

Exploitation of common resources – simple reasons to be different

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Abstract. Intraspecific competition in even-aged populations of plants and animals is very rarely the subject of ecological research. Even more rarely are ecologists interested in the important outcomes of this competition - the unequal partitioning of resources for which competition takes place and the resulting from it individual variability in the growth rate of individuals, their survival rate and the production of offspring. There are various reasons for this. The statistical methods used by ecologists deal with average values. Classical models of mathematical ecology describe the dynamics of the densities of populations, and are therefore interested in variables that by their nature neglect the important fact that a population is made up of individuals. It is also not without significance that it is generally very difficult to study interactions between individuals. The present study aims to discuss some very simple examples of how individual variability in the amount of resources taken up by individuals from the environment can arise because of the physical nature of these resources, without considering interactions between individuals. Three examples will be presented: individuals of a phytoplankton species that move chaotically in a column of water illuminated from above, sedentary organisms randomly distributed on a two-dimensional plane, and predators hunting for food in the form of particles. In all these examples, the measures of resources obtained by individuals indicate the existence of individual variability, and their distributions have a positive skewness (there are more individuals that obtained few resources than individuals with many resources). The influence that the costs of obtaining resources from the environment and interactions between individuals may have on such form of individual variability will be discussed also.

Key words: intraspecific competition, individual variability, resource partitioning.

Introduction

In ecological bioenergetics, there is an established scheme for representing the energy balance of an individual (Duncan & Klekowski, 1975). It looks like this. Let C denote the amount of resources brutto (usually measured in energy units) taken by an individual per unit of time from the environment. This is the so-called consumption rate. If we subtract from C the amount of energy excreted by the body in a unit of time in the form of undigested residues, we get the so-called rate of assimilation denoted by A . This is the energy

available per unit of time that the body can use for various life functions, such as, for example, growth and reproduction. However, the implementation of these vital functions requires energy inputs. We usually measure it by the body's respiration rate and call it the respiration rate R . Only now can we write an equation showing how much net energy the body has to perform vital activities. We will denote it by P and call it the rate of production. It is described by the following equation:

$$P = A - R . \quad (1)$$

By conducting a large number of experiments, ecologists learned what are the rates of C consumption, A assimilation, R respiration and the related rates of body weight change and offspring production for many animal species. However, almost all of these experiments were conducted firstly in the laboratory and secondly according to one of two schemes. Either the energy balance of a single organism was examined, or the total values of energy balance parameters for a larger number of individuals were examined, the results were then averaged by dividing the obtained values of energy balance parameters by the number of individuals participating in the experiment. In this way, for example, the dependence of the rate of consumption and assimilation on the amount of resources available in the environment was discovered, which, as it turns out, can be described by the equation proposed by Ivlev (1961) or the dependence of the rate of respiration on temperature (Ivleva, 1981).

In the last two decades, the so-called individual-based approach to modeling the dynamics of ecological systems has been developing very intensively (Uchmański & Grimm, 1996, Grimm & Railsback, 2005, Railsback & Grimm, 2012). It consists in a mathematical description of the fates of individuals in the population. As stated earlier, the production of P can be used by the organism to grow Δw and

produce offspring E according to the following equation:

$$P = \Delta w + E . \quad (2)$$

Thus, if in the individual-based model we want to describe the fates of individuals in the population, their growth and then the production of offspring, the question arises about the individual variability of energy balance parameters. More formally, the question can be presented as follows. Let there be N individuals in the even-aged population. Consider two different individuals with the numbers i and j ($i \neq j$). Let us denote the assimilation rate of the first one by A_i and the second one by A_j . If these individuals use common resources, their rates of assimilation can be different:

$$A_i \neq A_j \quad (3)$$

or equal

$$A_i = A_j . \quad (4)$$

Models

Phytoplankton in a light gradient

The space is a two-dimensional plane vertically positioned and illuminated from above. N phytoplankton cells are randomly distributed on the plane in the initial time step. At each time step, each cell rotates a random angle from 0° to 360° and takes one space step forward. This mimics the random movements of cells moved by thermal movements of water in the upper layer of the water column illuminated from above.

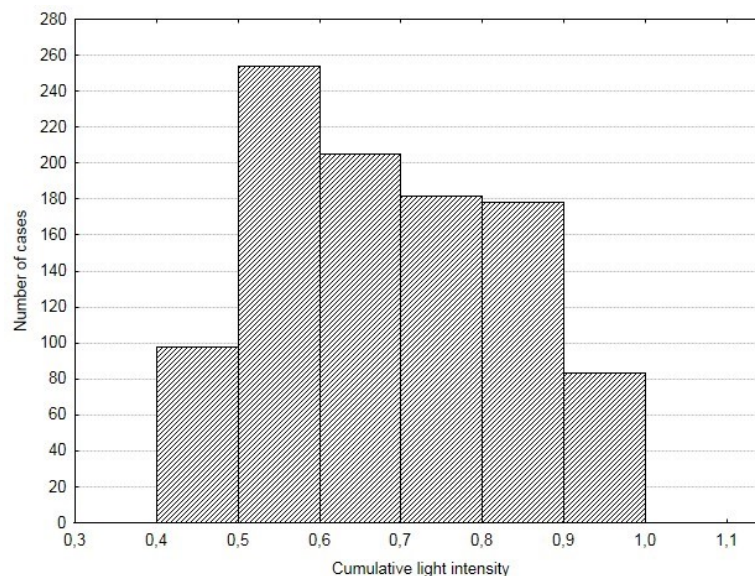


Fig. 1. Distribution of cumulative light intensities for $N = 1000$ and one thousand time steps. $I_{max} = 100$ and $\varepsilon = 0.01$. The relative values of cumulative light intensities in relation to the maximum value obtained by phytoplankton cells are plotted on the horizontal axis.

After the particle has made its move, at each time step, the light intensity that the phytoplankton cell encountered at the point where it found itself is recorded. It depends on the distance of the current cell location from the top edge of the space according to the equation:

$$I_i = I_{max}e^{-\varepsilon z_i}, \quad (5)$$

where I_{max} is the light intensity at the top edge of the space, ε is the light absorption coefficient, i is the cell number, I_i is the light intensity currently touched by the i -th cell located at a distance z from the top edge of the space. At each time step, calculations were performed for each cell according to equation (5), and the results were added to the individual history of light intensities that each cell encountered during its movements in subsequent time steps.

Fig. 1 shows an example of the distribution of cumulative light intensities for a thousand of cells moving randomly for a thousand time steps in a light gradient. A similar distribution would be obtained if the space in which the cells move was a one-dimensional vertical gradient of light or a three-dimensional volume illuminated from above.

Sessile organisms randomly distributed on a surface

Sessile organisms live on a flat two-dimensional surface. It has been divided into many square cells of equal size that cover the entire surface. Sessile organisms were randomly distributed on this surface. This was done in such a way that the x and y coordinates of the cells in which the organism could possibly settle were selected from appropriate uniform distributions. It was also done in such a way that no more than one organism could get to one cell. The living conditions of organisms are determined by the distances to the nearest neighbors, which are measured in the number of cells sharing the location of the neighbors.

Fig. 2 shows an example of such a situation. The space was divided into 900 cells. On such an area, 200 individuals are randomly distributed. Many cells are left blank. The living conditions of each individual were determined by the sum of the distances to neighboring individuals.

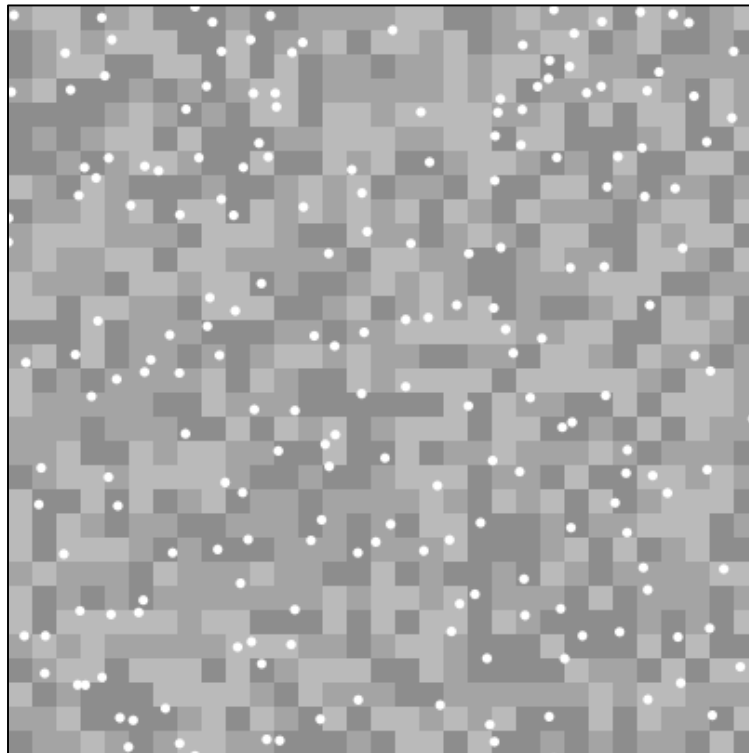


Fig. 2. Illustration of a surface divided into square cells. Various shades of gray have been used to show the cells, but these colors have no other meaning. There are 900 cells. The white dots represent 200 sedentary organisms randomly distributed across the surface. There can be at most one organism per cell.

Fig. 3 shows the results of two ways of calculating the cumulative distance to neighbors. Fig. 3A shows the distribution of cumulative distances to neighbors when only neighbors that

are within one cell distance were counted. In contrast, for the results shown in Fig. 3B, neighbors that were two cells apart were also counted.

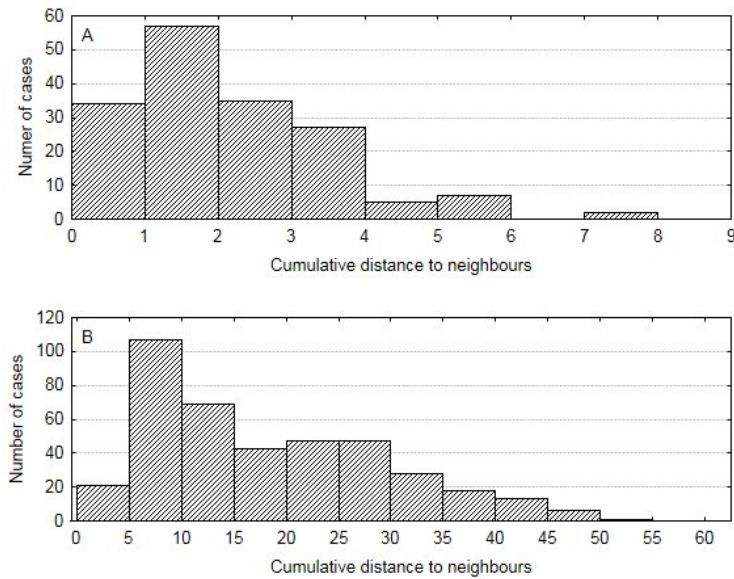


Fig. 3. Distributions of cumulative distances to nearest neighbors for 200 organisms randomly distributed over a surface of 900 cells. A - neighbors at a distance of at most 1 cell were counted. B - neighbors within 2 cells or less were counted.

Predators

The prey of a predator is particles. The predator has a probability p of catching a food particle. Simulations were carried out for 100 predators, each of which conducted 100 hunts. The results were illustrated with distributions of the number of food particles caught. Fig. 4A shows the results for $p = 0.1$, Fig. 4B for $p = 0.2$, and Fig. 4C for $p = 0.5$.

Calculations were also carried out for a situation where there are two species of prey particles in the environment. The probability of catching one is p_1 and the other is p_2 . Fig. 5 illustrates the two-dimensional distribution of the number of caught particles of both types by, as before, 100 predators in 100 hunts for each particle type.

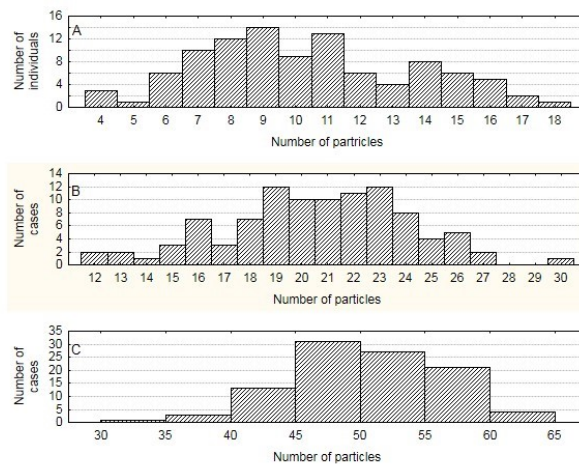


Fig. 4. Distributions of the number of particles caught by 100 predators, each of which made 100 hunts for different values of the probability p of catching a food particle. A - $p = 0.1$, B - $p = 0.2$, C - $p = 0.5$.

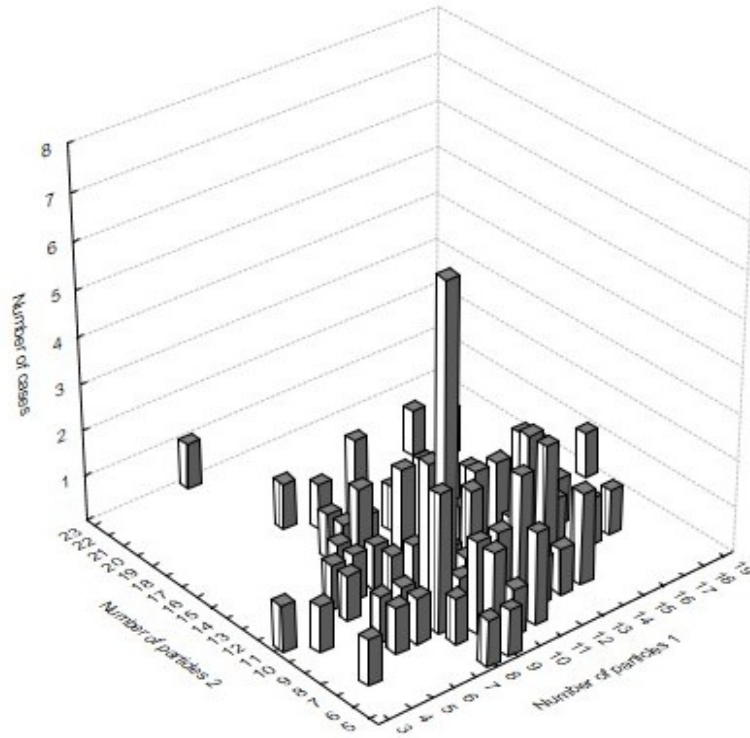


Fig. 5. Distributions of the number of caught particles of two types. In this example, there were 100 predators, each of which made 100 hunts for each type of prey. Calculations were made for $p_1 = 0.1$ and $p_2 = 0.1$.

Discussion

In theoretical ecology, when analyzing the causes of the observed phenomena, the so-called neutral or null models and hypothesis are often used (Hubbell, 2001; Chave, 2004; Leight, 2007). They are used to indicate random or non-biological factors that may cause the appearance of certain features of ecological systems. Typically, null models assume that there are no ecological interactions between the components of the system. Only in the next step are the modifications introduced to the behavior of the system by the above ecological interactions analyzed.

The examples presented in this paper are just such null models. They show that individual variability in the amount of resources acquired by individuals takes place and may result from the nature of the environment in which individuals live and the nature of the resources needed for them. Very general characteristics of the way of life of individuals common to all individuals in the population are also important, such as whether individuals are sedentary or moving in the environment. In the case of the latter feature, a distinction can be made between active and passive

movement. However, none of the examples above assumed the existence of ecological interactions between individuals consuming resources.

From a formal point of view, the models presented here are of two categories. Some of them, such as the description of the chaotic movement of phytoplankton cells in water, or the random distribution of sedentary organisms on the surface, require the construction of a simulation model. It allows the biological specificity of the problem to be taken into account, but the results are limited to the very specific values of the parameters used in the simulations. Additional analyzes need to be performed to make the results more general. The second category of models uses very well known facts in mathematics. The fact that a predator can be characterized by the probability of prey capture, and this is the fate of every predator regardless of its species, automatically causes that the distribution of the number of particles caught by predators will be a binomial distribution. On the other hand, in the case of two types of victims, it will be a polynomial distribution. Both of these distributions have features well known to mathematicians and an analytically

written formula describing their shape, which allows ecologists to make a very general statement about the results of such a predatory lifestyle.

Intraspecific competition in the above null models would be that ecological interaction that modifies the outcomes of resource partitioning between competing individuals. The result of such interactions may be correlations between the parameters of the individual's energy balance, such as the rate of assimilation and respiration. In the case of a positive correlation between the rate of resource assimilation and the rate of respiration, which in this case means the costs of obtaining resources, we will observe a decrease in individual variability in the amounts of resources obtained by individuals. There are documented examples of territorial fish species (Yamagishi et al., 1974), whose individuals feed on organic particles falling on the surface of the water. Individuals with the largest territories have the highest rate of resource consumption, but also the highest costs of maintaining these territories. As a result, they are not the heaviest individuals. In the case of a negative correlation between the rate of assimilation and the rate of respiration, the opposite effect can be expected - the individual variability in the amounts of assimilated resources will be greater.

The unequal distribution of resources as a result of intraspecific competition between individuals of the even-aged population sharing common resources is rarely of interest to ecologists. One can, of course, have some qualitative ideas about the situation here, which seem to be true not only in the case of ecology, but also in economics, or even in everyday life: if competitors interact with each other many times, then whoever obtained more resources in the past will also get more of them in the future. However, it is difficult to translate this general, qualitative principle of competition into a quantitative relationship that could be used in a mathematical model.

The only known indirect way of inferring the distribution of resources between competing individuals is by analyzing the shapes of weight distributions in even-aged populations of plants and animals. It shows that these distributions have positive skewness (Uchmański, 1985). This means that individuals with small weights predominate in an even-aged population. The number of heavy individuals is small. This

skewness increases as the number of competitors increases and the amount of resources in the environment decreases. Thus, factors that increase the intensity of intraspecific competition will also increase the weight differential of competing individuals. One may ask what should be the distribution of resources between competing individuals in order to obtain the above shapes of weight distributions. It turns out that this requires an unequal distribution of resources and an increase in these inequalities with increasing intensity of competition, for example caused by an increase in the number of competitors or a decrease in the amount of resources (Uchmański, 1987; Uchmański & Dgebuadze, 1990). Note that these features have already been revealed in one of the null models presented in this paper. Fig. 4 shows that the low probability of catching a food particle increases the skewness of the distribution of the number of food particles caught. However, when this probability is higher (e.g. equal to 0.5), the distribution becomes more symmetrical.

Only one example of the null model is known, which shows that under certain conditions an equal partitioning of resources between individuals using common resources is possible. This is an example from the category of models describing the so-called ideal free distribution of individuals (IFD - Fretwell & Lucas, 1970; Weber, 1998). Imagine individuals of herbivorous zooplankton actively moving in the water column. The light comes from above. Therefore, in the water column we have a food gradient that decreases with depth, which is, for example, phytoplankton. If we assume that this gradient is discrete (that is, the depth is measured with a constant spatial step and in each depth interval the amount of food is constant, although it decreases exponentially with depth) and within each depth interval the distribution of resources between individuals is equal, then freely moving individuals can always be distributed in this gradient in such a way that each individual in the entire gradient will have the same amount of food (Maszczyk et al., 2018).

Conclusions

Nature is diverse in many aspects. This diversity is usually treated as a kind of noise that needs to be removed in order to get to the heart of the matter. This is what theoretical ecologists do

when they build models of population density dynamics. Field ecologists and experimenters do the same when they study differences in mean values. The so-called individual-based modeling in ecology, which has been developed in recent decades, opens the door to the introduction directly to ecological considerations of individual variability in features important from the ecological point of view. As the examples presented in this work show individual variability in the amount of resources obtained from the environment will appear even without interaction between individuals. It is the result of the physical characteristics of the environment, resources and general characteristics of the behavior of individuals common to all representatives of the species. Interactions between individuals can only add a new dimension to such individual variability.

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