



# THE PRINCIPLES OF BIOCOENOLOGY

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THE present review is the exposition of a series of recent investigations in quantitative biocoenology. Its object is to demonstrate certain principles of an experimental approach to the structure of the associations of organisms or biocoenoses. In the study of these associations in the past, investigators laid stress on the morphological side, and scarcely felt the need for applying here an experimental, analytical method. However, it would be as illogical to limit oneself to the morphological investigation of the biocoenosis as to study an aeroplane as though it were an inert and static machine. It is now beginning to be generally recognized that the biocoenosis as a dynamic unit possessing a primitive organization ought to be studied with the aid of the analytical as well as the morphological method.

If a separation of the morphological point of view from the functional one was to a certain extent justified in the past development of cytology, and *idiobiology* in general, there does not seem to be any such justification in modern biocoenology. The laws of form depend here so evidently on the dynamics that any attempt to establish the properties of a structure independently of its transformations is destined to failure. But in our usual observations under natural conditions the complexity of the environment prevents the drawing of reliable conclusions as to the causes of the transformations. Great opportunities are therefore given here to the experimental method, which can be applied *in nature* as well as in the laboratory. The technical possibilities of experimenta-

tion in biocoenology are extremely great. We can directly see how the separate components and elementary processes of the struggle for existence become organized into a whole, and how the laws of form evolve out of the laws of dynamics.

In the present review the mode of approach to the study of organization of the biocoenosis is decidedly an analytical one. At the same time we emphasize the fact that we are only concerned with the principles of organization, and that there remains a great deal of experimental work for their further concretization. The literature on the elementary processes of competition between the components of a biocoenosis has been already summarized by me in *The Struggle for Existence* (1934) and *Vérifications expérimentales de la théorie mathématique de la lutte pour la vie* (1935), and there is no need to repeat it here.

## THE BIOCOENOSIS AS AN ORGANIZED UNIT

1. The recognition of the existence in nature of communities of living organisms or "biocoenoses" probably dates back to the ancient Greeks. In the modern period many botanists endeavored to understand the mutual relations among plants, and the following definition, due to Möbius (1877), is frequently quoted in hydrobiology:

Every oyster bed is in a certain degree a community of living organisms, a combination of species and a population of individuals which find here everything needed for their growth and multiplication. As yet science has no word by which such a community of living beings might be designated, no word for a community where a total of species and individuals is mutually limited and selected under the influence of

average external conditions of life. . . . I propose the word *biocoenosis* for such a community.

The turning point in the history of biocoenology has been the publication of numerous botanical investigations at the close of the last and the beginning of the present century, which demonstrated that the vegetable covering of the earth is divided into natural units of structure or associations. The establishment of a definable unit has automatically led to greater precision of observation and of thought.

If the significance of the biocoenosis as a unit of structure in the living cover of the earth (including animals and plants) does not leave any room for doubt, the degree of organization of this unit is far from being definitely understood. Morphological observations on the structure of biocoenoses show that the latter are characterized by a definite tectological composition and by a definite "texture." In other terms they consist of definite elements in a fixed numerical relation with each other. Elton (1933) remarks, for instance, that the total number of species in an association is a fixed one, and is determined by some important principle. The limitation of the number of species (of which we will become convinced further on) is apparently connected with the limited number of the "ecological niches" which can be utilized by different species without expelling one another, as the number of species saturating the habitat is greater in a more diverse environment. Consequently a biocoenosis consists of only a part of the forms that could potentially enter into its composition. It is already organized in the sense that its membership is a limited one.

The general criterion of an "organized" system is the presence of firmly established relations maintained by regulation and we

will evidently have to decide by means of some kind of dynamic method whether or not this definition holds true for the biocoenosis. *Do there exist any constant characters of constitution and of structure maintained by regulation? In other words, can certain combinations of organisms be stable ones, and the intermediates between them not, even under intermediate conditions?* The solution of this problem can be easily reached with the aid of the analytical method.

A comparison of the organization of a biocoenosis with that of living matter is sometimes made. But such a comparison is scarcely justified at the present time. First of all we have not yet any sufficiently clear understanding of the organization of living matter itself. The underlying units of its constitution are much smaller than those which are revealed by the microscope and scalpel. We can only hope that in the future we shall obtain a better insight into the laws of the molecular organization of living matter. The formation of an organized system on the primitive level of a biocoenosis ought to be therefore considered as an independent and important problem, which at the present time is quite ready for analysis.

2. Let us briefly examine certain observations in field conditions concerning the properties of the biocoenosis as a unit of structure. First of all arises the question whether there exists a sharp spatial separation of one type of structure from another. A number of botanists (Du Rietz, 1921, 1930; Chouard, 1932) give an affirmative answer to this question. In spite of the variety of conditions continuously passing from one value to another only a limited number of distinct associations can be usually established. One complex is sharply separated from another, and the intermediate combinations of species are not observed. However, no unanimity on the subject has been yet

attained (Gleason, 1926) owing to the complexity of field conditions.

To establish objectively how one kind of structure is separated from another an investigation is usually made as to transition of one type of distribution of organisms in space into another. The essential characteristic of the type of distribution in space is relatively simple. We calculate in how far the components of the biocoenosis are distributed in space at random (or not at random), and how sharply a statistical law of distribution peculiar to one association passes into another law in a new association. Regarding many components indications exist that they are not

investigation into  $N$  squares, count the number of individuals of a certain species found on the square ( $v_1$ ) and establish the mean value or abundance ( $v$ ). The statistical investigation shows that if the individuals (or components in general) are distributed according to the law of chance, the square of the standard deviation  $\sigma^2$  (of the variation series constructed with the values  $v_1$ ), divided by the square of abundance ( $v^2$ ) and designated as the relative square mean fluctuation  $\delta^2$  must be equal to the inverse value of abundance  $\frac{1}{v}$ :

$$\delta^2 = \frac{\sigma^2}{v^2} = \frac{1}{v}$$

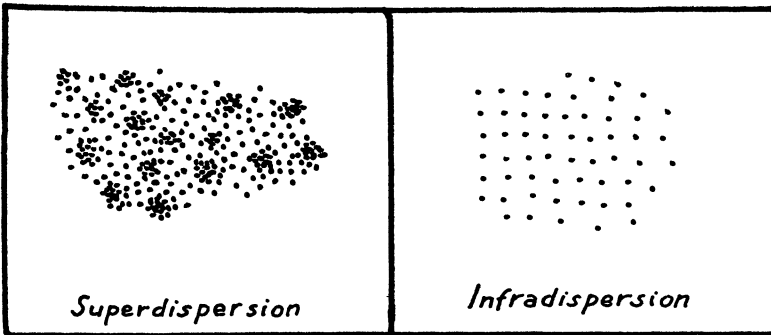


FIG. 1. TWO TYPES OF THE DISTRIBUTION OF ORGANISMS IN SPACE

scattered in the association according to the laws of chance, but are rather grouped into aggregations (Gray and Treloar, 1933; Allee, 1934). Then the character of the statistical distribution of such mosaic complexes or aggregations in the biocoenosis can serve as a criterion of the homogeneity of the latter. If the biocoenosis is homogeneous, the aggregations for their part can be distributed in it according to the laws of chance.

A very accurate method for investigating the character of the spatial distribution of the components in the biocoenosis has been elaborated by The Svedberg (1922). We can divide a plot under

Representing  $\frac{\sigma^2}{v^2}$  as the  $\delta^2$  found, and  $\frac{1}{v}$  as the  $\delta^2$  calculated, it can be said that if the components are distributed at random the ratio  $\delta^2$  found/ $\delta^2$  calculated must be equal to 1. This ratio is called *the coefficient of dispersion*. Every deviation from random distribution in space leads to a deviation from unity of the value of the coefficient of dispersion. Thus, for instance, if the components are distributed in aggregations the per cent of the squares bearing the number of components deviating from the mean value will be greater than we might expect from normal distribution. The  $\delta^2$  found will be greater than

$\frac{1}{v}$  and the coefficient of dispersion will be  $> 1$  (Superdispersion, Fig. 1). But if the components are distributed too regularly (for example the stems of moss when very close together) the coefficient of dispersion will be smaller than the unit (infra-dispersion).

3. The most important structural property of the biocoenosis is the existence of definite quantitative relations between the abundant species and the rarer ones. In this connection let us consider biocoenological terminology. The *abundance* of a species is characterized by the number of individuals on a unit of surface, and the degree of domination by the per cent of

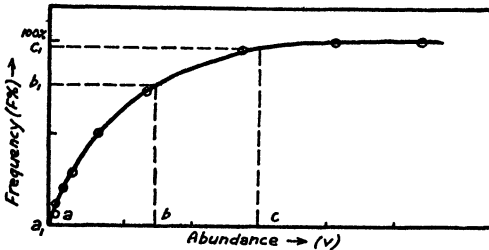


FIG. 2. THE RELATION BETWEEN ABUNDANCE AND FREQUENCY IN THE SNAIL, VALLONIA PULCHELLA (According to Beklemishev, 1931)

abundance of a given species in the abundance of the total population. Another characteristic represents the *frequency*, or the per cent of the samples in which the individuals of the given species have been found in proportion to the entire number of the investigated samples. If we have examined a hundred samples and found a definite species in twenty-five of them the frequency will be 25 per cent. Frequency represents a complicated statistical characteristic which depends on abundance, the size of the sample and the type of the distribution of the organisms on the plot. On a plot of large size we will find all the organisms of the biocoenosis and frequency will become simply transformed into a list

of the species. It is very important to bear in mind the connection between frequency and abundance with the constant size of the sample plot. This connection will depend on the character of distribution of the organisms in space. For the simplest case of a normal dispersion frequency will be an exponential function of abundance:  $F\% = 100(1 - e^{-v})\%$ , where  $F\%$  is frequency and  $v$  abundance. Figure 2 represents this relation often encountered in practice (Beklemishev, 1931; McGinnies, 1934). With the increase of abundance frequency approaches gradually to 100 per cent on the typical saturation curve.

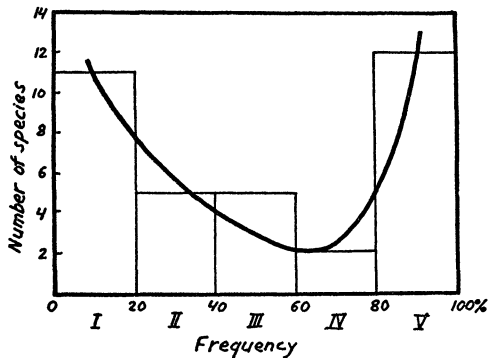


FIG. 3. A TYPICAL CURVE FOR THE DISTRIBUTION OF FREQUENCIES (According to Du Rietz, 1921)

In spite of the great complexity of such a characteristic as frequency many authors have often used it in the investigation of the structure of associations. With a certain moderate size of the sample plot (upon which the frequency of only the most abundant species attains 100 per cent and in others is still very low) we can group frequencies into, for instance, 5 classes: 0-20, 20-40, 40-60, 60-80, 80-100 per cent and determine the number of species which belong to each of them. Jaccard (1902) was the first to build such curves, and Raunkiaer established the following law (Raunkiaer, 1918; Kenoyer,

1927; Gleason, 1929): the greatest number of species belongs to class 0-20 per cent, i.e. they are rare. As the order of the class of frequency rises the number of species belonging to it decreases and reaches a minimum in the fourth class (60-80 per cent) and then rises again in the fifth class (80-100 per cent), attaining a second maximum on the greatest frequencies (Fig. 3). In this manner it becomes possible to separate out of the whole mass of species in the biocoenosis a certain definite group of the most frequent ones which Du Rietz (1921) calls *the constants* of the association. The size of the sample plot upon which these species attain a frequency of 90-100 per cent is called *the minimum area*. In a "real" association, according to Du Rietz, the number of "constant" species (with a frequency of 90-100 per cent) is considerably greater than the number of species in the middle classes of the frequency scale. In artificial "mixtures," on the contrary, it is the great number of species in the middle classes of the scale that is peculiar. In other terms in a "real" (or, evidently, in an "organized") biocoenosis *the predominating part of the biomass belongs to a separated group of frequent or constant species*. This is due to the fact that the organized association is the product of a long process of struggle for existence and of mutual aid. Here survived a few species or combinations of species that are more successfully adapted to particular ecological niches of the habitat and they constitute the basic biomass of the association. There is evidently no such structure in an unorganized mixture. Thus, according to Du Rietz, we can consider the structure of the association as the outcome of a long process of competition and selection.

4. We will soon see that the presence of a definite structure in the biocoenosis may or may not correspond to a state of organi-

zation. One can judge of this latter only by the dynamic and not by the morphological properties. But let us now consider certain difficulties in the work with frequencies. It has been repeatedly pointed out (Gleason, 1929; Romell, 1930) that frequency represents a complicated statistical characteristic, and that in this connection the causes of an accumulation of species in the maximal (fifth) class of frequency require a special analysis. *Does this accumulation reflect the very essence in the structure of the biocoenosis—a certain natural separation of a group of constant species—or is it a statistical artifact?* The possibility of the latter has been mentioned by Gleason (1929). Let us now turn to fig. 2 and suppose that in a certain definite class of abundance, *ab*, fall ten species and that in another analogous class, *bc*, fall also ten species. Taking into account the relation between abundance and frequency it can be easily seen that the first ten species will be dispersed upon a larger section of the frequency scale,  $a_1b_1$ , than the second ten species ( $b_1c_1$ ). In this manner, owing to the exponential relation between abundance and frequency, the most numerous species widely distributed on the scale of abundance can become artificially grouped on a very small section of the scale of frequency. The considerations advanced by Romell (1930) lead also to a notion of the great statistical inclusiveness of the last class of frequency, although his arguments are of a somewhat artificial nature. If we add to this the influence upon frequency of the size of the sample plot and of the character of the dispersion of the organisms in space we will easily come to the following conclusion: *for obtaining an objective representation of the structure of the biocoenosis we must have recourse to some characteristic simpler than frequency.*

The most convenient for this purpose is

the abundance of organisms. In fact it often turns out that the constant species are at the same time the dominant ones, i.e. they predominate as regards abundance (Katz, 1930). Du Rietz (1930) directly introduces the existence of constant dominants in every layer of vegetation into the definition of a phytocoenosis. It is therefore interesting to examine upon existing facts to what extent the group of the most abundant or dominant species is naturally separated in the structure of a biocoenosis. We can analyze the relation between the class of abundance and the number of

the classes of abundance in the lichen stratum of *Pinetum*-association, and curve (2) that of 23 species of plants in the association of *Filipenduletum*. In both cases the sharp separation of two types of species—the abundant and the rarer ones—is quite apparent. The total population is sharply divided into two categories: the numerically dominant species and the non-dominant ones, represented by a small number of individuals. Consequently we arrive here at a conclusion corresponding to that of Du Rietz—the basic biomass of the biocoenosis belongs to a few dominant

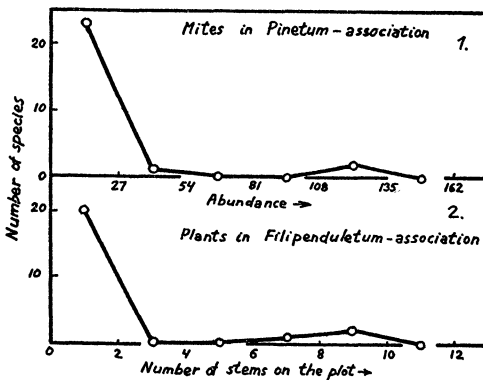


FIG. 4. THE RELATION BETWEEN ABUNDANCE AND THE NUMBER OF SPECIES

(1) Distribution of 26 species of mites. Data from Beklemishev, 1931. (2) Distribution of 23 plants. Data from Beklemishev and Igoshina, 1928.

species belonging to this class. It is often supposed (Gleason, 1929; Beklemishev, 1931) that this relation is of a simple statistical character. In other words the greater the class of abundance the less numerous is the number of species belonging to this class, and in this way no natural separation of a group of abundant species can be observed. However, it is not difficult to see that the situation frequently differs. In Figure 4 are given the curves we have constructed on the basis of the data of Beklemishev and his collaborators (1931). The curve (1) shows the distribution of 26 species of forest mites in

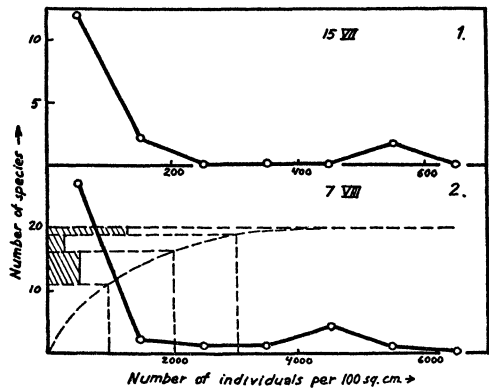


FIG. 5. THE RELATION BETWEEN ABUNDANCE AND FREQUENCY IN THE POPULATING GLASS PLATES SUBMERGED IN THE WATER

(1) young and (2) mature biocoenoses. Data from Duplakov, 1933

species. (For such calculations abundance ought to be expressed in biomass, and not in the number of individuals.)

5. An interesting example from hydrobiology shows that a specific structure can exist in organized as well as in unorganized biocoenosis. Thus Duplakov (1933) following the method of Hentschel (1916) investigated the process of population of glass plates plunged in summer into the water in the shore zone of a lake in Middle Russia. Three days after the beginning of the experiment (15.VII) there was on the glass a typical immature and unstable biocoenosis in which the group of

dominant species was at the same time sharply apparent. On the basis of his data we constructed the curves given in Figure 5. The dominants of the immature biocoenosis were simply the species abundantly represented in the surrounding medium, fixing upon the glass and growing rapidly. Such a feature of an organized state as the regulation of the composition was here entirely lacking. The biocoenosis changed rapidly and only later become somewhat stabilized as regards its qualitative composition. In such a mature biocoenosis (7.VIII) one can also distinguish a group of dominants, but now consisting of species that have shown themselves best adapted to separate ecological niches in the habitat. Figure 5 shows how in the distribution according to the classes of frequency these dominants give a peak in the higher class (dotted diagram). It appears that in working with land vegetation it is more difficult to observe a definite "structure" in unstabilized systems as the process of population is here less regular than in the water of the lake. In this connection botanists use another structural method for recognition of the stabilized biocoenosis (Chouard, 1932). Peculiar to the latter is the presence of a sharply outlined type in the number of species per unit of surface: the variability in the number of species in the sample is represented by the normal variation curve. In the case of unstabilized biocoenoses owing to the irregularity of dispersion there is no sharply outlined typical number of species holding good for the entire territory. The variation curve of the number of species in the sample is irregular and shows several peaks. But in the case of a glass plate being populated in the lake the course of the population is so regular that an immature biocoenosis also possesses a "type." In this way the existence of a definite struc-

ture shows often, *but not always*, a stabilized state of the system. The necessity of a combined morphological (structure) and dynamic (stability) approach to the understanding of organization of biocoenoses is obvious, and it is already recognized by botanists (Du Rietz, 1930).

6. Turning to the structure of stabilized systems we must point out the important principle elaborated by Clements (1916) concerning the very process of stabilization. His observations on vegetation led him to the idea of a gradual development of a stable type of association or *climax* which, owing to its stability, does not allow of any intrusion of new species whereas the unstable intermediate associations admit such an intrusion. The structure of a stabilized system is evidently connected with the fact that some best adapted species have occupied the principal ecological niches. The group of dominants will be the more numerous the greater is the number of different niches or, in other terms, the more the association is "ecologically specialized" (Du Rietz, 1921; Lundbeck, 1926). In a more homogeneous environment the number of dominants falls (Frey, 1927). In any case we can say with certainty that at the basis of the structure of a biocoenosis lies the "niche" structure. The group of rare species is apparently a heterogeneous one and includes the immigrants coming from neighboring habitats, and those individuals that find convenient conditions for living on the various plots existing together with and between the basic niches. The fact of the group of abundant species being usually separated from that of the rarer ones represents a proof of the absence of a continuous transition between the dimensions of the fundamental niches and those of the additional plots. This regularity is especially apparent in the separate layers or *sinusia* of the biocoe-

nosis (Du Rietz, 1930), as the structural properties are here not so much overshadowed by the statistical variability of dimensions of the basic niches.

Summarizing, it can be remarked that the biocoenosis possesses a definite structure whose degree of organization must be investigated experimentally. Field observations raise before us the following problem: How under continuous change of the environment from one value to another can arise stable, spatially separated structures whose composition is maintained by regulation? In other words, how does a state of organization arise?

ON THE PRINCIPLES OF ORGANIZATION

1. The simplest way of answering these questions will be to begin an examination of the principles of organization by pointing out that there exist biocoenoses of two types: the *unstable* and the mature or *stable* ones. The process of development leading to stabilization can be particularly well observed on the population of glass plates plunged in natural fresh waters. Recent observations (Ivlev, 1933) show that the process of development of such a biocoenosis falls pretty regularly into two periods: a period of *accumulation* with a simultaneous growth of all the principal components of the biocoenosis, and a later period of *reconstruction*, when under the influence of competition and of other biocoenotic relations a part of the components is suppressed and begins to diminish in number whilst others develop in even greater abundance (Fig. 6). However, in fresh waters of our latitude a final stabilization of the system is never attained. Having reached a certain stability it continues uninterrupted alteration under the influence of variation of the external medium and finally dies off almost completely in the winter period. It is therefore easy to understand why the idea of

"moving equilibrium" is particularly wide-spread among hydrobiologists (Resvov, 1924).

Recently Duplakov (1933), whom we have already mentioned, carried out a very careful investigation of the process of population of glass plates submerged in Lake Glubokoe (near Moscow), and we

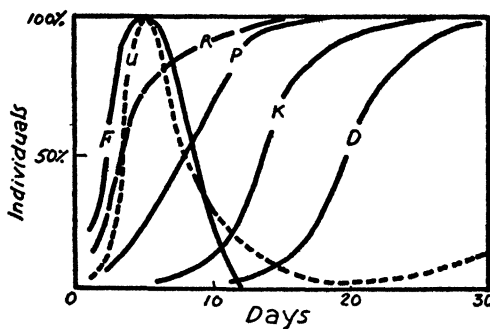


FIG. 6. THE DEVELOPMENT OF POPULATION ON THE GLASS PLATE SUBMERGED IN THE MOSCOW RIVER  
*F*-non-motile *Flagellata*, *U*-non-motile *Protozoa*, *R*-moving *Rotatoria*, *P*-moving *Protozoa*, *K*-non-motile *Rotatoria*, *D*-*Diatomaceae*. From Ivlev, 1933.

TABLE I

The increase of the number of species in a biocoenosis. (Glass plate submerged in Lake Glubokoe.) According to Duplakov, 1933

DAYS AFTER BEGINNING OF THE EXPERIMENT	NUMBER OF SPECIES
1	13*
3	20
5	33
7	33
9	43
26	47
42	45

\* Five of these will disappear on the ninth day.

will discuss here some of the results obtained. Table I shows that the number of species in the populating biocoenosis continuously increases after the submersion of the glass plate into the water and attains a certain stability towards the ninth day (43 species). This number remains approximately constant up to the forty-second day. The slight alterations



occur only at the expense of accidental immigrants represented by an insignificant number of individuals. Some of the first settlers soon disappear, but from the ninth to the forty-second day the qualitative composition of the biocoenosis remains almost the same. These data are therefore in accord with the view of Elton (1933) as to the constancy of the number of species in a biocoenosis, which was based upon the macro-components.

Figure 7 represents some typical curves of growth of separate components. After 24 hours of submersion of the plates one can find *Vorticella* upon them. The num-

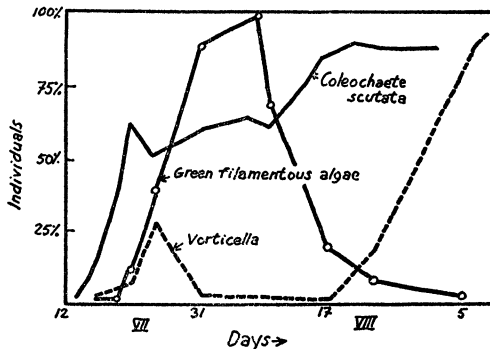


FIG. 7. SOME TYPICAL CURVES OF GROWTH OF SEPARATE COMPONENTS ON THE GLASS PLATE SUBMERGED IN THE WATER  
From Duplakov, 1933

ber of these increases very rapidly and reaches a maximum after 12 days. After this the number of *Vorticella* decreases considerably under the influence of the developing filamentous algae (*Oedogonium* and *Spirogyra*), whose growth is intense in the light (whilst in the dark they are incapable of disturbing the animal nature of the biocoenosis). The expulsion of *Vorticella* from the biocoenosis by the filamentous algae can be explained by the fact that an abundant development of the latter prevents the nutrition of *Vorticella*. Indeed, by its mode of nutrition *Vorticella* belongs to the "sedimentators," and requires for the absorption of the sus-

pending nutritive particles a free circulation of the water which surrounds them. The developing flakes of green algae interfere with this circulation. Towards autumn the filamentous algae finishing their cycle die off, and *Vorticella* develops again.

The curves of development of the lamellate green algae (*Coleochaete* and *Stigeoclonium*) are of peculiar interest. In Figure 7 is traced the curve of growth of a number of individuals of *Coleochaete scutata*. Soon after the beginning of the experiment numerous germinating algae settle down on the glass plate and begin to develop into small lamellae. Later the increase of the number of the lamellae ceases owing to a lack of room. The larger lamellae push off or cover over the young growing algae which have settled on the glass. The overgrowth of the glass by the filamentous algae is also an obstacle to their development. However, at the moment of the strong dying off of the filamentous algae and of another species—*Coleochaete soluta*—owing to seasonal causes, the species *Coleochaete scutata* increases very rapidly, taking possession of the liberated places, and later remains at a new fixed level.

It can be said with perfect assurance that the biocoenosis is subject to regular development and attains a certain state of stability which, however, is very strongly altered by the seasonal variation in the lake. The main factors of development are the biocoenotic relations between organisms—competition, destruction and mutual aid—, and if there were no seasonal changes these would be the only factors of development. The type of the external medium defines the relative advantage of some components over others and, consequently, the type of development itself, but this type is realized only by means of the biocoenotic forces (in the case of constant external

conditions). In the associations of large terrestrial plants the rôle of seasonal variations is not so profound, and it is therefore possible to observe distinctly the stability of the final states or climaxes (Phillips, 1934). The possession of organization and of regulations is usually connected only with these final states and these categories consequently represent an outcome of the process of regular development.

2. If the organization is the outcome of development we must evidently establish the factors governing the dynamics of development and express them in the form of differential equations. The solutions of these equations will indicate the stationary states and furnish complete information about the regulation of these states. The experiments made under constant laboratory conditions can easily verify the theoretical conclusions. We can also analyze the influence of the external factors on the stationary states of the system. To what extent do the properties of the system fail to change in proportion to external alterations or, in other words, why are intermediate combinations of organisms impossible under intermediate conditions? How far do the properties of the system change in an abrupt manner with the threshold values of external factors, etc.?

For the details of these calculations the reader is referred to the two books by Gause (1934, 1935) and the paper by Gause and Witt (1935); we will only briefly examine here some of the fundamental principles. The dynamics of development of a biocoenosis resulting from interaction between species can lead, for example in the simplest case of two components, either (1) to a complete expulsion of one component by the other,

associations in the same ecological niche and on the consequent expulsion of some components by others may be found in Nicol (1934). He writes: "M. Beijerinck's view of the condition of associations of bacteria responsible for the production of commercial preparations of soured milk may be expressed by saying that these associations are in unstable equilibrium. On account of this instability it is not possible to continue inoculation of fresh milk from a properly soured sample indefinitely; after a very few transfers the balance has been so much disturbed that an undesirable product results from fermentation. Commercial quantities of yoghurt are therefore made from continually renewed mixtures of the single species, which are maintained in pure cultures in milk."

or else (2) to a *stabilization*, that is to the establishment of a stable combination of the two components. Both theory and experiment show that a complete expulsion of the less adapted species by the better adapted one can only take place in the case of two species belonging to the same ecological niche in the habitat. The stabilization which interests us more immediately can take place in the case of each of the species possessing an advantage in its own ecological niche (a "two-niches" stabilization) or in the case of a mutual (or a one-sided) help between the species (symbiotic stabilization). If we write a theoretical equation of the interaction between the species in such a case we will come to the following conclusion. The process of interaction between the first species ( $N_1$ ) and the second ( $N_2$ ) will lead to a stable mixed population which will be dynamically maintained. This can be easily seen on the graph with  $N_1$  plotted on the abscissae and  $N_2$  on the ordinates (Fig. 8). This stable population ( $A$ ) will represent a "knot" as the mathematicians call it. In other words all the curves of the interaction between species will meet in this point. If we begin with small concentrations of both species ( $a$ ) they will increase until reaching "stable" values ( $A$ ). If we now destroy the equilibrium artificially by

In addition to the experiments mentioned by Gause (1934) interesting data on the instability of microbic

introducing more  $N_2$  than necessary and less  $N_1$  than is necessary for equilibrium ( $a_1$ ), the "stable" combination ( $A$ ) will be automatically recovered. In this manner the mathematical theory shows quite clearly how the regulation of a type (or of a stable combination) can result from the interaction between species.

Theoretical considerations of this kind are to a certain extent confirmed by the experimental work. The stable combination of species and its regulation can be observed in a mixed population of two infusoria one of which, *Paramecium aurelia* ( $N_2$ ), utilizes more actively the bacterial

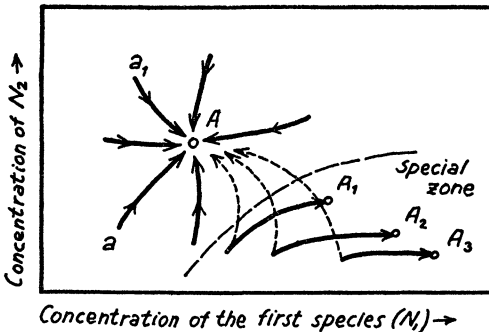


FIG. 8. THE BEHAVIOR OF A MIXED POPULATION OF TWO SPECIES BELONGING TO DIFFERENT ECOLOGICAL NICHES

The dotted lines show the direction of the curves of interaction in the absence of a "special zone."

components of the mixed diet suspended in the upper layer of the liquid, whilst the other, *Paramecium bursaria* ( $N_1$ ) utilizes more actively the yeast settling on the bottom, although both infusoria can live in the entire territory of the microcosm (Gause, 1935). At the same time experimental work points to a certain limitation in the regulation of the typical combination of two species. This regulation is not possible from all the points on the surface  $N_1, N_2$ . If we bring the population into a "special zone" (Fig. 8) where a new factor not taken into account before is in operation (a peculiar sensitivity of  $N_2$  to the metabolic products of  $N_1$  and

$N_2$ ), the "stable" combination ( $A$ ) cannot become reestablished and we will obtain  $A_1, A_2, A_3$ , etc. It is easy to show what are here the alterations in the equation of the interaction between species (Gause and Witt, 1935). Observations of this kind are well known to ecologists. In the population of glass plates, for instance, it may be observed that certain forms enter into a "young biocoenosis" and occupy in it a corresponding place ( $N_2$  enters readily when  $N_1$  is not numerous), but can scarcely enter into an "older biocoenosis" (a great deal of  $N_1$ ), as Karsinkin (1936, in press) remarks. This can also be compared to the facts of an incomplete regeneration of climaxes in the plant associations (Ilinsky and Pozelsky, 1929). Usually certain species cannot regain possession of the places that they occupied before.

3. We can conclude that the first feature of an organized biocoenosis—the regulation (within certain limits) of a stable combination of species—can be successfully observed in an experimental way and accounted for theoretically with the aid of a differential equation. The meaning of a regulation in the case of two species belonging to different ecological niches consists in their expelling one another into the zones of maximal effectiveness, so that every disturbance of such a stationary state leads automatically, owing to competition, to the reestablishment of the stable proportion. Such a regulation can take place also in the case of a symbiosis, when with definite relations between the concentrations of the species the greatest advantage for them is attained (see Gause and Witt, 1935). Let us now consider the second feature of the biocoenosis as an organized unit. Many authors have pointed to the fact that with an uninterrupted change of external factors the types of stable combinations of organ-

isms pass abruptly from one to another or, in other words, that the intermediate combinations of organisms are impossible under intermediate conditions. It seems that this important principle can also be theoretically and experimentally demonstrated with simple biocoenosis.

The idea of a theoretical demonstration represents an application of the mathematical conceptions of Poincaré concerning the *change of stability* in a system. If we assume that a definite biological system is under the influence of the temperature gradient which modifies the relations between the fitness of the species, the calculation will show that at fixed moments the system will undergo *qualitative* changes. One type of stable combination will be succeeded by another type of stable combination. The technical details of such calculations can be found in Gause and Witt (1935). Here we can only note that the changes in question are the result of purely biocoenotic causes: after a certain threshold some components cannot withstand the competition but at the same time continue to exist as pure populations. However, under complex natural environment we have to take into account two factors participating in formation of types: (1) biocoenotic, and (2) physiological factors, i.e. the falling out of components in passing their physiological thresholds which takes place both in pure and in mixed populations. These two groups of factors are often closely interwoven and we will now analyze them on a concrete example.

4. Let us consider briefly the results of several new experiments of the author with artificial biocoenoses of Protozoa in order to illustrate the possibilities of the experimental method here. In these experiments a study was made of the influence of a gradual change in a factor of the external medium (hydrogen ion concen-

tration, *pH*) on the formation of the biocoenoses. An attempt was made to answer the two following questions: (1) What are the differences in structure between the unstabilized and the stabilized biocoenoses?, and (2) How sharp is the separation of one type of biocoenosis from another under such conditions?

The experiments were made in tubes for centrifugation with 5 c.c. of the liquid of the following composition: To one liter of twice distilled water add 40 mg. CaO (in boiling water), pass through CO<sub>2</sub> until dissolved, and then add MgSO<sub>4</sub> (5%)—0.5 c.c., Ca(NO<sub>3</sub>)<sub>2</sub> (1%)—0.5 c.c., K<sub>2</sub>HPO<sub>4</sub> (1%)—0.5 c.c., and FeSO<sub>4</sub>—2 mg. to one liter. This medium is favorable to the majority of the Protozoa and its *pH*

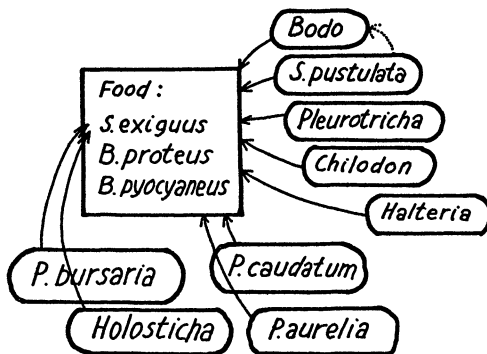


FIG. 9. THE FOOD-CHAIN IN THE EXPERIMENTAL BIOCOENOSIS OF PROTOZOA

is close to 7.9. For a gradual acidulation was used  $m/20$  KH<sub>2</sub>PO<sub>4</sub> and the following *pH*'s were established in separate cultures: 7.6; 7.3; 7.0; 6.6; 6.3. The experiments were made in a thermostat at 24.5°C. with an artificial light according to Hartmann (300 watt). Every day a centrifugation and a change of the medium were made, and likewise the number of individuals in 0.5 c.c. was counted. After the counting the protista were put back into the culture and thus there was no rarefaction of the population. The food consisted of three species of microorganisms which were taken off a solid medium by means of a platinum loop and shaken up in the salt solution. To 30 c.c. was added one loop of *Saccharomyces exiguus*, half-loop of *Bacillus proteus* and half-loop of *B. pyocyaneus*.

Figure 9 shows the food-chain of our biocoenosis consisting of nine species of

TABLE 2

Growth of the number of individuals in experimental biocoenoses under different pH of the medium

(Number in 5 cc.)

DAYS	pH	<i>Paramecium caudatum</i> 0.5 c.c.									DAYS	pH	<i>Paramecium caudatum</i> 0.5 c.c.								
		<i>P. aurelia</i> 0.5 c.c.	<i>P. bursaria</i> 0.5 c.c.	<i>Synglychia pustulata</i> 0.5 c.c.	<i>Planorbis grandis</i> 0.5 c.c.	<i>Holosticha</i> sp. 0.5 c.c.	<i>Halteria grandinella</i> 0.5 c.c.	<i>Chilodon cucullatus</i> 0.01 c.c.	<i>Bodo</i> sp. 0.01 c.c.	<i>P. aurelia</i> 0.5 c.c.			<i>P. bursaria</i> 0.5 c.c.	<i>Synglychia pustulata</i> 0.5 c.c.	<i>Planorbis grandis</i> 0.5 c.c.	<i>Holosticha</i> sp. 0.5 c.c.	<i>Halteria grandinella</i> 0.5 c.c.	<i>Chilodon cucullatus</i> 0.01 c.c.	<i>Bodo</i> sp. 0.01 c.c.		
0	7.9	6	6	5	3	2	3	3	10	9	7.9	6	5	4	36	290		10			
	7.6	6	6	5	3	2	3	3	10		7.6	3	15	1	24	140		60			
	7.3	6	6	5	3	2	3	3	10		7.3	5	19	4	8	140		40			
	7.0	6	6	5	3	2	3	3	10		7.0	20	8	2	11	140	0.5	5			
	6.6	6	6	5	3	2	3	3	10		6.6	1	7	10	8	180	1	7			
	6.3	6	6	5	3	2	3	3	10		6.3	3	14	27	4	5	80		60		
1	7.9	1			2	1	1		10	7.9	8	4	4	3	88	230		22			
	7.6	4	3				2			7.6	3	31	1	20		240	1	3			
	7.3	1	1	1						7.3	1	9	38	7	10	300		4			
	7.0		1	1		1	1			7.0	10	32	1	8		144	1	8			
	6.6	1	4		1		1			6.6	1	5	26	1	8	240		8			
	6.3	3					2			6.3	2	10	30	3	3	60		11			
2	7.9	1	1	1	1		10		12	7.9	10	1	2	6	88	300		6			
	7.6	1	1		3	1	7			7.6	3	8	36	1	10	320		6			
	7.3	2	2		2		6			7.3	2	8	40	3	8	230		4			
	7.0	1	5	1	6		8			7.0	1	7	40	3	4	140	1	3			
	6.6	3			4		12			6.6	1	12	37	7	7	230		9			
	6.3	1	5	2		1	3			6.3	3	16	47	6	5	44		12			
4	7.9		3		7		37	47	14	7.9	8	4	13	120	370	1	4				
	7.6	1	2	1	15		7	120		7.6	1	4	70	3	8	120		3			
	7.3	3	1	1	14		21	40		7.3	12	58	3	6	110		3				
	7.0	1	3	5	15		40	24		7.0	3	10	37	2	12	120	1	4			
	6.6	1	5	7	10		68	40		6.6	1	6	37	2	16	125		18			
	6.3	7	2	14	2		24			62	6.3	2	14	52	12	4	44		8		
6	7.9		4	1	9	5	50	22	15	7.9	5	1	8	4	240	350	1	8			
	7.6	1	2	2	22		30	12		7.6	3	58	5	8	80		4				
	7.3	2	6	8	1	24	34	16		7.3	16	70	4	8	100		6				
	7.0	1	9	11	2	15	46	12		7.0	2	3	70	2	4	110		8			
	6.6	1	4	13	2	6	80	10		6.6	8	62	3	10	100		16				
	6.3	1	10	16	2	4	24			8	6.3	3	12	66	4		88		5		
7	7.9	1	6	3	22	5	100	24	16	7.9	2	2	8	8	220	260		9			
	7.6	2	2	8	26		55	22		7.6	10	80	3	13	60		5				
	7.3	1	4	16	1	24	90	8		7.3	13	68	5	8	88		6				
	7.0	1	7	10	1	9	60	5		7.0	4	75	2	14	84		12				
	6.6	2	5	8	3	11	95	5		6.6	8	70	3	10	105		12				
	6.3	4	9	19	4	3	40			6	6.3	2	12	90	5	4	102		6		
8	7.9		2	1	9	11	240	26													
	7.6		14	1	30		230	44													
	7.3	2	3	25	6	8	140	16													
	7.0		3	10	1	10	120	6													
	6.6	3	7	11	3	7	150	30													
	6.3	1	8	24	4	2	90	10													

Protozoa. As a prototype for this biocoenosis was taken an association really existing in nature. It was merely somewhat simplified by a reduction of the number of components, and an important new condition was introduced: the nutritive and physico-chemical properties of the microcosm were maintained at a fixed level. The mean absolute results of the experiments are presented in Table 2, which shows the growth in the number of individuals under different conditions.

in mature biocoenoses (sixteenth day). They are separated into two sharply individualized types—the phosphateless ( $pH = 7.9$ ) and the phosphate ones. A very strong increase in the concentration of the latter scarcely alters the type of the biocoenosis. Thus we have evidence of the formation of individualized units resulting from the process of development.

Turning to a more detailed analysis of the results we must point out that  $KH_2PO_4$  together with a change of  $pH$  exhibits an additional specific effect on the protozoa (Beers, 1933 and Gause, 1934). In our experiments there took place a strong depression of *Holosticha* by the phosphate

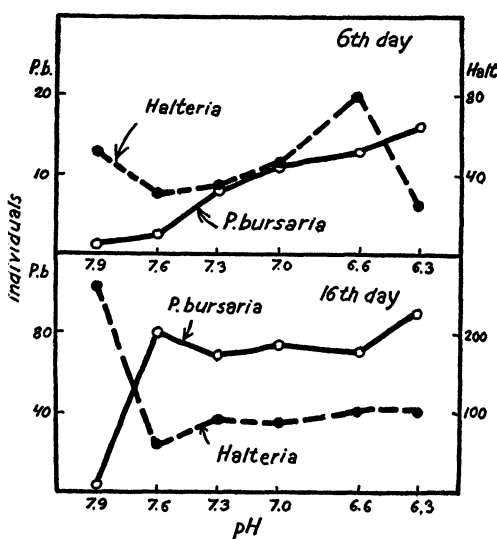


FIG. 10. THE RELATION OF SPECIES TO pH OF THE MEDIUM IN A YOUNG (SIXTH DAY) AND AN OLD (SIXTEENTH DAY) BIOCOENOSIS

An examination of Table 2 enables us to conclude that in a young immature biocoenoses (fourth and sixth days) there is no sharp separation into individualized types at different  $pH$ , and the differences between the types are continuous. This is illustrated by Figure 10 which shows that on the sixth day the densities of *P. bursaria* and of *Halteria* do not form any distinct types on the  $pH$  scale, and that no sharp differences exist between "phosphateless" and "phosphate" cultures. An entirely different picture is to be seen

TABLE 3  
The separate growth of population of *Paramecium bursaria* under different pH of the medium. Number of individuals in 0.5 cc. Food: *S. exiguus*

DAYS	pH					
	7.9	7.6	7.3	7.0	6.6	6.3
2	9.5	8	8	9	10	11
4	19.5	14	13	17	18	24
5	41	35	46	54	41	40
6	67	58	44	60	50	51
7	86	70	80	70	61	86

(through not an immediate destruction, as *Holosticha* has been registered on the second day of growth). This depression is already quite distinct in the immature biocoenosis, and is therefore of a physiological and not of a biocoenotic nature. With the further development of the biocoenosis the place of *Holosticha* is taken by *P. bursaria*, which later begins to crowd out *Halteria* and is responsible for a sharp leap in the changes of concentration of the latter as regards  $pH$ , which did not exist before. We can say with certainty that the insufficient development of *P. bursaria* in a phosphateless biocoenosis ( $pH = 7.9$ ) is due to the presence of *Holosticha* for, when growing separately,

*P. bursaria* develops in almost the same way in a phosphateless and in a phosphate medium (Table 3). In this way *Holosticha* falls out owing to physiological causes and lets *P. bursaria* into the biocoenosis on one side of the ecological scale, while on another section *P. bursaria* is pushed out (or, more exactly, not admitted) biocoenotically by *Holosticha*. The differences between the types of biocoenoses appear as a result of a complicated interweaving of biocoenotic and of physiological causes, and the stable types themselves change abruptly.

TABLE 4  
Calculations of the volumes of species

SPECIES	LENGTH IN DIVISIONS OF THE OCULAR-MICROMETER	VOLUME ( <i>P. caudatum</i> = 1)
1. <i>Paramecium caudatum</i> .....		1
2. <i>P. aurelia</i> .....		0.396
3. <i>P. bursaria</i> .....	39.9	0.405
4. <i>Halteria grandinella</i> .....	9.8	0.036
5. <i>Pleurotricha grandis</i> .....	32	0.101
6. <i>Chilodon cucullulus</i> .....	14.5	0.016
7. <i>Bodo</i> .....	2.25	0.00043
8. <i>Stylonychia pustulata</i> .....	63.6	0.770
9. <i>Holosticha</i> .....	30.3	0.098

In order to obtain an idea on distribution of the biomass between the separate species at different stages of growth of the biocoenosis we measured the species under the microscope and calculated their volumes (Table 4). These data have only the character of a very first approximation to the biomasses, as with differences of shape in the species a calculation of their volumes cannot be a very exact one. With the aid of these coefficients we can see that the surplus of biomass of *P. bursaria* in the biocoenosis with  $pH = 7.6$  as compared to  $pH = 7.9$  coincides almost completely with the deficiency in the biomass of *Holosticha* and *Halteria*. If we

take the mean data for the fifteenth and sixteenth day we obtain: (1) an excess of *P. bursaria*:  $67.5 \times 0.405 = 27.3$  and (2) a deficiency of *Holosticha* and *Halteria*:  $230 \times 0.098 + 235 \times 0.036 = 30.95$ . Therefore from the view-point of biomass these components mutually replace one another. An exact coincidence is hardly to be expected here owing to the approximate calculation of the volumes and the differences in productivity of formation of the biomass by different species at the expense of the same food material (Gause, 1934).

TABLE 5  
Distribution of biomass between different species in the experimental biocoenosis on the sixth and sixteenth days of growth.  $pH = 7.9$

SPECIES	VOLUME PER 0.5 CC.	
	6th day	16th day
<i>P. aurelia</i> .....	1.58	0.79
<i>P. bursaria</i> .....	0.40	0.81
<i>Stylonychia</i> .....	0.77	6.16
<i>Pleurotricha</i> .....	0.91	0.81
<i>Holosticha</i> .....	0.49	21.55
<i>Halteria</i> .....	1.80	9.37
<i>Bodo</i> .....	0.47	0.19

If we turn now to the distribution of biomass between the different species (Table 5) we will be able to note a certain difference between the immature and mature biocoenoses. In a young biocoenosis (sixth day) there are, as biocoenologists say, no "constants" in the association, that is no natural separation of the group of abundant species from the rarer ones. But such a separation appears on the sixteenth day when we have a group of rare species (0.79; 0.81; 0.81; 0.19) and of abundant species occupying the fundamental ecological niches (6.16; 21.55; 9.37). Therefore one can succeed in observing under experimental conditions the appearance of the structural properties of the biocoenosis which are usually men-

tioned in field observations. We can only remark that such a structural property is not always proof of the maturity and stability of the system. We have already had an occasion to point out that in the population of glass plates in the lake there is a very abundant fixation (and growth) of the components which will not be able afterwards to survive in the competition, and thus a structure may arise even in an immature system.

We can endeavor to summarize briefly

our review by pointing out that the fundamental problems raised by field investigations—the regulation of a stable combination of species and the separation of the biocoenoses into individualized natural constructive unities or types in spite of an uninterrupted change in the external conditions—can be successfully analyzed with the aid of the experimental method. The great potentialities of this method for the future of biocoenology admit of no doubt.

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