

Density or variability: is it time for a paradigm shift in ecology?

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Abstract. In ecology, the paradigm of density is commonly used. It is used to construct mathematical models and to plan and interpret ecological experiments. This leads to mathematical models using differential equations in ecology. It seems, however, due the fundamental discontinuity in ecological systems, which appears in the form of discrete individuals in the population, we should use in models of population dynamics a paradigm that speaks of the variability of these individuals and the discontinuity of basic demographic processes in populations. This should result in the further development of individual-based modelling in ecology as well as the development of experimental individual-based ecology. The paradigm of dependence on density in a slightly altered form and the assumption of the continuity of ecological processes can continue to be used in those branches of ecology that deal with the cycling of matter and the flow of energy through ecological systems.

Key words: population density, density dependence, individual variability, individual-based models, individual-based ecology.

1. Introduction

There are two ways of learning about nature in the natural sciences (Heller & Życiński, 2010; Lemańska, 2001, 2013). One of them is to observe and experiment with nature. The other is to build mathematical models of natural phenomena and processes and then to study the properties of such mathematical structures. They are not indifferent towards each other. They complement and strongly influence each other. Experiments are used to verify the mathematical models, and the theoretical generalisations formed on the basis of mathematical models strongly influence the interpretation of the results of observations and experiments. In different natural sciences, there are different accents between these ways of learning about nature. In physics, both ways of understanding inanimate nature work together (Tegmark, 2014). That is why physics can boast of great achievements in building theories well verified through experiments (Wigner, 1960). In biology,

things are different. Experiments rule here, and the theory, in the sense in which it occurs in physics, is underdeveloped and even less bounded by the rules of mathematics. That is why biology is still the science of details above all. Let us take a closer look at these problems using the example of ecology and try to show the way out of this state.

2. Ecology

In ecology, two categories of processes and phenomena are considered (Golley, 1993). These are either processes and phenomena related to the dynamics of populations forming ecological communities or the processes of the cycling of elements or energy flow through ecological systems. These two categories are, of course, interlinked and represent two sides of the same coin. Both are also important in explaining the fundamental question in ecology: the causes of biodiversity and its persistence.

Ecology is, above all, an experimental science. It is filled with content that comes from experiments and observations of nature. An ecologist performing an experiment is generally free to choose what kind of results they want to obtain within the experiment and what they want to observe. However, the design phase of the experiment, observation and especially the interpretation of their results are burdened with certain ecological thinking patterns. These patterns are particularly evident when one enters the area of so-called theoretical ecology, which uses mathematical models. It should be stressed that these thinking patterns were shaped in the first decades of the last century and have taken root in ecology very strongly. There are no signs that ecologists are beginning to see the need to look at these standards of thinking in ecology developed by mathematicians with a certain distance.

3. Ecological paradigms

What are these thinking patterns? First, it is the belief that the course of ecological processes depends on the density (Andrewartha & Birch, 1954). Density is understood by ecologists as the number of individuals per unit of space where they live. Because the density is determined by calculation and not by direct measurement, it is a real number. This scheme is used primarily to interpret the results of experiments and observations of this category of ecological processes and phenomena, which concern the dynamics of populations forming ecological communities (see for instance the theory of population regulation (Tamarin, 1978)). It also occurs when ecologists analyse the processes of energy flow and circulation of elements in ecological systems. The second thinking pattern is the belief in the continuity of ecological processes (Komarov, 2007). It is also used to analyse the results of experiments and observations in both categories of processes and phenomena studied in ecology, although the nature and origin of this thinking pattern is different from the first one and its justification is also different. The intensity of the use of this pattern in both areas of ecology is also different.

Those who were the first to try to build mathematical models of ecological processes are to blame for introducing these thinking patterns, namely, Vito Volterra and Alfred Lotka, as long as we concentrate on the most prominent names (Kingsland, 1995). They used the density concept as a state variable in simple mathematical models describing the dynamics of two interacting populations (Volterra, 1931; Maynard Smith, 1974; Bazykin, 1985; May & McLean, 2007). From a mathematical point of view, these were quite simple systems of two differential equations. I do not suppose that this was due to a deep knowledge of ecological processes.

Mathematical methods were used, which were the closest at hand and, at the same time, known to mathematicians for centuries, with a well-known mathematical apparatus needed to analyse the properties of their solutions. Such a way of proceeding was the simplest solution when mathematicians were requested to build a mathematical model of the dynamics of ecological systems. However, I believe that this occurred at the expense of the quality of these models (Grimm & Uchmański, 1994). It also had very far-reaching consequences. The second thinking pattern, namely, the conviction of the continuity of ecological processes, both when we are talking about the dynamics of numbers (or, in fact, the dynamics of density) and about the circulation of elements and the flow of energy, was a natural consequence of the use of such and not another mathematical apparatus. Later, also difference equations appeared in the description of the dynamics of ecological systems (May, 1976; Sharkovskij, 1983), but it was still the same thinking patterns: population density as a state variable, although its value was given in discrete time steps.

4. Reasons for ecological paradigms

Why have both of these schemes taken root in ecology and are still in force to this day? First, they were well-known mathematical methods with a very good apparatus used to analyse their properties. Moreover, the apparatus was used with great success to describe the course of physical processes. One should remember that a large proportion of those who introduced mathematical methods to ecology were physicists. Second, it happened that the results of the first mathematical models used in ecology qualitatively fit very well with what experimental ecologists had been knowing for a long time. The model describing the dynamics of two competing species illustrated the principle of competitive exclusion and, in turn, the model of the predator-prey system typical of this system oscillations of the densities of both species. Whether this was a proof of the correctness of these models, or rather a coincidence, it is hard to say. However, it was undoubtedly of great importance for the success of this approach in the eyes of ordinary ecologists unfamiliar with the possibilities of mathematical language. Third, it should be mentioned here that it is difficult for ecologists working with living nature to assess the correctness and importance of this approach proposed by mathematicians and physicists because traditionally then, and even today, the education of ecologists does not include a serious and systematic study of mathematics, such as, for example, at the level of physics students. The fact that among ecologists there has always been a tendency to generalise and construct verbally theories is also not without significance. The abovementioned models provided very illustrative grounds for this.

5. Consequences of ecological paradigms

What conclusions on the nature of ecological systems and their dynamics have therefore been reached by ecologists with the abovementioned mathematical basis? In the theory of dynamic systems, which is primarily used in theoretical ecology, the types of dynamics that are the solutions of differential equations or their systems have long been known. Such dynamics has also been attributed to ecological systems. The most important conclusion, which left its deepest mark on the thinking of ecologists, was that many dynamic systems are characterized by singular points and asymptotic stability. This type of dynamics has started to be attributed to ecological systems by ecologists. A certain concern of ecologists was aroused by the possibility of emerging deterministic chaos, which was observed in some solutions of difference equations, but this fact, years after mathematicians discovered this phenomenon, left only a marginal trace in ecology. This whole range of possible types of dynamics, but also the fact that what was observed was population density and what caused such changes in density were different types of dependence on density, mainly of average rates of reproduction and mortality, were used in the past and are still used by ecologists to analyse the dynamics of real ecological systems.

6. Validation of ecological paradigms

Let us draw our attention at this point to an essential fact, which makes it very difficult to verify the theoretical deliberations. The point is that ecologists have very limited experimental material concerning the dynamics of ecological systems. Our perceptions of dynamics of the system of two competing species and the dynamics of the predator-prey system come almost exclusively from laboratory experiments on microorganisms, for which the duration of generation is so short that they can be observed under controlled conditions for long enough. There are, of course, some well-known exceptions, such as indirect information on the dynamics of lynxes and hares, compiled on the basis of the number of skins of these animals bought by the Hudson Bay Company at the turn of the 19th and 20th century, or statistics on the number of *Homo sapiens* worldwide. However, they do not contribute much to understanding the nature of the dynamics of these systems.

Let us try to assess the validity of the thinking patterns that classical theoretical ecology has imposed on ecologists. It is necessary to start the argument by considering the issue of the continuity of processes in ecological systems. We have previously said that ecology uses two ways of describing the dynamics of ecological systems: through

the cycling of elements or energy flows through ecological systems or through the dynamics of the populations that form them. In the latter case, the thinking patterns in force in ecology have imposed on ecologists the need to use population density, not population number. It seems that the assumption regarding the continuity of ecological processes is justified in the former case, that is, when we build a mathematical description of the circulation of elements or the flow of energy through ecological systems. Let us imagine the lake ecosystem and the cycling of an element within it. This element, dissolved in water in various forms, flows with the waters of the river that feed the lake, it flows with rainwater from the area surrounding the lake, and there may also be air transport of this element. All these processes are constantly taking place with different intensities. At times, it may be zero, but the real function equal to zero can also be continuous. In water, the element participates in biological transformations. They are the result of the activity of the species inhabiting the lakes – the uptake of this element by organisms and also its partial excretion. Since these processes are described on a lake-wide scale, in other words, we are building a mathematical description of the activity of all organisms at the same time, the course of these processes is continuous, even though the activity of individual organisms consists of them. The state variable in the model using differential equations will in this case be the elemental content of particular compartments of the lake ecosystem. If the system is well mixed or we are using partial differential equations, it may even be the concentration of this element variable in time and space, which is something that, from a formal point of view, resembles a population density because the latter is a concentration of individuals in space. A similar argument to the one presented above can also be used for other ecological systems, for example, the soil or even the whole biosphere.

Things are different in regard to building mathematical models of dynamics of populations composing the ecological system. In this case, we should question the validity of the assumption about the continuity of processes influencing population dynamics, as well as the advisability of using density as a state variable, and in principle, we should also deny the correctness of the use of mathematical methods derived from the arsenal of dynamic system theory.

In the case of population dynamics models, discontinuities are revealed at several levels. First, and this is the most important cause of discontinuity, the studying population dynamics means counting the individuals, and the individual is by its nature a discrete unit. The question arises as to whether population density, i.e. the average number of individuals per unit of space, can replace consideration of the fates of individuals in demographic analysis. I think not. The basic argument is that, when we look at the nature

around us, we can easily notice that individuals are variable. This variability is formed of several components. First, the features of an individual are not constant over time. They change as the age of an individual changes. The individual is born, grows, undergoes different stages of the life cycle, reproduces, and finally dies. They pass these life stages most often not synchronously. Second, so-called individual variability occurs. This means that individuals of the same age and sex will be different. These differences may be the result of accidental events in an individual's life or genetic differences between individuals, but most often they are the result of different kinds of ecological interactions between individuals, among which intraspecific competition probably plays important role.

7. Variability as an ecological paradigm

Intraspecific competition is associated with an uneven distribution of resources among competing individuals (Łomnicki, 1988), as there is no reason to expect competing individuals to share resources equally or according to needs. It is usually the case that an equal distribution of resources or a distribution according to the needs of individuals occurs when there are sufficient resources to meet the demands of each of the individuals in a population. However, when there is a shortage of resources, and with such a situation each individual has a chance to meet sooner or later in its life, then some individuals get more, others get less, and still others get nothing. The uneven distribution of resources may also be the result of the physical conditions in which the individual lives. For example, the seeds distributed randomly on the soil surface are transformed into plants, each of which has different neighbours at different distances. This creates different growth conditions for each of them (Harper, 1977). Similarly, the individuals of all predatory species have only a certain chance of catching their prey in a single hunting act. If the hunt is repeated many times, even if each individual has the same chance of catching its prey in a single hunt, the cumulative success of each individual will vary (Feller, 1961). In fact, in most cases, predators will also differ in the probability of catching their prey, which may depend, for example, on the number of prey they have previously caught.

Differences in the quantities of resources obtained by individuals will translate into differences in the rate of growth of the individuals, their weights at maturity will vary, and consequently, the number and quality of offspring produced by these individuals will also vary (Koyama & Kira, 1956; Obeid et al., 1967; Ogden, 1970; Weiner, 1985; Weiner & Thomas, 1986).

If, therefore, we allow for discontinuities in the form of discrete individuals in our considerations of the dynamics

of the populations, then immediately their variability becomes a key problem. Imagine that the amount of available resources is decreasing. This may be due to their exploitation by individuals. Let us start with a population of identical individuals. Generations do not overlap. Identical individuals share resources equally. So long as there are enough resources for the individuals to reproduce, their progeny will form the next generation. Let us assume that, at the beginning, there are enough resources that each individual can produce three offspring, and then only two. In both cases, the population will grow. As resources continue to decline sooner or later, there will be such a quantity of resources that the production of the offspring of each individual will fall to one offspring. Then, the population will remain constant. With a further decline in resources, it may turn out that none of the individuals (they are identical) will be able to produce even one offspring. Population goes extinct. Let us note that although there are no individual variability in this example, the assumption of individual discontinuity remains valid. Its consequence is that we are using natural numbers. The size of the population, and the number of offspring produced by an individual are natural numbers.

The population composed of variable individuals will behave in a different way in a crisis of lack of resources (Uchmański, 1999, 2000a). If the majority of individuals are unable to produce even one offspring, there is a great chance that there will be at least one individual in the variable population who will be able to do so. All that is necessary is for the individual variability to be large enough. The population will last. However, because it is small at times of demographic crisis, the resources will have time to recover, and the population cycle will start again. We will have cyclical increases and decreases associated with similar resource dynamics in the case of variable individuals, while in the case of identical individuals we will see an initial exponential population increase and then the extinction of the population.

Are classical population dynamics models that use population density as a state variable able to make allowances for these effects? I guess not. Population density can always be calculated in any situation and for any population if we develop an appropriate method for counting individuals per unit of space. It is also possible to correlate this density with other population characteristics, such as population average offspring production or average mortality. We will certainly find that these correlations are statistically significant. However, this does not mean that it is a mechanism that drives population dynamics. Classic models of population dynamics are created when these correlations or regressions, and therefore statistical rather than causal dependencies, are converted into continuous functions and thus treated as causal dependencies. Therefore, are the dynamics they

produce compatible with population dynamics that take into account individual variability? Neither is it. Moreover, the classical models of population dynamics cannot be used for those populations for which unique density cannot be calculated. These include those populations whose individuals lead sedentary life. All terrestrial plant species have to be included in this category because, in their case, the local density value is very variable in space (provided that we do not deal with plantations) and does not agree with the globally calculated population density value. If we consider individual variability, it is easy to construct a computer algorithm to describe the structure or dynamics of such a population, and indeed, in ecology, such models have been constructed many times (*e.g.* Wyszomirski, 1983). In the past, classical models of population dynamics have been applied to all other populations on the assumption that individuals in a population are well mixed and that population density reflects the ecological situation in that population well, thus neglecting the essential fact for the functioning of ecological systems that individual variability exists.

This neglect of ecological reality and details in the case of classical population dynamics models is particularly evident in the logistic equation. Its solution has become an ecological benchmark of single population dynamics. There are no directly introduced resources in this equation, which gives rise to the mistaken belief that it will be possible to use it for any kind of resource. Therefore, the dynamics produced by this equation – an initial increase and then a population density set at a certain fixed value called carrying capacity – are considered to be typical of each single population dynamics. This is not true. The right-hand side of the logistic equation is constructed in such a way that it actually describes a situation where individuals in a population use a resource such as a space that is filled by individuals up to the capacity limit of that space. This effect appears in explicit form in models that take into account individual variability and are built for populations of sedentary organisms, for example, in forest stand dynamics models. We already know that classical population dynamics models cannot be used in this case. The solution to the logistic equation cannot be a standard for the dynamics of a single population because the kind of resources used by individuals in a population can vary greatly. It is possible to build a classical model of population dynamics, in which resources of renewable type are introduced directly, so that we do not make the mistake of a logistic equation. We will then obtain population density oscillations, but we will not obtain effects characteristic for an approach that takes into account the different degrees of variability of the discrete individuals.

8. Consequences of paradigm change

The postulate to change the paradigm in ecology from looking for dependence on the density of important ecological processes to studying the variability of basic objects – individuals – that create ecological systems and drive their functioning, requires thinking about two problems. First, what mathematical instrument should be used to build mathematical models of the dynamics and functioning of such perceived ecological systems? Second, do we have sufficient information from experiments and observations to support the construction and validation of such models?

In view of what has been said above, where we are dealing with the dynamics of populations forming ecological communities, the traditional mathematical approach, *i.e.* differential and difference equations, including density as a state variable, should be abandoned. The nature of the phenomena associated with these processes boils down to the recognition of the important role of individual variability, and this in turn entails the need to follow the differential fates of individuals. This perception of the role of mathematical models in ecology is what the so-called individual-based approach has been advocated since the early 1990s. A closer look at the methods used in the individual-based models allows for an important generalisation concerning the mathematical nature of ecological processes and ecology in general. When we talk about the essence of that part of nature that is dealt with by physics, we talk about its mathematical nature or mathematicity, understanding under this term that we can study the nature of physical processes and phenomena by analysing the properties of the mathematical structures that describe it (Heller, 2014). In this sense and with such a mathematical apparatus, which was mostly developed for the purposes of physics, we cannot talk about the mathematicity of that part of living nature that is dealt with by ecology. Living nature exists and functions in a form of individuals, and the life of each individual is the realisation of a certain algorithm. Therefore, we should rather talk about the algorithmicity of living nature (Uchmański, 2020a).

Since the first individual-based models appeared in ecology, their number has increased prodigiously. At the end of the 1990s, it was possible to review them and write a review article (Grimm, 1999) and books (Grimm & Railsback, 2005; Railsback & Grimm, 2012) summarizing the achievements in this field to date. There was also a postulate to create a uniform standard procedure for the construction of individual-based models and for the unification of their description in the form of the so-called ODD protocol (Grimm *et al.*, 2006), so that it would be possible to recreate the model by a person who is not its

author. Today it would be impossible to discuss all efforts in the field of the construction of individual-based models. The basic problem boils down to the fact that what we find now in the ecological literature are detailed simulation models of individual phenomena and processes (DeAngelis & Grimm, 2014). With the great diversity of nature, the possibilities in this respect are virtually limitless. However, there is a lack of order in all these attempts. It makes impossible to generalise and formulate more general hypotheses or theories on this basis. This greatly weakens the position of the individual-based approach in relation to the traditional view of these problems, where the density-dependent paradigm is well established and provides a general view of ecological problems.

As mentioned above, the paradigm focusing on individual variability simply justifies the need to apply individual-based models in ecology where we are dealing with population dynamics. The way in which these models are built makes a comparison with mathematical objects known as fractals (Uchmański, 2020b). They are very complex and irregular geometric structures when we consider them as a whole. It is difficult for us to understand principles according to which they were created. However, fractals can be built in a very simple, even boring, way. A fractal is a complicated geometrical structure because it is created by repeatedly adding a small and simple geometrical element called a module to an already existing structure (Prusinkiewicz & Lindenmayer, 1990; Kaandorp, 1994). Things are similar in ecology. We have modules – individuals, we know their characteristics and interactions between them. From these modules, we form a population. The emerging image is complicated, as there are many modules. It is difficult to understand how nature works when we look at it as a whole. However, we can do the same as in the construction of fractals, where different modules repeatedly iterated give different structures at the end of this process. We can build typical models for typical ecological situations from individuals. These must be subject to experimental verification, but let us leave it to the ingenuity of the experimental ecologists. We cannot naively expect one equation – let us say a logistic equation – to describe all single populations. We are working with an object whose basic feature is diversity. For different species, for different ecological groups, and for different ecological situations, we will have different models. From them, it will be possible to describe a larger whole and understand how it works. We need to look for typical patterns in nature, which will serve to verify the models built in this way (Grimm et al., 1996; Grimm et al., 2005).

9. Experimental ecology of individuals

The first step in putting these matters in order would be to refer to the experimental side of this problem. We know very little about the ecological aspects and ecological effects of individual variability because, by removing it from the scope of their interest as something disturbing, we do not see it. The blame for this state of affairs probably lies in the methods of statistical processing of experimental data, which are widespread in ecology and consist mainly of comparing average values. If it were to be customary in ecology to use statistical methods that involve examining confidence intervals (Altman et al., 2000), perhaps the situation would be different. The subject of experimental ecology of individuals should concentrate on the ecologically important characteristics of the individuals, taking into account their variability and the influence of interactions between the individuals on individual variability. Contrary to the appearance, this is not a very wide range of issues. After all, each individual does the same thing: it is born, grows, reproduces, and then dies. During its life, it has to deal with other individuals of the same or different species. Their presence usually disturbs them, but sometimes this fact is helpful. The individual is using the resources of the environment to develop and reproduce. The presence of other individuals forces them to share these resources with others. All of these are ecological processes, in the diversity of which we should seek order, be able to catch the similarities and differences, despite their great diversity at first glance.

I believe that such classification, the search for differences and similarities, is possible to apply. For example, we have individuals who lead a sedentary life and who move relative to the environment. This fact alone in each of these categories means that there are great similarities in the nature of the interaction between individuals, whether they are trees or hydroids on the one hand, and plankton-eating fish and, for example, insect eating lizards. Individuals can compete globally or locally. Those who lead a sedentary life do so locally, competing only with their nearest neighbours. We also have unitary and modular organisms, with different types of growth, as well as those with simple and complex development. This classification should also take into account the dimensions according to which the resources needed for individuals can be classified. We have resources that are well mixed and continuously present in the environment or distributed on islands. Resources and the individuals using them can roam freely within the environment, but it is also possible that the individuals live inside spatially limited resources, as is the case with insect larvae that feed inside the fruit. Resources can also exist in the form of particles of different sizes and values for the individuals using them, which in turn can be divided into those that actively hunt

for these particles or passively filter the carrier in which the resources are suspended. In the latter case, I would see similarities, for example, between spiders building networks between plant twigs and sedentary water filter feeders. After all, there may be different types of space in which individuals live – for example, one-dimensional, linear, flat, two-dimensional or three-dimensional, and the resources in this space may be distributed in different ways: evenly, randomly, with a certain gradient, staying stationary relative to the space or moving. In the case of sedentary organisms, spatial statistics of the distribution of these organisms are an important issue that needs special attention (Wiegand & Moloney, 2014).

The main issue, the reason why these experiments are worthwhile and should be carried out, is, of course, the problem of individual variability, its scope, causes, mechanisms of creation, and ecological consequences. Individual variability is the greatest unknown in contemporary ecology (Sutherland et al., 2013). Without an experimental analysis of this problem, it will be impossible to develop further systematic approaches to the individual-based modeling of the dynamics of populations forming ecological systems.

The classification presented above, taking into account at the same time the types of organisms, their growth and use of resources, the types of interaction between individuals, and types of resources, would allow the construction of typical experiments for typical situations. This would allow us to get out of the chaos of detailed ecological situations, detached from contact with others, to find similarities between them, to point out significant differences and to try to make generalisations. The results of experiments and observations made within the framework of such an experimental ecology of individuals could be translated into standard algorithms, which in turn could constitute elements of future standard individual-based models of population dynamics of different animal, plant and microorganism species.

In fact, there was a period in the history of the 20th century's ecology when there were circumstances that were conducive to the emergence of the ecology of individuals in this sense. Unfortunately, this opportunity has not been used. In fact, after the Second World War, ecological bioenergetics (Kleiber, 1961) was developed in some countries of Middle-East Europe. Among other things, it covered the energy balance of individuals of very different species. It measured the consumption and assimilation of food by individuals, constructed growth curves for individuals, and measured the production of offspring and the rate of respiration (Grodziński et al., 1975). Highly sophisticated and precise experimental methods were applied. All this information is essential from the point of view of the ecology of individuals and the possibility of developing an individual-based

approach in ecology. However, the arrangements of the experiments were such that either single individuals isolated from interactions with other individuals were studied or a group of individuals, but in the latter situation, average individual characteristics were measured. In both cases the experimental method excluded the possibility of obtaining information about the results of interactions between individuals and their variability.

The natural way to develop ecological bioenergetics would be to analyse the individual variability of all the above elements of the energy budgets of individuals and the impact of interactions between individuals on them. Unfortunately, when ecologists dealing with ecological bioenergetics have matured to such a step, dramatic political changes have occurred in these countries, reforming science and introducing other methods of its management. This has led, among other things, to the collapse of bioenergetics. In recent years, tentative attempts have been made to reactivate ecological bioenergetics and direct it towards studying individual variability caused by interactions between individuals. The results are very promising. They provide information exactly what individual-based ecology and individual-based models need (e.g., Khvorostova, 2010). Recent attempts to study so-called dynamic energy budgets (see Kooijman, 1993, and later papers) are also connected with the abovementioned applications of ecological bioenergetics.

10. Need for an ecological literature review

Another task facing the ecology of individuals today is to review the existing ecological literature, where there is a lot of valuable information that can be gathered and systematized to make significant progress. In fact, we have seen an example of this in the recent past. A review of the literature on weight distributions of individuals in even-aged populations dating back to the 1950s has shown that these distributions are positively skewed, *i.e.* they consist of many light and few heavy individuals (Uchmański, 1985; Pfister & Stevens, 2002). In addition, the skewness of these distributions increases when the food conditions in which the individuals live deteriorate and when population density increases. These regularities concern both plants and animals. The authors of these observations and experiments attributed these results, which are a kind of regularity, to intraspecific competition and the unequal distribution of resources among competing individuals. The general rule seems to be as follows: whoever has gained more resources in the past will gain more resources in the future. With these experimental results in front of our eyes and knowing their interpretation, we could think about constructing

a mathematical scheme that, assuming a certain equation for the growth of an individual, would allow us to obtain such distributions of the weights of individuals growing simultaneously and using common resources.

The aforementioned ecological bioenergetics currently provides helpful concepts. The energy balance of an individual growing before the reproduction period comes down to a very simple equation: weight gain equals the difference between the rate of food assimilation and the rate of respiration. It only remains to be guessed, therefore, how different the assimilation of individuals growing under competitive conditions should be to obtain the positively skewed weight distributions commonly observed in even-aged populations. It turned out that for sedentary individuals and competing locally with their closest neighbours the rate of assimilation of an individual is lower when the larger the neighbours are located closer to it (Benjamin & Hardwick, 1986). For individuals competing globally with other individuals in the even-aged population, it is possible to indicate the appropriate function linking the rate of assimilation to the weight achieved by the individual (Uchmański 1987; Uchmański & Dgebuadze, 1990). The weight of an individual in both above examples is a measure of its past, net energy gains, i.e. after deducting the cost of living

Such schemes may be included in algorithms describing the dynamics of a single population. In this way, for example, we can build a forest stand dynamics model with a fairly high degree of generality, which makes it possible to study the general dynamic properties of this type of system (Wyszomirski et al., 1999; Komarov et al., 2003a). The case of global competition can also constitute the basis for building a single population dynamics model. It turns out that the dynamics of such a model have different characteristics from those produced by classical models. The main difference is that we now have discrete individuals which variability is shaped by intraspecific competition (Uchmański, 2000b; Grimm & Uchmański, 2002). We may then find that, with low levels of resources and intense competition, there is no individual able to reproduce in the population. Then, the population will go extinct. Such an event is inevitable. If a population of variable, discrete individuals passes through successive phases of low and high abundance, then sooner or later, this must happen in the minimum population size. This is the same effect that we observe in gambling or when we track random walk. Repeated exposure to danger must sooner or later lead to disaster. The only difference is when this happens. A population made up of more variable individuals will last longer. Such an effect cannot be expected in classical models of single population dynamics.

The above scheme is focused on the weight of the individual. We have in this scheme the resources and their

unequal partitioning among individuals as a result of intraspecific competition, which affects the weight of the individual, and this in turn is important for the survival and production of offspring (Peters, 1983) – a larger individual has the opportunity to reproduce or produce more offspring. Of course, the number of individuals is also important here because its increase means more individuals share the resources. This scheme contains and replaces all elements that the classical models have in common with the concept of density dependency. In the latter case, these dependencies, pushed into a mathematical scheme of differential equations, give a different picture of the population dynamics. The mathematical apparatus used is not indifferent to the subject of mathematical description. I believe that the algorithm proposed in the above individual-based approach is closer to the roots and rejects a significant part of the mathematical inertia that greatly distorts the final result.

One may imagine a scheme using a feature other than the weight of the individual that will be variable in the population and will affect the production of offspring. In the above-described scheme focused on the weight of an individual, modifications are possible that do not change the dynamics of the system (Kenkel, 1990; Czárán, 1998; Berger & Hildebrand, 2000; Bauer et al., 2004; Grabarnik, 2007; Berger et al., 2008). For example, in the models of local competition between sedentary individuals, instead of the function describing the dependence of the resource assimilation of an individual on the weight of its neighbours and the distance to them, the concept of so-called zones of influence can be used. Competition that also leads to an individual's weight differentiation would now be represented by the overlapping of the zones of influence of neighbouring individuals and their unequal partitioning in the common parts of these zones.

11. Conclusions

I believe that the paradigm emphasizing the importance of individual variability for the dynamics of ecological systems is fully capable of replacing the paradigm using density dependency. This new paradigm allows the construction of mathematical models to be schematised, as well as setting the direction in which experimental research should be directed. The problem is that by using this new paradigm to construct models of population dynamics in ecological systems, we obtain different results than by using the density-dependent paradigm (see for example Pfister & Stevens, 2003). This requires the experimental verification of these models. It should be remembered, however, that in fact we know very little about the dynamics of natural populations, and our scant information on this comes from a very limited number

of laboratory experiments carried out on only certain groups of organisms, and the interpretations of these experiments are tainted by thinking in terms of density dependence.

As has already been stated, there are areas of ecology where traditional mathematical methods – differential equations – are successfully applied. These are areas of ecology that deal with the processes of energy flow or the circulation of matter in ecological systems. Here, the use of differential equations seems to be justified. In these areas of ecology, we are dealing with processes that are taking place over time and in many cases in space in a continuous manner. The variables in these models are not the density, just the concentration or the total amount of, for example, a certain element. The values of these variables change over time and can be described in a fully justified way by continuous functions. There are several reasons for this. The processes of circulating elements in ecological systems are to a large extent determined by physical and chemical phenomena and processes, where such mathematical methods have always been used or even invented to describe such processes. Liquid flows, for example, very often take part in such processes. There is also a large proportion of the activity of living organisms in these processes. However, now we are dealing with other effects of their activities. In the case of demographic models describing population dynamics, after growth periods of different lengths, an act of reproduction occurs, the nature of which is extremely discontinuous even when an individual produces many offspring. In the case of element cycling, however, the participation of living organisms is reduced to those manifestations of their activity that occur constantly during their lifetime. For example, the excretion of elements or their absorption occurs almost continuously, although with varying intensity. In addition, the effect of the continuity of these processes is strengthened by the mass of these phenomena, as they occur in all organisms present in the environment. The fact that the use of traditional mathematical methods in the construction of models of element cycling and energy flow through ecological systems is a correct procedure is proven by numerous practical applications of these models. Let us recall here the mathematical models of the phenomenon of lake eutrophication or the models of carbon circulation on the scale of particular ecological systems or of the entire biosphere.

In physics, the phenomenon of the concerted contact of different descriptions of physical systems is known. Thermodynamics is a macroscopic description of a gas system. Statistical physics sees this system on a microscale. Both descriptions are compatible (Reif, 1967). The concepts used in thermodynamics – for example, temperature – have a very precise microscopic explanation in statistical physics. I think the question whether two descriptions of ecological

systems – through the dynamics of the populations that make up them and the cycling of matter in them or the flow of energy through them – come together at a certain point is justified, although unlike in physics. Each of these descriptions addresses something different. They are the result of two different views on ecological systems, views that see different aspects of their functioning. Descriptions concerning the cycling of elements or energy flows provide, in a sense, information about the environment in which individuals live, rather than providing another view of the dynamics of their numbers. The compatibility of these two descriptions of ecological systems can be presented in other ways. Imagine that we are building a model of the dynamics of a natural forest stand. We are following the recommendations of the paradigm that emphasises the importance of individual variability. Therefore, it will be important for us to have differences in the size of the growing trees due to their uneven distribution on the forest surface and the variability in seed production. Now let us add to this model a description of the physiological processes taking place in each tree and related to the absorption of carbon dioxide during photosynthesis and its secretion during respiration. Let us add also a description of root and soil organisms activity. We will finally obtain a description of carbon circulation in the forest ecosystem, which should follow the same models made by traditional methods using differential equations (Komarov et al., 2003b; Komarov & Chertov, 2007; Chertov & Komarov, 2007).

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