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EXPERIMENTAL POPULATIONS OF MICROSCOPIC ORGANISMS

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I

In an attempt to discuss the problem of experimental populations, a living and rapidly developing chapter of experimental ecology, it is perhaps best to concentrate on the consideration of all the possibilities, and particularly of all the limitations inherent in this new biological *Wissenzweig.* The origin of this line of investigations appears to be deeply rooted in the quite natural desire of human beings to master the laws governing the structure and activity of the biosphere in which they live, in order to modify it and to adapt it to their own ends. The problem of the biosphere, of that specific envelope of our planet saturated with populations of living beings, is at present attacked from at least three different angles. Firstly, in biocoenology by describing, qualitatively and quantitatively, associations of living organisms under field conditions. Secondly, in biological geochemistry by analyzing the chemical consequences of activities of these populations. And thirdly, perhaps the most recent line tries to discover general principles of organization in these population systems by means of experimental analysis.

Various opinions concerning the rôle of experimentation in biocoenology are extremely contradictory, and one may still meet active scepticism denying any significant rôle of experimentation in this particular field. "The data," as it is often said, "obtained in the laboratory under 'unnatural' conditions are of extremely little value and sometimes are even misleading." On the other hand, to overrate the potentialities of the experimental method would perhaps be equally dangerous. It therefore appears best to mention them briefly.

It is interesting to find late in the past century an analogous discussion concerning the rôle of experimentation in zoölogy. We meet O. Hertwig's claim to a specific restriction of application of experimental method by physics and chemistry, and its uselessness in biology: *"das Experiment habe seine eigentliche Bedeutung im Gebiete des Anorganischen. Da die anorganischen Körper verhältnissmäßig unveränderlich seien, so müssen sie durch den Menschen gezwungen werden, sich zu verändern, und erst dadurch werden sie der kausalen Forschung zugänglich gemacht."* We meet further Driesch's energetic and clear cut reply in defence of experimentation in biology: *"das Experiment wird nicht allgemein Veränderungen herbeiführen, sondern will Veränderungen (Vorgänge) nach Belieben isolieren oder variiren. . . . Ganz dasselbe, was den Wert des Versuchs in den anorganischen Disziplinen ausmacht, trifft nun auch vom biologischen Versuch su."*

The rôle of experimental method in biology is now generally recognized, and by extending it to the study of biological "associations" we appear to be making a perfectly logical step of lowering it to the next hierarchical level. At the same time there appears to be a certain specificity in that particular level, which is at least worthy of some attention. In the study of an individual organism it is usually relatively easy to distinguish between inherent organismal properties which are due to a specific order of matter which makes it living, and relatively secondary variations in these properties which are associated with differences in environmental conditions. Putting it in another way, the living matter appears to be rigorously organized, and the very existence of this organization admits of no doubt. At the same time the degree of organization of "associations" of living beings is of an entirely different order of magnitude. The principles inherent in these associations as such (*e.g.* regulation in composition, etc.) are not always clear owing to a relatively more efficient rôle of the environmental situation. The field studies have therefore the advantage of showing us the exact behavior of such-and-such an association under such-and-such a set of environmental conditions, which is sometimes of immediate use for practice. At the same time no claim can be made to an adequate theoretical understanding of the principles of its organization by field observations alone, and definite room is therefore left for application of the experimental method.

The position of experiment in biocoenology has much in common with the rôle which relatively simple physical facts, obtained through experiment, play in the science of meteorology. It is certainly true that at the bottom of all weather variations lie some definite physical facts, which have been, and surely will be productively studied under simplified laboratory conditions. It is equally true that an adequate understanding of some weather phenomena could never have been attained without laborious experimental work of this sort, and nobody will ever doubt of its importance. At the same time an attempt to forecast weather on the basis of such laboratory investigations *alone* will scarcely meet with any approbation.

To sum all this up: although an individual organism is either *somewhat* modified or perfectly eliminated by environment, a biocoenosis is really *made* under rigorous control of environment. Those features which are specific for a developing biocoenosis as such and hold true under any set of conditions are therefore not very evident at first, but they undoubtedly exist and are worthy of experimental analysis. It is therefore the object of experimental study of populations to find out some very general principles underlying the organization of biological associations.

II

Populations of *microscopic* organisms appear to be particularly suitable for experimental work because (1) it is very inexpensive to undertake all the manipulations required, and (2) these manipulations can be accomplished in a very short while. My early studies on populations were conducted in field conditions on various grasshoppers about ten years ago; they were continued in the laboratory on *Drosophila* cultures in milk bottles. But finally I found populations of various yeasts and infusoria to be extremely suitable for work of this sort. To the list of our laboratory animals have recently also been added mites inhabiting wheat flour, semolina and some other substrates. These are extremely small and must be counted under a microscope; in this way we are right to rank them among populations of microscopic organisms.

In search of some general principles governing the structure of associations I have first used the simplest possible method, that of analysis into elementary constituting processes. An attempt was made to investigate, under carefully controlled laboratory conditions, the trend of elementary processes of the struggle for existence between various species and the consequences to which they lead. Complete information concerning all details could best be obtained from my books on the subject (Gause, '34; '35) and all additional information from three papers (Gause and Witt, '35; Gause, '36; Gause, Smaragdova and Witt, '36).

A mixed population in the test-tube was first made of the two species of yeast, and then of the two infusoria, *Paramecium caudatum* and *Paramecium aurelia,* presenting equal requirements regarding the kind of food and mode of its consumption or, in other terms, occupying identical " ecological niches " in the microcosm under investigation. The outcome of such an experiment was always identical and clear-cut: only one species, the better adapted for living under given conditions, was finally left in the population, which in this way had become *pure*. It is also interesting that it was possible to calculate *in advance* which one of the two species would be left, from an equation of growth for such a mixed population.

In so far as a mention has just been made of mathematical equations it seems best to say a few words concerning the rôle of this method in the study of experimental populations. It is sometimes argued, and not without sound reason, that when a mathematician tries to introduce all even secondary details specific for some experimental population into his theoretical calculations, he can scarcely get conclusions of any permanent value for understanding real animal life in the field. The conditions, and consequently the conclusions, will surely be different in the field. This reasoning originates from a real difficulty of recognizing some underlying fundamental principles of associations of organisms in the complex of their details. Mathematics will be of value in the study of populations which will seek principles and not merely unimportant details.

The danger of the neglect of details is scarcely to be emphasized, for it is too evident that any separation of the " meanly net " from its " gist " is only possible when the net is carefully and definitely understood. But what is the kind of " gist " that a mathematician could help us to get out " net "? Since we are dealing with quantities, with numbers of animals, we will be supplied with qualitatively different *types* of variations of these numbers. We will be exhaustively told how different types of interaction between organisms in associations lead to different types of the steady states of these systems: either to continuous periodic variations in numbers, or to a continuous stable mixed population capable of autoregulation, etc. Using technical terms of mathematicians, the principles we are looking for are nothing but types of qualitative solutions of differential equations for various population systems.

The first such principle we have heretofore observed experimentally and accounted for theoretically, both in infusoria and in yeasts, is that the steady state of a mixed population consisting of two species occupying an identical " ecological niche " will be the pure population of one of them, of the one better adapted for the particular set of conditions. The second type of the steady state we are now going to discuss appears to be particularly interesting from the viewpoint of a field naturalist. Certain suggestions concerning its nature were at first given theoretically by Lotka, Winsor and myself, and since then it has been experimentally demonstrated for two population systems in infusoria. If we take a test-tube containing a mixed diet consisting of bacteria and yeast, and populate it with the two species of infusoria, *Paramecium aurelia* and *Paramecium bursaria,* the first of which will prefer bacteria and the second yeast sediment on the bottom, we will apparently have to deal with a mixed population of two species occupying two different ecological niches contained within the same microcosm. Both species can certainly eat each kind of diet, but each one of them is particularly well-adapted to its own mode of nutrition. The outcome of such an experiment shows the existence of a specific steady state, the stabilization of a steady mixed population of both species. Two species occupying different ecological niches in the habitat continue to live together indefinitely in essentially stable equilibrium, in which each one occupies the niche where it is more efficient. This appears to be the second principle of biological association yielded by experimentation and accounted for by theory.

The theoretical interest of this principle lies also perhaps in the fact that it gives a satisfactory account of regulation in association, on a very primitive level of its organization. In fact, not any but only a certain *definite* combination between the two species possesses the property of maintaining stability. Any deviation from it will automatically, owing to continuous process of competition, lead to re-establishment of the steady state.

All this appears to hold true, as far as the mixed population of *Paramecium aurelia* and *Paramecium bursaria* is concerned. Certain significant differences have, however, been found in cases of *Paramecium caudatum* and *Paramecium bursaria.* The re-establishment of a disturbed equilibrium did regularly take place when *Paramecium caudatum* was in excess, but ceased to operate in case of excessive increase of *Paramecium bursaria.* Subsequent experimental analysis has shown that this is due to a specific sensitivity of *Paramecium caudatum* to the waste products excreted by *Paramecium bursaria;* the former is in this way unable to increase in dense populations of the latter. What is essential in these data is perhaps the realization of relative parts played by a more general principle of automatic regulation and of a more special disturbance if this regulation changes under some conditions due to specific biological particularities of experimental animals. An interplay of these two parts is responsible for the design of complicated natural phenomena as we see them.

III

Another group of elementary processes of interaction between species in associations, that of *direct* struggle for existence, should perhaps be only briefly mentioned. It was at first observed on infusoria, and later on mites inhabiting both semoletta and wheat flour, that an interaction between predators and prey in a closed habitat can lead either to extinction of both in case of sufficient voracity of the former, or to oscillation in numbers under conditions of continuous immigrations of predators and prey from the outside. An essentially different behavior was observed in a less voracious system consisting of *Paramecium* devouring yeast cells, where continuous variations in numbers of both species were demonstrated under some conditions. Certain advances in both experimental technics and theory enabled us to conclude that this type of variation is essentially due to two factors: (1) the impossibility for infusoria to consume yeast cells to the very end with the resulting threshold of consumption, and (2) a peculiar relation between the increase of predators and the density of prey, that give to these variations their specific shape.

The two mentioned types are nothing but elements that participate in the complicated design of real natural events.

IV

Although analysis into constituting entities almost always precedes the study of coordination of these entities into units of higher order, it seems reasonable to ask at this stage what we can hope to obtain from experimental populations of microscopic organisms for understanding biological associations in their complexity? In this connection we should like to mention some new possibilities that seems to open regarding the very mode of experimentation. If we want to pass from elements subject to laboratory analysis, to an interplay of these elements, something intermediate should evidently be taken between highly complex field biocoenoses and extremely simple laboratory mixed populations. Elements of complexity, if you like, should also be studied in their *relatively simple* form. Some opportunity for this is offered by the study of fouling by various microscopic organisms of glass plates submerged in natural waters. The first such attempt was made by Hentschel in Hamburg in 1916, and a very effective extension of this method is due to several Russian authors. The submerged glass plate begins to be covered by various microscopic organisms in a very orderly way, which steadily grow in number and enter into competition with each other. A stage of a relatively stable mature biocoenosis is finally reached, but it is still subject to continuous alterations in composition due to variations in environmental conditions.

It is perhaps particularly convenient that it is extremely easy to interfere experimentally from the outside with the competition and other relations in this rapidly developing biocoenosis on the glass plate. Some organisms can be easily eliminated with different intensity by a thin needle. In the summers of 1935 and 1936 I used the opportunity of experimentation with such biocoenoses of microscopic organisms on glass plates in a lake near Moscow.

For the beginning of the study of complexity in biological associations, there seem to be at least two problems worthy of experimental attack. These are the principles of regulation and of biocoenotic discontinuity. The first of these was already briefly mentioned in the discussion of elementary constituents, and about the same picture was observed in the study of complexes on glass plates. In one series we had two dominating algae, *Microneis* and *Lyngbia,* that competed for space and later reached a temporary equilibrium. When *Lyngbia* was artificially rarefied in a very considerable proportion, the equilibrium was disturbed, but later on became re-established again owing to competition. The complexity of populations on glass plates is enormous in comparison to that in test tubes, and in the future are expected to exhibit various disturbances of a proper regulation in composition, of the type we have previously described for *Paramecium bursaria.*

The essence of the principle of biocoenotic discontinuity could perhaps be outlined in this way. How, under a continuous gradient of environmental factors that steadily pass from one value to the other, can discontinuous units of structure come into existence, known as associations of living organisms? The data obtained in the field alone are not always entirely satisfactory considering the extreme difficulty of recognizing both the elements of continuity and discontinuity. Some experiments have been recently made by me in which the effect was studied of the continuous alteration in the active reaction of the medium upon an artificial biocoenosis consisting of nine species of infusoria in the test tube. At early stages of growth the differences between mixed populations (that were at the start identical) appeared to be continuous, and discontinuity in composition was recognized only later in their development. One species, *Holosticha,* was depressed on a part of the environmental scale due to physiological causes, mainly because of its sensitivity to increased concentration of phosphates. In this way it let another species, *Paramecium bursaria,* come in, which was otherwise not admitted due to the biocoenotic reason of the presence of *Holosticha,* being itself relatively insensitive to phosphates. In its turn *Paramecium bursaria* depressed a third species, *Halteria,* and thus we have discontinuity of alteration if the composition of associations as regards the environmental gradient has become steadily established.

In the light of all the data available it is scarcely admissible at this stage to wave experimental study of microscopic populations aside and content oneself only with observations of nature as it stands before us in the field. But neither do we expect to find in the experimental population a universal panacea of all our troubles. What we need are more careful investigations of this sort, out of which in the next decade will perhaps evolve another series of general principles of biological associations.

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