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Ecology: Changing options

Long and slow development

Ernst Haeckel, a leading German naturalist, who studied – among others – the life of coral reefs came in 1869 to the conclusion that the organisms living there are mutually dependent and also are affected by the environmental conditions. He proposed a new term „ecology" to delimit the set of his findings on mutual relations between organisms and their environment. He could not, however, predict that the word ecology may become – at the last quarter of the 20th century – frequently spoken by common people all over the world.

The word ecology is now often misused, e.g., used mostly to denote human actions preventing pollution, contamination, habitat destruction, etc. On one hand we know the meaning of ecology – Krebs (1972) showed schematical connections of ecology to a few close branches of biology, i.e., genetics, evolution, physiology and behaviour (Fig. 1) – and ecological research is often supported by the methods elaborated in other biological disciplines as well as known from physics, chemistry or statistics. On the other hand, ecological research was done even long before the term ecology was created. An example is the model of rabbit population growth proposed as early as in 1202 by a mathematician known as Fibonacci. He made some assumptions of how many progeny rabbits produce per year, how many years rabbits reproduce and live, and from that he created a model of increase of the rabbit population size in consecutive years expressed in numbers of pairs: 1, 1, 2, 3, 5, 8, 13, etc., known in mathematics as Fibonacci series (please, note that any value higher than 1 in the series is the sum of the 2 preceeding ones).

Studies on population ecology, and especially on the rate and form of population increase, had been an important part of ecology for many years. 18th century – the beginning of the industrial era – brought about a renewal of population ideas induced by pauperization of substantial part of human population in such countries like United Kingdom or Germany. Malthus (1798) predicted that human population would grow exponential-

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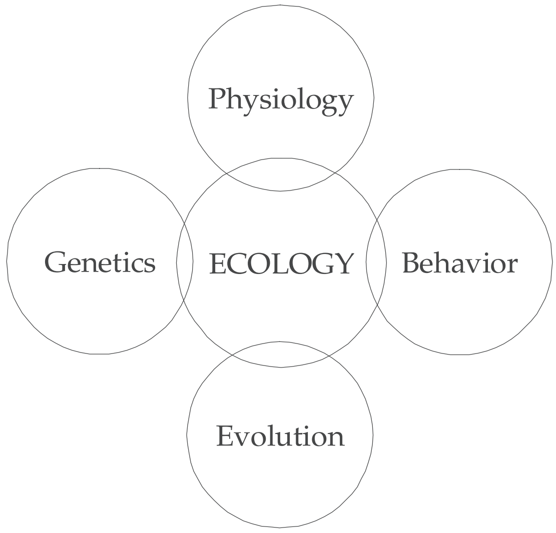


Fig. 1. Ecology and some related biological sciences (slightly modified from Krebs 1972).

ly, while food resources could increase linearly. Such situation could result in a sudden increase of human mortality rate and a decrease in the population numbers. However, his idea was rejected by a French mathematician Verhulst (1838) who proposed another model of population growth, commonly known as logistic growth curve. His model predicted that after a period of exponential growth, the rate of the growth would steadily decrease – due to decreasing life conditions (availability of food and shelters) – and finally would be equal to 0. The ideas presented by Malthus and Verhulst (Fig. 2) were widely discussed in the first half of the 20th century, when vast areas of uniform crops (in farmland and forestry) were destroyed by various pests, like insects and rodents.

In the beginning of the last century there was a controversy between the representatives of multi-factor approach to evaluation of population dynamics of numbers (Howard and Fiske, 1911) and those who claimed the importance of a single factor, like Bodenheimer (1928), seeking – for instance – for the predominant impact of climatic conditions that limited the period of the appropriate weather conditions for breeding. Early 30ties drew the attention to the population itself, as a reason for limiting its density. Nicholson (1933) and Smith (1935) are generally considered as inventors of the idea of density-dependence. This idea postulates that population density (i.e., the number of individuals living concurrently per unit of area or volume) increases until an equilibrium between density and environmental capacity is reached. The formal (mathematical) model of density-dependence is the logistic curve of population growth. Va-

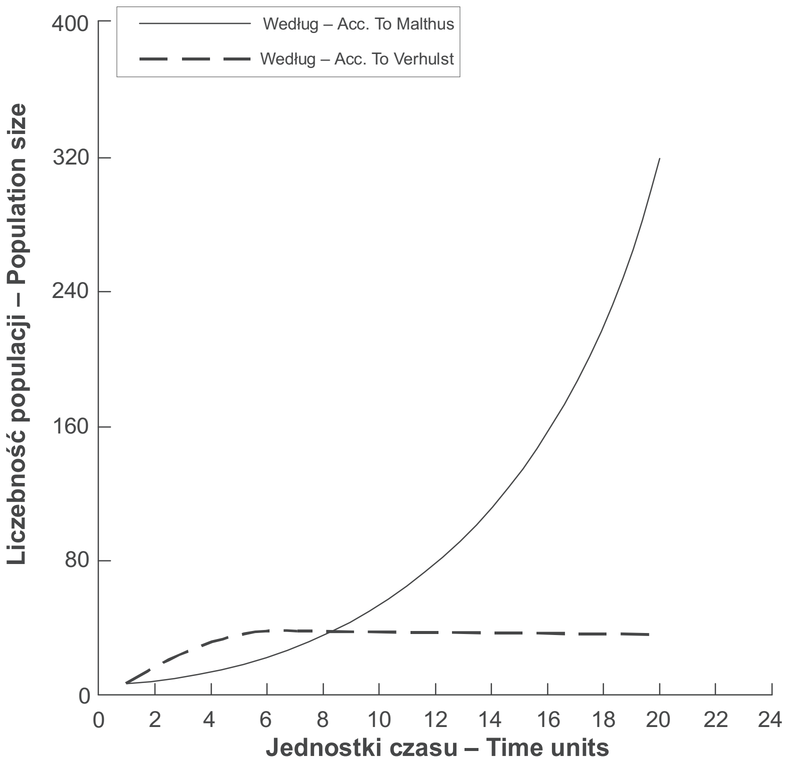


Fig. 2. Population growth according to Malthus (exponential) and Verhulst (logistic).

riation in population density were explained by Nicholson as a result of changes in environmental capacity: He compared density changes to a baloon changing its elevation in relation to variations of air pressure. Others sought the reason for fluctuations of density in a delayed response of individuals (such as response in mortality and natality) to changing conditions.

Even though the density-dependence was a predominant theory of population growth, it was also a subject of criticism. For example, Andrewartha and Birch (1954) drew the attention to the fact of treating population density as a mean equal in the entire population range, while in reality the density varies in space and also the range of population area may expand and contract. The same criticism applies to the mathematical model of logistic growth curve of population numbers: Space is lacking in that model. Another serious doubts about reality of density-dependence resulted from experiments made by Petrusewicz (1957) on the so-called induced population growth. His investigations on laboratory mice populations provided evidence that population growth was mostly dependent on social relations between individuals: Introduction of a strange individual to a caged population only for a limited time (a few days) resulted in a disturbance of the social structure (dominant individuals lost their position and other, formerly subordinated ones, took their social rank), and such disturbance lead to a new increase of population numbers despite stable size of the cage and food delivery.

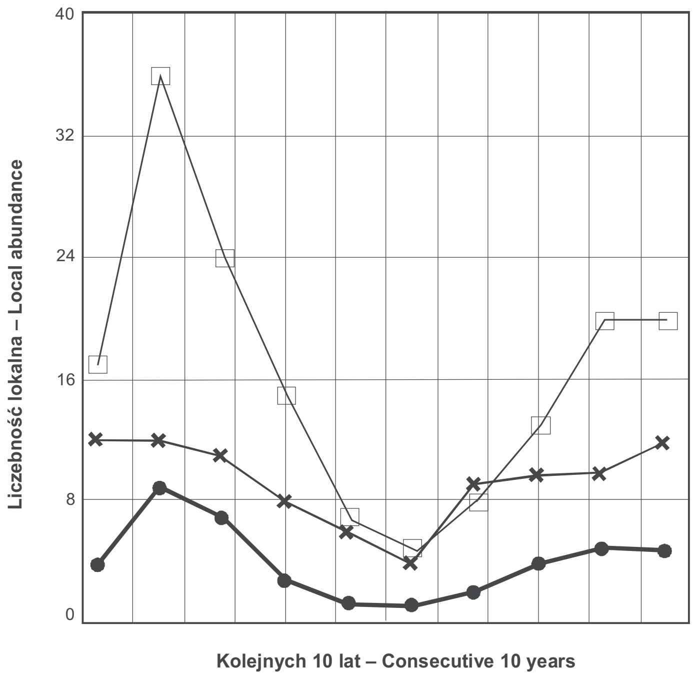
Contemporary studies on dynamics of population numbers have split into problems of metapopulation (consisting of relatively isolated local populations) and local population. In late 60ties the problem of metapopulation dynamics was raised up by Den Boer (1968). He postulated that local populations have limited life-time, that is often disappear and the site previously occupied by a local population can be deserted for some time. If conditions present in all local populations are even, or similar, then it is very probable that all of them may vanish at the same time, and the metapopulation becomes extinct. However, if the conditions in the sites occupied by separate local populations differ, then there is no risk of concurrent extinction of all of them, and those that survive form a source of individuals that may recolonize the deserted sites, unless the dispersal power of the individuals is such low or the sites are so distant that succesful recolonization is impossible (Fig. 3).

On the other hand, the studies on local populations are focused on the importance of differences between individuals (e.g., Łomnicki 1978). Single population theory is at present paying attention to individual features (not only genetic ones, but also sex, weight, social status, age, etc. are considered to be paramount factors differentiating individuals) and to the social order (e.g., such forms of social relations that exist among solitary, colonial or territorial mode of life). Contrary to the basic claims of the density-dependence where individual fate depended on density of the population, now it is presumed that individual features and social relations between the local population individuals, or even neighbouring individuals (Bujalska and Grüm 1989), affect the population growth rate and its density.

Rapidly changing challenges

In mid 60ties of the passed century consciousness of difficult alimentary conditions of people in many countries could be considered a signal for scientists for a thorough investigations on biological productivity, its limiting factors and means of increasing the efficiency of agriculture. These were the basic tasks for announcing the International Biological Program. IBP was based on studies of old Tansley (1935) idea of ecosystem, called in some countries also biogeocoenose. The ecosystem concept is fo-

A



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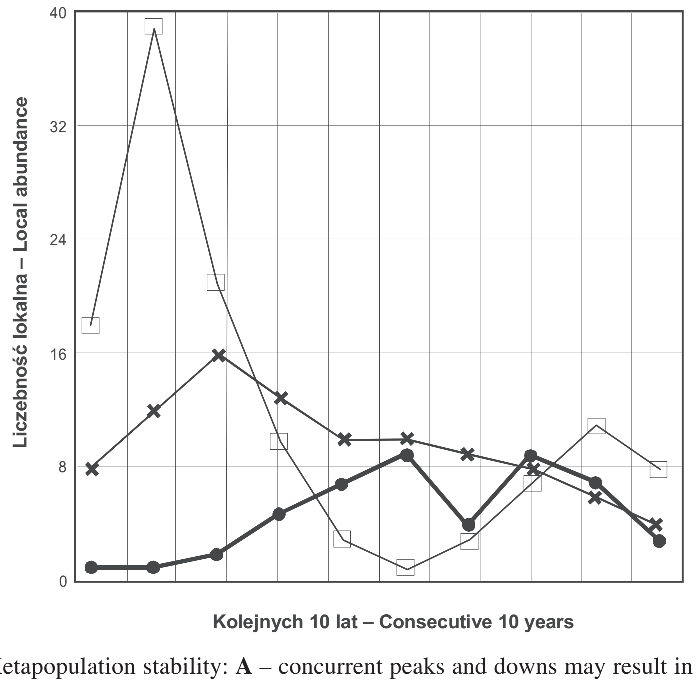

Fig. 3. Metapopulation stability: **A** – concurrent peaks and downs may result in extinction because of lacking source of organisms at the lowest abundance, **B** – diversified peaks and downs prevent extinction due to constant presence of individuals able to populate deserted sites.

cused on the transfer of solar energy reaching our globe: This energy is used by green plants to produce organic matter consumed by plant eaters. The latter are the source of energy for carnivorous animals. Dead bodies of plants and animals decay and in this process such organisms like bacteria or fungi are involved. The final result of decaying organic matter are various inorganic compounds (mineralization) used again by green plants to build their bodies. In an ecosystem there are primary producers (green plants), and secondary producers (unable to photosynthesis), among which one can distinguish primary consumers (phytophagous animals), secondary consumers (feeding on phytophages, or on other carnivorous animals), and finally destruents (living on dead bodies). The energy built in the organic matter has to be used for maintenance of living processess (metabolism), that is dissipating, and also to be built in the body or allocated into progeny. Thus, each consecutive (higher) level of the ecosystem structure achieves less energy than the preceeding one, because:

$P = C - (R+FU)$,

where: P – biological production (expressed in terms of biomass or energy units), C – consumption (energy consumed), R – respiration (energy lost for metabolic processes), FU – energy contained in feces and urine.

The studies on ecosystems in terms of energy transfer introduced a new methodology in considering any changes in objects of ecological investigations: This change relied on estimation of cumulative values as a contradiction to former comparison of the consecutive „snapshots” (e.g., the total consumption of food during life replaced former estimates of daily food consumption in chosen stages of individual life). It was the main scientific merit of the program. On the other hand, IBP lasted only a few years and, perhaps, it was to short time to induce serious controversies and discussions on the ideas of ecosystem, energy flow, or matter transfer. Similarily, the short life of the program resulted in estimates of only mean values and this did not allow for linking the former knowledge on population dynamics and dynamics of interspecific relations (e.g., competition) with new achievements in the area of biological productivity, though some attempts were presented (e.g., Myrcha 1975). The final result of the IBP was the knowledge on a very small proportion of solar energy reaching our globe that is utilized by land plants (approximately between 1 to 2 percent), and on high percentage of energy lost by each organism during metabolic processes necessary to maintain its life. An important effect of IBP was also a very extensive international co-operation between scientists involved in that program.

IBP was followed by another international program called MAB, this acronym standing for Man And Biosphere. The latter program was created due to increasing knowledge on the environmental changes induced by human activities, including unwanted effects of progress in civilization, such as rapid accumulation of pollution, contamination or destruction of natural habitats. MAB essentially can be considered as a prolongation of IBP: The basic unit of study were ecosystems and their vulnerability to human impact.

Nowadays, two topics have attracted attention of ecologists from many countries. One of them is due to common recognition of diminishing energy resources like petroleum and coal. Therefore, new sources of energy are sought, and among them the renewable energy sources seem to be most wanted. The energy of wind and water, the latter provided by electric power plants installed on big rivers, appear not only renewable but also clean, i.e., free from pollutants like carbon oxides or solid particles contained in smoke. Another renewable energy resource is biological production of plants: For instance straw can be used to heat houses, and grain is naturally important element in feeding humans and their farm animals.

There were expressed various opinions on international exchange of goods and import of energy resources from developing countries to highly industrialized ones. The question has been whether such international exchange promotes the development of the „source" countries or it is a form of exploitation of natural resources by those highly industrialized. Some scientists claimed that each country should use the sources of energy located within its borders, and such a policy would favour maintenance of balanced and reasonable use of natural resources.

The two last decades of the past century brought about the idea of sustainable development, and an organization called Worldwatch Institute has issued numerous volumes of the „State of the World". The basic idea of that Institute is to monitor the civilization progress and the accompanying changes in natural environment, with special attention to energy resources, human population growth, reduction of waste materials, recycling etc. Durning (1991) asked an important question: „How much is enough?". This was stimulated by enormously growing human consumption and doubts whether or not the earth can support that growth.

Another contemporary task that ecology has to face is preservation of biodiversity. The reasons for that are different, ethical (we cannot deprive future generations of the beauty of nature), genetical (diversity of genotypes is important for future use in agriculture, medicine etc.) or, ecological (biological diversity provides stability of ecosystems).

There is a long history of studies on biological diversity, starting with such questions like why there are so many species? Why various species in a locality are represented by different number of individuals? The latter question was asked and studied quantitatively very early, with a presumption that the reason was habitat conditions and environmental demands, different for separate species. Other hypotheses were also considered, like such exposing rate of colonization of a new environment (MacArthur and Wilson 1967), or the impact of interspecific competition that may eliminate some weak competitors by stronger ones (Schoener 1983). Later on methods of estimation of species diversity were proposed, and one of them originating in information theory has been commonly accepted. It is the Shannon-Weaver equation, and particularly its component called „eveness".

$H = -Sum^{s}_{i=1}\ p_i \log p_i$ ....(diversity index)
where: s – number of species, p_i – share of ith species in all s of them
$J = H/H_{max}$ ....(eveness)

Species diversity is a function of the number of species in a habitat. The eveness reaches its maximum when all the species are represented by the same number of individuals, that is the habitat is equally well suited for all the species living there. The eveness decreases when the species are represented by different number of individuals, that is the habitat is suitable for only one or a few of them (Fig. 4).

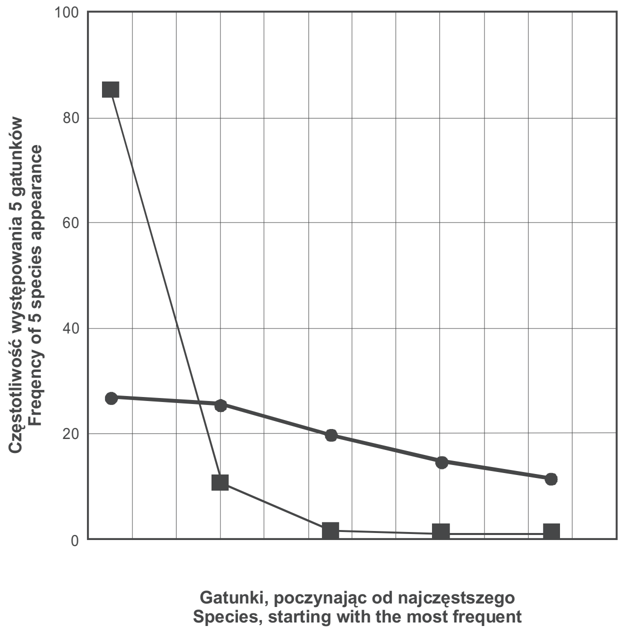

Fig. 4. Two hypothetical distributions of numbers in 5 species forming a community can illustrate the idea of biodiversity: In one distribution only one species is very numerous, and in terms of eveness it represents lower biodiversity (conditions are favourable only for that one), in another distribution all 5 species exhibit similar abundance (conditions are favourable for all of them).

Ecologists quarelled about the importance of diversity for ecosystem stability, understood as the intrinsic property of a system to withstand external disturbance and to recover from changes due to external factors. According to some of them (Dunbar 1960) diversed ecosystems, that is rich in species, are more stable than poore ones (having only a relatively small number of species). The argument was that elimination of a few species does not deprive functioning of a rich ecosystem, while it may destroy existence of a poor ecosystem. This opinion was, however, rejected by others (Wolda 1978) showing that the most rich ecosystems, like tropical forests in South America, are very vulnerable to clear-cutting: they never can be restored in the same shape.

Conclusion

The above short review of changing topics undertaken by ecologists since the invention of the word „ecology" shows that this branch of biology has always been stimulated by human needs. Besides, theoretical approach to the problems studied for many years underwent consecutive changes, shown for example in studies on population ecology. Another important aspect of ecological investigations is that this branch of biology has lately become part of global policy related to rapid growth of human population and its still growing demands.

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Ekologia: zmieniające się cele

STRESZCZENIE

Terminu „ekologia" po raz pierwszy użył Ernst Haeckel w 1869 r. Ekologia zajmuje się współzależnościami pomiędzy organizmami i ich środowiskiem i korzysta z dorobku wielu dyscyplin biologicznych (Fig. 1), a także innych nauk przyrodniczych i ścisłych. Przez wiele lat ważną częścią ekologii były badania nad populacjami, zwłaszcza zwierząt i ludzi. Należy tu wymienić modele wzrostu populacji proponowane przez Malthusa i Verhulsta (Fig. 2), które do chwili obecnej stanowią istotną część podręczników ekologii populacyjnej. Jednakże, w tej dziedzinie ekologii w ostatnich 50 latach zaszły istotne zmiany: odrębny problem stanowią badania nad stabilnością metapopulacji (Fig. 3), a w teorii pojedynczej populacji znaczną uwagę przykłada się do właściwości osobników, ich płci, wieku, sąsiedztwa i innych cech indywidualnych.

Szybki rozwój cywilizacyjny i powstanie społeczeństw konsumpcyjnych stanowią źródło zmiennych celów jakim stawić musi czoło także wiedza ekologiczna. Począwszy od lat 60-tych ubiegłego stulecia zarysowała się międzynarodowa współpraca naukowa w ekologii: powstawały takie projekty jak Międzynarodowy Program Biologiczny ukierunkowany na określenie środowiskowych warunków maksymalizacji produkcji biologicznej, czy też program pod nazwą Człowiek i Biosfera – odpowiedź na narastającą degradację, zanieczyszczenia i zatrucia naturalnego środowiska.

Współczesne zagrożenia ekologiczne to narastająca eksploatacja naturalnych zasobów, zwłaszcza kopalnych źródeł energii, oraz zubożenie zasobów biologicznych wyrażające się zmniejszeniem różnorodności biologicznej (Fig. 3). Współcześnie usiłuje się odpowiedzieć na pytanie jak poradzić sobie z rosnącą konsumpcją: jakie zużycie zasobów umożliwia obecny stan naszego globu?

Z niniejszego, krótkiego przeglądu wynika iż rozwój wiedzy ekologicznej jest stymulowany potrzebami ludzkiej populacji, a ta wiedza stała się argumentem w prowadzeniu globalnej polityki rozwoju społeczeństw i ich przyszłości.