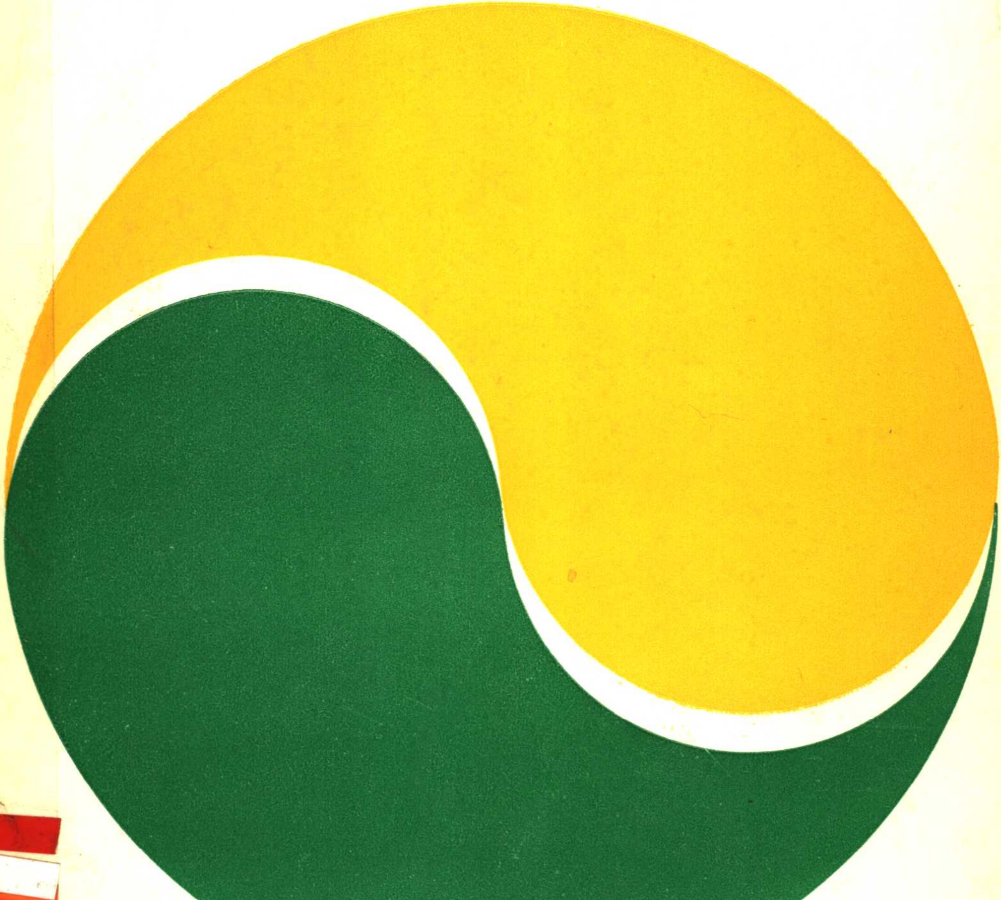
Przemysław Trojan

Ecosystem Homeostasis



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ECOSYSTEM HOMEOSTASIS

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FOREWORD

The concept of ecological homeostasis is central to all the most important problems of theory and practice in contemporary ecology. It sets out to explain the structure and the functioning of the mechanisms involved in stability, regulation and persistence of ecological systems.

Theoretically, the concept helps to define the principles of the organization of ecosystems as self-regulating entities. These principles will serve as the basis for the study of community structure and the related problems of ecosystem control. A better understanding of the relationships between the structure of ecosystems and homeostasis is at present particularly desirable, as some ecologists are inclined to believe that structural investigations of plant and animal communities are of a purely phenomenological nature and have no connexion with the general theory of ecosystem organization (Łomnicki, 1978). Unfortunately, high accuracy in measurement of matter cycling and energy flow in ecosystems is not matched by a corresponding consideration of these processes as subject to rigorous regulation and control by the homeostatic mechanisms operative within such systems.

No less important is the theory of homeostasis in solving practical problems set to ecology by the economy of natural resources. Many crucial questions concerning the economy of the biosphere as a whole or the management of landscapes and ecosystems cannot be answered without a theory of ecological homeostasis. Such applied sciences as agriculture, forestry or fishery will find here important clues to the phenomena which occur in particular ecosystems. Ecological threats and disasters sweep over our forests and fields. They are caused by a mass occurrence of phytophages, whose population control presents a problem of growing complexity. As a result, ecosystems intensively exploited by Man are defined as unbalanced, lacking an internal regulation or having a restricted regulation. It is the nature of such problems that should be explained by the theory of ecological homeostasis.

There are numerous indications that protection of the endangered species by setting up national reserves is inadequate. Fear that such species may be exterminated by Man has often been replaced by the certainty that their elimination will be accomplished by nature itself. Therefore, developing a theory of ecosystem organization is not a goal for a remote future, it is a problem to be tackled today.

Ecology will not be able to achieve success in the practical sphere of ecosystem engineering until the mechanisms which make up the core of ecosystem homeostatis have been understood.

The task of creating a concept of ecological homeostasis lies within the scope of ecology rather than any other science dealing with ecological problems. Actually, the results achieved by other sciences so far show very little promise in this respect.

There does not seem to be much agreement among ecologists as to what kind of methodology would be the most suitable for homeostatic studies. Many ecologists are quite radical in their conflicting views. On the one hand, reductionists point out (on the basis of obvious facts) that ecosystems, in their living part, consist of nothing but individuals of different species. Therefore they claim that individuals and their characters should be at the root of all models of ecosystems as homeostatic units. On the other hand, holists stress that one cannot see the trees without seeing the wood (Odum, 1977). They indicate that the ecosystem acts as an entity and its properties cannot be predicted from an analysis of individuals alone. Both methods slip into idealism either through admitting the inexplicability of ecological phenomena or through making a fetish out of the functions ascribed to ecosystems, which control their organization and internal activity. The first goal of this book is to discuss the above two kinds of methodology and to specify the premises that underlie the author's analysis of ecosystems as homeostatic units.

One can differentiate between three approaches to the study of ecosystems currently in use (Odum, 1972). The simplest of them, the hological approach, treats the whole ecosystem as a 'black box' (i.e. a unit whose function may be evaluated without specifying the internal contents) with emphasis on inputs and outputs. The merological approach is based on careful identification of particular components of the system, on the study of their properties and on an attempt to build up an integrated structure from them. The third (system) approach, has developed recently. It consists in reducing ecosystems to simple models suitable for computer analysis. Each of the three approaches excited great enthusiasm followed by bitter criticism. These controversies show how important the right choice of method is.

The study of ecosystem homeostatic organization is fraught with various difficulties, chiefly accounted for by three causes. First, many concepts and definitions of the basic units in an ecosystem's internal organization are rather vague. They are either too heterogeneous (e.g. the notion of the trophic level) or too narrow (e.g. the notion of the link in a trophic chain or of the biological species) for the purpose of bringing order into the internal complexity of an ecosystem. All attempts to apply cybernetic schemes in ecology involve subordinating the ecological material to the requirements of mathematical analysis and, consequently, simplifying it in a way hardly acceptable to an ecologist.

The second cause of difficulties is the complexity of ecosystems. The composition of each terrestial community is highly differentiated. It comprises, as a rule, several thousand species displaying varied ecological requirements, many of which we can only suspect because of a very limited knowledge of their precise quantitative parameters.

The third cause resides in the specific responses of individuals and populations operative in a community. Outside the community an individual may display selectivity, preferences and a diet different from those recorded within a community. In the course of laboratory studies populations frequently exhibit features other than those observed in natural communities, while their numerical dynamics rarely resembles the cycles observed in nature.

It should also be noted that an ecologist engaged at present in homeostatic studies is exposed to a great pressure of public opinion, especially on the part of the scientific community. Many natural scientists have their own idea of an ecosystem which, they believe, fits the theory of ecosystem homeostasis. This accounts for a multitude of differing postulates addressed to ecologists, who are expected, in fact, to do only one thing — to elaborate a method of building up an ideal ecosystem of the future. Such an ideal ecosystem would have nothing but advantages. It should display persistence and no changes in time. It should also be well balanced and possess mechanisms maintaining its internal equilibrium. The system, thus, should exhibit resistance to environmental stresses and show no fatigue, retaining full functional efficiency of its components despite the impact of pollution and contamination. The major characteristics of such systems should embrace high productivity, suitability for commercial exploitation and prompt undisturbed restoration of natural resources essential to Man.

All these demands involve the necessity of defining the notion of the ecological equilibrium, of explaining its essence and of reducing it to a measurable form. It is also necessary to determine the constituent parts of ecological mechanisms responsible for such equilibrium and to understand their action. It is not quite clear yet how nature functions on the ecosystem level. Nor do we know whether it is possible to combine high production and exploitation in an ecosystem which displays good regulation mechanisms, stabilizing the system as a whole. Discussion of the above problems against the background of ecosystem organization is another task of this book.

The action of homeostatic mechanisms shows up most vividly in critical situations. A destructive or deforming impact of pressures evokes homeostatic responses in ecosystems, such as triggering off their inner reserves or attempts to compensate for the losses. These processes are coupled with far-reaching transformations of communities, crucial for an understanding of ecosystem organization. Extremely unfavourable environmental conditions lead to degradation of communities, but its description in terms of the homeostasis theory is still highly inadequate. The history of the last few decades has recorded examples of ecological disasters chiefly due to strong and lasting anthropogenic pressures involving the contamination of entire ecosystems or their components, which are essential homeostatically.

Homeostatic mechanisms appear, develop and function within an ecosystem. The evolution of ecosystems is as long as that of the biosphere, since palaeontology does not know examples of the existence in nature of isolated species that would not form a community. Principles of evolution so far have been discovered only in relation to the individual. Of primary importance for evolutionary advance is to guarantee the system's functioning, to provide reserves and surpluses, which are kept in store under normal conditions to be utilized when need arises in critical situations.

Nature, thus, shows no shortsightedness nor resorts to actions having an immediate but temporary effect. It is not parsimonious either. But still some authors contrast the rationality in the structure and functioning of an organism with the inconsistencies in the ecosystem structure (Eckhardt, 1968).

How is evolutionary progress expressed at the ecosystem level? Are there systems displaying a higher or a lower adaptive value as regards structure and function? Are there primitive and modern ecosystems? Is nature, observed through ecosystems, as purposeful and perfect as the studies of organisms suggest?

According to evolutionary concepts based on population studies, the classical evolutionary game consists in a continuous differentiation of the living world, of all biological species. But the evolution actually takes place within the existing ecosystems, that is under the stress and control of their homeostatic mechanisms. Therefore, stimulation or restriction of evolutionary processes should have their source within the community and its organization. The evolutionary achievements of individuals, or, to be exact, of a population, have a chance to pass through the selection sieve only when they at the same time become instrumental in the improvement of ecosystem organization. After all the entire natural increase of a population is eliminated in the course of its interactions within a well-balanced community. Only part of the individuals survive to ensure a stable size of the population. The severity of control effected by a community in respect of all its components is, ecologically, an obvious fact, but up till now it has only been alluded to as an aspect of evolutionary studies (Schmalhausen, 1968).

In his urge to gain control over nature Man has mastered or set in motion forces so great that in many parts of the world they have brought about ecological disasters. Strong anxiety for the fate of the environment expressed in the report of the former UN Secretary General U'Thant has initiated a broad discussion concerning the place of Man in the biosphere. This discussion has not only an ecological but also a philosophical aspect, involving such problems as the relations between Man and nature and the question to what extent Man is the ruler of nature and to what extent he is its slave. An ecologist must study the relationships between Man and the ecosystems, and the place of the human population in the economy of communities, both natural and man-made. He should also verify the justice of the accusation that Man's interference is the chief force devastating otherwise well-functioning communities (Odum, 1959) or of the contrary belief that the human population can be regarded as the carrier of equilibrium in ecosystems. This is again a question concerning the criteria and the measures to be employed in an attempt to define the rôle of the human population and of other species composing an ecosystem.

In the end of the sixties an opinion prevailed that Man is a product of the evolution of the biosphere and that his fate is associated with a given, fairly balanced system of ecological relations within the biosphere. Thus, the possibility of escaping beyond the biosphere, of isolating the human population from its natural environment and making it independent of nature has proved to be an illusion, which admittedly may materialize in a spaceship, but has no prospects for the numerous and constantly developing human species, which always remains bound to various ecological systems exploited as the source of food. A possible disturbance of equilibrium, persistence and productivity in such systems is charged with the danger of a disaster for *Homo sapiens.*

All the numerous problems discussed above are basically coupled with the concept of ecosystem homeostasis. Ecological reactions of the systems which occur in nature are, in fact, very simple. They consist in the maintenance of the earlier level of numerical abundance, in its decrease or increase. The causes for such reactions are varied, occurring regularly or at random and often depending on the action of homeostatic mechanisms.

The distinction between the phenomena rooted in the organization of ecosystems and those of a random nature only seems to be easy. An ecologist, who, as a rule, can very accurately trace the course of an event, faces much greater difficulties trying to ascertain its causes. It is generally assumed that the action of homeostatic mechanisms is of a protective and preservational kind. One ought to take into account, however, that fixed homeostatic reactions have evolved in the course of historical development. Simple and once reliable mechanisms of spatial orientation in nocturnal insects may drive them towards fatal collisions with the sources of incandescent light. An unprejudiced scientist has every reason to ask whether the appearance of new environmental stimuli may turn the homeostatic mechanism into a factor of self-destruction in ecosystems.

The present book has emerged from thinking on recent concepts and current studies of the ecological foundations of environmental protection conducted in Poland during the last decade.

The book owes a great deal to the suggestions and criticism of my friends Professor Andrzej Szczepański and Professor Adam Urbanek. I am especially grateful to Mrs Irina Bagaeva who undertook the far from easy task of translating the Polish text into English. Mrs Jadwiga Kobuszewska devoted exceptional care to the editing of both the original and the English versions of the book, while Mr Andrzej Karabin prepared illustrations in a competent manner. I am grateful to all the above-mentioned persons for their generous help in the preparation of the book.

1. BASIC IDEAS OF THE CONCEPT OF ECOSYSTEM HOMEOSTASIS

1.1. Historical and contemporary aspects of the concept of ecological homeostasis

The concept of the ecological homeostasis has become a widely discussed issue of contemporary community ecology. Much of what is debated today as the principles and criteria of homeostasis was also the source of theoretical generalizations in the past. The criterion of durability was put forward by Aristotle in his '*Historia animalium*', where he discussed the relationship between the individual and the species. Individuals come and go, while species last for ever. This persistence of natural species had a different meaning in Ancient Greece, where it motivated Plato's idealism in natural history. The persistence of a biological system as a criterion either of evolutionary success or of adaptability has remained among ecological and evolutionary concepts.

The concept of biological equilibrium is a product of the 18th century teleological approach to biological phenomena. It was grounded by Linnaeus (1787, 1789) is his works '*De oeconomia naturae*' and '*De politia naturae*', which contain his views on the economy of nature. Biological equilibrium is based on the interrelationships of all nature's components. Its maintenance involves not only propagation and subsistence of organisms but also their destruction, since the death of some organisms is indispensable for the existence of others. Understood in this way, the notion of ecological equilibrium was for Linnaeus a complement of the concept of the hierarchical order which he ascribed to nature (Nowiński and Kuźnicki, 1965). One could also find here considerations concerning the struggle for life in its later Darwinian sense as a factor of general order in nature.

The discussion about the foundations of community ecology that developed in the first half of the 20th century embraced all basic issues associated with the theory of ecological homeostasis except its mechanisms. The notion of the superorganism as suggested by Clements and Shelford (1939), the ideas of autarchy, self-regulation and autonomy of communities are now all part of the homeostasis concept (Friedrichs, 1927; Thienemann, 1942). The critics of the application of organismal concepts to ecology (Tansley, 1935) emphasized the fact that ecosystems were open systems, but did not question the possibility of their autonomy and self-regulation.

A heated discussion is going on as to the methodological foundations of ecological theories. The dividing line passes between the reductionists and the holists. The urgency of the problem for Polish ecologists is well illustrated by the number of opinions published in the journal '*Wiadomości Ekologiczne*' (Advances in Ecology) in response to Łomnicki's (1978) paper suggesting reductionism as the sole method in ecology. Petrusewicz (1978) advanced the principles of an integrative approach to the analysis of ecological compound units. Of great importance also is the connexion between two trends of discussion: one about the methodological basis of ecology and the other concerning the foundations of biology.

As part of the latter discussion, Urbanek (1974) proposed several postulates associated with the historical aspect of biological sciences, three of which seem to be particularly relevant.

(1) The historical principle states that biological sciences cannot do without a historical method in their attempt to explain the phenomena and processes of the organic world. This also embraces the structure of living organisms. A question arises as to the applicability of this principle to the ecosystem study. The answer is difficult to find, since ecology has never taken into account the historical aspect of ecosystem organization. Recent palaeoecological studies reveal a great influence of ecological concepts, and attempts are being made to apply them to fossil material (Kaufman and Scott, 1976) without considering the historical side of the phenomena examined. Another problem is the applicability of the historical method to the study of community structures. Though this method is valid at the organism level, it has been impossible so far to recognize ancestral or newly acquired structures in compound units, such as populations and communities.

(2) The problem of immanent and configurational features of ecosystems is an important, though not fully appreciated, trend of contemporary methodological discussions in ecology. Establishing universal principles relevant to all ecosystems that have existed in the history of the biosphere as opposed to those which define only their recent properties may provide a break-through in present-day ecology.

(3) In Simpson's opinion immanent uniformism makes it possible to show that the history of life is not uniform, but consists of unique

events. His concept finds a lot of evidence in organismal biology and ecology, for both the organisms and the communities of the past were quite different from the recent ones.

The concept of ecosystem homeostasis is also closely linked with cybernetics and information theory. The achievements of physiologists in elucidating homeostatic mechanisms functioning in organisms together with the rapid development of cybernetics have had a strong impact on ecology of populations and communities, where regulation phenomena may be described in terms of cybernetic models and information theory. Here, a great achievement was by all means Christian's (1950) model of population control in rodents associated with the concept of the ecological and physiological stress. But ecology is under greater pressure of physiologists (Langley, 1965; Dawidowicz, 1970) and mathematicians engaged in the systems theory (May, 1974) than that of ecologists themselves. The latter tackle these problems with great caution or even mistrust. This is due to two reasons. Systems ecology is based in principle on great simplification associated with the necessity to adapt the model to the analytical potential of computers. On the other hand, the known ecological parameters are too few to satisfy the requirements of even such simplified models (Margalef, 1968). Attempts to use simulation of ecosystems as a solution of environmental problems usually end in failure (Odum, 1972), which is hardly an incentive to further cybernetic studies in ecology.

Another argument in favour of caution in using cybernetic methods in ecosystem analysis is lack of certainty whether the principles fully successful in studying the homeostasis of organisms are equally applicable to the investigation of populations and communities. Therefore, community ecologists are first of all trying to learn the rules governing the existence of ecosystem, often referred to as the ecological or evolutionary strategy.

One more important subject of research is the structure of communities, which does not easily succumb to the scientists' efforts because of the complexity of the ecosystems, inhabited as they are by thousands of species and millions of individuals. This multitude and diversity is not easy to identify, but an even more difficult task is to establish the existing interrelationships and the functions of particular constituents. No wonder that some ecologists, e.g. Eckhardt (1968), sound pessimistic, stating that the structure of an organism is highly rational while that of an ecosystem is much less so, as it consists of numerous components capable of performing similar functions. But according to Schmalhausen (1968) this diversity of structural components is, in fact, the result of the action of the mechanisms controlling the organization of ecosystems. All these points, closely linked with the concept of homeostasis, require further discussion, elucidation and drawing definite conclusions.

1.2. Methodological aspect of the concept of ecosystem homeostasis

Theoretical deliberations on the concept of the ecosystem, community and ecological homeostasis are points at issue in a methodological debate rooted, as was mentioned above, in the views of Aristotle and Linnaeus. The thirties of the 20th century saw the advance of a holistic understanding of community as a superorganism. Now, over forty years later, the dispute between holists and reductionists has been renewed. In addition, an integrative approach is being developed which, though supported by not too many ecologists, has a sound methodological core. This debate is of fundamental significance for the theory of ecosystem homeostasis, therefore it is in a way a must to adopt an unequivocal attitude towards it. Philosophically, this problem involves the relationship between matter and idea, whereas ecologically this basic subdivision is expressed in the relationship between part and whole and also between structure and function.

The reductionist trend in contemporary ecology is methodologically based on negation of holism (Łomnicki, 1978). Particularly strong objections against the understanding of community as a superorganism concern the low explicative value of this concept which can explain everything in general and nothing in particular. Reductionists challenge the direction given to community investigations by holism. 'It seems entirely misleading, however, to expect that holistic descriptions will allow us to understand the integrative mechanisms of a community and, moreover, to manipulate them. So far, there is no indication of such prospects, for these descriptions are purely phenomenological' (Łomnicki, 1978). Łomnicki has also formulated a methodological creed of reductionism as a negation of holism. Instead of starting from individuals, of which our knowledge is the most complete, we choose a larger system, which might yield to analysis, such as an ecosystem, a community or a population, and set to describe it in much the same way as classical zoology or botany used to described new species. Since an ecosystem is often a poorly integrated unit with vague limits there is a danger of studying not the real subjects but creations of our own mind fairly remote from reality. Subdividing such a superorganism into smaller components, e.g., trophic levels, we still remain within the scope of highly abstract notions, operating with units that are highly heterogeneous, until we get down to the level of an individual of a given species.

According to the reductionist views, a model for ecology may be provided by population genetics and the study of microevolutionary processes. Proceeding from our knowledge about the organism, e.g. Mendel's laws, and making several simple assumptions as to the relationships between individuals, we construct a mathematical model of behaviour of a set of individuals, i.e. of a population. During laboratory or field studies of populations we check up to what extent our model corresponds to reality, and when it does not, we look for further relations based upon the genetics, behaviour or ecology of individuals and introduce them into the model.

These considerations are accompanied by clearly defined methodological recommendations. It is believed that their violations lies at the root of all the failures of ecology. They concern two problems: '(1) the rule referred to as Ockham's razor, which requires that entities should not be multiplied unnecessarily, i.e. that complex concepts and notions should not be introduced where phenomena can be explained without them; (2) application of reductionism wherever possible, that is explanation of higher levels of organization through the properties of the lower ones. It is debatable whether biological phenomena may be ultimately explained in terms of physics and chemistry (or rather in terms of physics, chemistry and natural selection), but there is no doubt that in ecological systems there is nothing but individuals of different species, an abiotic habitat and various relations between these components' (Łomnicki, 1978).

These considerations go together with a conviction that advance in ecology was achieved in those cases where the subjects of investigations were individuals and their relationships, where the results of studies were presented as accurately as possible with the help of mathematical models and where these models were used to predict the behaviour of entire systems. Progress was achieved when ecological studies were based on the knowledge of genetics, physiology and also animal behaviour (Łomnicki, 1978).

The views of contemporary ecologists engaged in mathematical simulation of population phenomena have their predecessors in the resolute statements of Bodenheimer (1958) and Andrewartha (1967). The latter, though admitting the principle of three levels of ecological complexity, still regards reductionism as the only way to the understanding of the regularities they involve. 'So we may conveniently recognize three levels of complexity in the laws of ecology. Firstly, there are the laws governing the physiology and behaviour of individuals in relation to their environments... Secondly, there are the laws governing the numbers of animals in relation to the areas that they inhabit: this is sometimes called population ecology. And thirdly, there are laws governing communities, which may be thought of as groups of interacting populations'.

Andrewartha believes that a scientific approach to these three levels of organization should be as follows: 'It seems reasonable to proceed upwards through these three levels of complexity — that is to approach the study of populations through physiology and behaviour, and to approach the study of communities through the ecology of population. And it seems likely that a science of community ecology may eventually be built on the base provided by population ecology'.

A reductionist reasoning is a kind of appeal of common sense in ecological studies, for this is how one can understand the demand that what is less complex and better known should come before what is more complex and difficult to analyse. But common sense and methodological correctness are two completely different things. One can raise two objections to the reductionist approach. The first of them concerns the limits of reduction (Trojan, 1978). Contemporary reductionists in ecology believe the concept of the biological individual to be the lower limit of reduction. Many years ago Raabe (1954) reminded us of the complexity and ambiguity of the notion of the individual. A molecular biologist would like to proceed with reduction further and to analyse ecosystems on the basis of physical and chemical laws operating at a molecular level. An ecologist, however, easily accepts the view that an individual is usually a separate entity, isolated from the environment or other organisms and, as such, suitable for analysis. But suitable does not mean the only one acceptable methodologically. Anyway, this suitability may immediately turn into its opposite, if one assumes the point of view that the genetic properties of an organism provide a good ground for ecological analysis. What should be the response of a community ecologist? Does there exist empirical evidence concerning the inheritance of environmental tolerance range? What genes account for food selectivity? What genetic laws govern the transfer of different types of behaviour: aggressive (in predators), tolerant or protective? Genetics is chiefly confined to investigating the principles governing replication of the organization of an individual, but its relations with the environment largely remain within the scope of interpretation and not of empirical data. Ought an ecologist to assume all the parameters essential for his model of an ecosystem by analogy with the inheritance of properties in pea seeds or of morphological characters in *Drosophila*? What methodological prerequisites allow him to make this choice?

Another objection which should be raised concerns the principle of additivity. The adoption of this principle is a consequence of assuming the reductionist attitude to the study of populations and communities. The additive approach is a survival of mechanistic views, according to which a compound system such as community, or biocoenosis (B), is the sum total of the properties inherent in populations (p) composing it.

$$B = p_1 + p_2 + p_3 + p_4 \cdots + p_n. \tag{1}$$

Similarly, a population (P) is the sum total of individuals (i) of which it is composed.

$$P = i_1 + i_2 + i_3 + i_4 \ldots + i_n. \tag{2}$$

Such reasoning is bound to arise out of reductionist methods. Where individuals are the only subject of studies, there is no room for introducing components other than those obtainable from the analysis of individuals. A question arises whether a study of individuals is capable of elucidating every phenomenon occurring in population and community systems. The assessment of energy flow in a population is a typical example of using reductionist methods to evaluate phenomena occurring in compound systems. This path is full of pitfalls, methodological ones in particular. Models employed to estimate energy flow are not equally reliable and the accuracy of their results is generally unverifiable, though the results of measurements conducted under similar experimental conditions are reproducible. McNab's (1963) reductionist model accounts for all the parameters that may affect the amount of food required by a single individual. Grodziński's (1966) model cautiously restricts the estimations to the average diurnal values with corrections taking into account various ecological and physiological events. However, Trojan and Wojciechowska (1969) have shown how unreliable are the estimates based on reductionism. Corrections calculated for various relationships between metabolism and different