through the rodent population changed to a much lesser extent than its abundance (and, therefore, biomass).

CONCLUSIONS

The results of this study show that an increase in intrapopulation diversity, i.e., in differentiation of individuals by relevant parameters, should inevitably result in a higher efficiency of energy flow through the population: with all other conditions being equal, the total energy input with food should increase, while energy expenditures should decrease. These parameters are the type of area colonization (extensive or intensive; Shilov, 1977) by different intrapopulation groups, the expression of responses to the presence of other individuals within detection range (the response may not necessarily be antagonistic), and size characteristics (body weight). The greatest effect should be achieved when the population is subdivided into alternative groups.

In this context, it appears relevant to refer to the hypothesis of behavioral polymorphism proposed by Chitty (1960), which largely stimulated population-ecological research but failed to provide the final response to the question as to what factors account for the cyclic pattern of population dynamics (Krebs, 1978). Our results show that, to optimize the input of matter and energy into the population system, individuals spending little time on contacts with others (tolerant, or better indifferent) should live under conditions

of a low local density, whereas those sensitive to the presence of other individuals, under conditions of a high density. To some extent, this is reminiscent of Chitty's scheme, i.e., succession of behavioral stereotypes in the course of population cycles. However, the difference is that, according to our conclusions, the increased efficiency of the energy flow should result not from succession of these groups but from their coexistence. In addition, the results of our analysis may shed new light on the functional significance of the phenomenon of alternative types of growth and development discovered in small rodents (and not only in them) and, in general, provide deeper insight into the functional-ecological significance of biological diversity at different levels of organization of ecological systems.

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