FLUCTUATIONS

in

THE STRUGGLE FOR LIFE

THEIR FUNDAMENTAL LAWS AND RECIPROCITY

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1. Since 1900 the statistical and mathematical work in biology has intensified. It commenced with statistics, and it was in 1900 precisely that an eminent English mathematician, Karl Pearson, founded the journal *Biometrica*, which has rendered an immense service to the sciences. It was Pearson who recognized that the problems that were posed by the theories of evolution, transformism, and natural selection must be envisioned from the demographic viewpoint, but it was not immediately adopted by scholars. It has taken some time to convince them.

After Pearl, one of the greatest living biological statisticians, the theories in question seem to have been on their deathbed for some years.

Nonetheless, the ideas of evolution and the struggle for existence have aroused great interest *prima facie*. They have been the object of innumerable writings that have exceeded everything that had been done on the other questions of reality.

However, despite the contributions of celebrated authors, the writing and experiments that have been performed on these subjects during the last half-century have not arrived at any conclusions of great import. That is the opinion of Pearl, who added that it is the new path along which one will engage genetics, and that it is the new studies on population and demographic dynamics that have resuscitated transformism and the struggle for life by showing that these theories preserve a surprising vitality.

Presently, these studies continue to progress from either the experimental and practical viewpoint or the mathematical and theoretical viewpoint. Ross, and principally Lotka, Elton, Gause, Thompson, and many others, must be cited for their calculations, experiments, and their practical struggle against pestilential insects in agriculture.

Among the most recent works, I would like to point out the beautiful volume that was published by Kostizin in the Colin collection.

Two new branches of biology have thus developed in recent times: mathematical biology and experimental biology.

I have had occasion to speak on that subject in Paris several time already. I first gave a series of lectures on the struggle for life at l'Institut Henri Poincaré that have been collected into a volume that was published in 1931. Last year, at a conference, I showed that one can advance in biological dynamics in a manner that is analogous to what was followed by rational mechanics by introducing a variational principle of the same type as Hamilton's, reducing the fundamental equations to the canonical form, developing some theories that are analogous to the energetic theories, and finally, by stating *the principle of least action for life.*

I.

2. I shall begin by giving a summary of the general theory.

If one has just one species whose population is N_1, and if the growth coefficient is the positive number ε_1 then the law of Malthus will be expressed by:

$$\frac{dN_1}{dt} = \varepsilon_1 N_1 ,$$

and the population will increase in an exponential manner. Likewise, if the population of a second species is N_2 then one will have:

$$\frac{dN_2}{dt} = - \varepsilon_2 N_2 .$$

The growth coefficient will be the negative number $- \varepsilon_2$. The population will then decrease in an exponential manner, and the species will be exhausted.

If the two species live together, but they have no reciprocal action with each other, then the preceding two equations will be verified simultaneously.

However, suppose that the individuals of the second species eat those of the first, so the growth coefficient of the first species diminishes as the population of the second one increases, whereas the growth coefficient of the second species will increase with the population of the first one, whose individuals form its food. If we assume, in a first approximation, that these increases and diminishments are linear then we must replace ε_1 and ε_2 with $\varepsilon_1 - \gamma_1 N_2$ and $- \varepsilon_2 + \gamma_2 N_1$, where γ_1 and γ_2 are constant positive coefficients. That is why one must replace the preceding equations with the following ones:

$$(A) \qquad \frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 N_2) N_1 , \qquad \frac{dN_2}{dt} = (- \varepsilon_2 + \gamma_2 N_1) N_2 .$$

We leave aside the integration of these equations, which has defined the subject of several papers, and pass on to the general case of *n* species.

In order to study that case, I have employed *the principle of encounter* in my preceding works. We now show, in a very summary manner, that one can also obtain the same results by generalizing the process that was just used in the case of two species.

Imagine a biological association of n species that have populations N_1, N_2, …, N_n and suppose that the individuals of the one species eat those of the other.

Their growth coefficients, which will be ε_1, ε_2, …, ε_n if each species is isolated, will be modified due to their mutual actions.

If we always suppose that these modifications are given by terms that are linear functions of the populations then the growth coefficients for the species r and s will be written:

$$\varepsilon_r + \sum_{s=1}^{n} A_{sr} N_s , \qquad \varepsilon_s + \sum_{r=1}^{n} A_{sr} N_r .$$

Now, it is obvious that A_{sr} and A_{rs} must be constant and of opposite sign, since if the species s eats the species r then A_{sr} must be negative; however, the species r is then eaten by the species s, and as a result, A_{rs} must be positive. If the two types have no reciprocal action then one will have $A_{sr} = A_{rs} = 0$. In addition, one will have that all of the A that have the same indices will always be zero. What is the significance of A_{sr} and A_{rs}?

It is obvious that A_{sr} measures the effect that is exerted on the growth of the species r by the presence of each individual of the species s in the biological association, while A_{rs} measures the reaction that is exerted on the growth in the species s by the presence of each individual of the species r. Now, these two effects cannot be made equal in absolute value, in general.

For example, suppose that one is dealing with two species: One of them consists of large fish, while the other one consists of small fish, and suppose that the individuals of the former eat those of the latter. One easily sees that the introduction of a large fish that eats the small ones will have a greater effect on the growth of the latter species than it will on the growth in the species of large fish, while the introduction of a small fish will have no other effect than to increase the food for the large fish to a lesser degree.

One can take that remark into account by making a new hypothesis, which is very easy to accept, moreover, and which consists of giving different values to the individuals according to whether they belong to one or the other species. The inverses of these values will then be equivalent to the individuals of the different species.

Call these values β_1, β_2, …, β_n and in turn, those of the equivalents $1/\beta_1$, $1/\beta_2$, …, $1/\beta_n$, which corresponds to saying that $1 / \beta_r$ individuals of the species r are equivalent to $1 / \beta_r$ individuals of the species s. By virtue of that hypothesis, one can take:

$$A_{sr} = \frac{1}{\beta_r} a_{sr} , \quad A_{rs} = \frac{1}{\beta_s} a_{rs} , \quad a_{sr} = - a_{rs} ,$$

and then the growth coefficients of the different species will be given by:

$$\varepsilon_r + \frac{1}{\beta_r} \sum_{s=1}^{n} a_{sr} N_s , \qquad \varepsilon_s + \frac{1}{\beta_s} \sum_{r=1}^{n} a_{rs} N_r .$$

One will then have:

(B) $$\frac{dN_r}{dt} = \left(\varepsilon_r + \frac{1}{\beta_r} \sum_s a_{sr} N_s \right) N_r \qquad (r = 1, 2, \ldots, n)$$

as an extension of equations (A) to the general case of n species.

The process that we just followed is not as rigorous as the one that we employed in our preceding work, but perhaps it is more intuitive and simpler.

One can also write equations (B) as:

(1) $$\beta_r \frac{dN_r}{dt} = \left(\varepsilon_r \beta_r + \sum_{s=1}^{n} a_{sr} N_s \right) N_r$$

in which:

$$a_{sr} = - a_{rs}, \qquad a_{sr} = 0, \qquad \beta_1, \beta_2, \ldots, \beta_n > 0.$$

If a_{sr} is positive then that will signify that the species r eats the species s, while if it is negative then contrary statement will true – i.e., the species r will be eaten by the other one. If $a_{sr} = 0$ then the individuals of the two species do not affect each other.

The quantities ε_1, ε_2, …, ε_n are the growth coefficients of the species when each species is isolated. One takes them to be positive when the species is effectively augmented and negative for the ones that tend to be exhausted.

3. If the equations:

(2) $$\varepsilon_r \beta_r + \sum_{s=1}^{n} a_{sr} N_s = 0$$

are satisfied then the populations N_1, N_2, …, N_n will stay constant.

Equations (2) are *the equations of equilibrium* or *the stationary state.* We suppose that the determinant (*fundamental determinant*):

$$\begin{vmatrix} 0 & a_{12} & \cdots & a_{1n} \\ a_{21} & 0 & \cdots & a_{2n} \\ \cdots & \cdots & \cdots & \cdots \\ a_{n1} & a_{n2} & \cdots & 0 \end{vmatrix}$$

is not zero.

In order for that to be true, it is necessary that the numbers of species must be even, since that determinant is half-symmetric. Moreover, one can prove that if n is odd then one will generally have that some of the species will tend to exhaust or grow indefinitely. That will produce a complete modification of the biological association that loses its stability. We then suppose that *the number of species is even and that the determinant is non-zero.*

In addition, one makes the hypothesis that the roots of equations (2) must be positive. We denote them by q_1, q_2, …, q_n, and we will then be certain that there exists an equilibrium state and that these numbers will give the equilibrium populations.

4. One infers from equations (2) that:

$$\sum_{r=1}^{n} \varepsilon_r \beta_r q_r = 0.$$

That is why it is necessary that the ε_r should not all have the same sign in order to have equilibrium, since the β_r are all positive.

Vary the ε_r by $\Delta\varepsilon_r$, so the roots of equations (2) will vary by Δq_1, Δq_2, …, Δq_n. Consequently, due to equations (2), one will have:

(3) $$\beta_r \Delta\varepsilon_r + \sum_{s=1}^{n} a_{sr}\Delta q_r = 0,$$

so

(4) $$\sum_{r=1}^{n} \beta_r \Delta\varepsilon_r \Delta q_r = 0.$$

If the quantities $\Delta\varepsilon_r$ are non-zero and all have the same sign then the Δq_r cannot all be zero [*see* (3)] and the ones that are non-zero will have different signs [*see* (4)].

II.

5. Now, let us envision the fundamental laws of fluctuations. The statement of the first one is as follows:

If one has an even number of species, and if there exists a stationary state then upon starting with a non-equilibrium initial state, one will produce fluctuations that do not die out.

One says that one has *fluctuations* of a population if it has maxima and minima for infinitely large values of time.

They *die out* if the oscillations become as small as one desires for sufficiently large values of time.

In order to prove that law, one must begin by obtaining an integral of equations (1).

Suppose that equations (2) have the roots q_1, q_2, …, q_n . One can then write:

$$\varepsilon_r \beta_r = -\sum_{s=1}^{n} a_{sr} q_s ,$$

and upon eliminating $\varepsilon_r \, \beta_r$, equations (1) will become:

$$\beta_r \frac{dN_r}{dt} = \sum_{s=1}^{n} a_{sr} (N_s - q_s) N_r \, .$$

Upon multiplying these equations by $\dfrac{N_r - q_r}{N_r}$ and summing over the index r from 1 to n, they will become:

$$\sum_{r=1}^{n} \frac{\beta_r}{N_r} (N_s - q_s) \frac{dN_r}{dt} = 0,$$

since $a_{sr} = -a_{rs}$; i.e.:

$$\sum_{r=1}^{n} \left(\beta_r \frac{dN_r}{dt} - \beta_r q_r \frac{1}{N_r} \frac{dN_r}{dt} \right) = 0,$$

and upon integrating:

(5) $$\sum_{r=1}^{n} \left(\beta_r N_r - \beta_r q_r \log N_r \right) = C,$$

in which C is a constant.

Set:

$$\beta_r \, (N_r - q_r \log N_r) = P_r \, .$$

Upon differentiating, one will get:

$$\frac{dP_r}{dN_r} = \beta_r \left(1 - \frac{q_r}{N_r} \right), \qquad\qquad \frac{d^2 P_r}{dN_r^2} = \beta_r \frac{q_r}{N_r^2} \, .$$

The minimum value of P_r is then obtained by taking $N_r = q_r$, and will be:

$$p_r = \beta_r \, q_r \, (1 - \log q_r).$$

On the other hand, one will see that the values of N_r and P_r correspond in the following manner:

$$N_r, \quad 0, \, \ldots \to q_r, \, \ldots \to \infty,$$
$$P_r, \quad \infty, \, \ldots \leftarrow p_r, \, \ldots \to \infty \, .$$

(The arrow indicates the sense in which it increases.)

Since:

$$\sum_{r=1}^{n} P_r = C$$

(in which C is finite if the N_r have finite initial values), one will infer from this that *each N_r must be kept between finite, positive numbers.*

It is obvious that if the $N_r = q_r$ then one will have $\sum_{r=1}^{n} p_r = C$, and conversely, when C has that value, one will have that $N_r = q_r$.

That is why the necessary and sufficient condition for the constant C to be equal to $\sum_{r=1}^{n} p_r$ is that the state of the biological association must be stationary.

Equations (1) give:

$$\beta_r \frac{d \log N_r}{dt} = \left(\varepsilon_r \beta_r + \sum_{s=1}^{n} a_{sr} N_s \right),$$

and upon integrating this from t_0 to t, one will get:

$$\frac{\beta_r}{t - t_0} \log \frac{N_r(t)}{N_r(t_0)} = \varepsilon_r \beta_r + \sum_{s=1}^{n} a_{sr} \frac{1}{t - t_0} \int_{t_0}^{t} N_s(\tau) d\tau .$$

Since $N_r(t)$, $N_r(t_0)$ must be found between finite, positive numbers, it follows that upon letting t grow indefinitely, the left-hand side of the preceding equation will have the limit 0, and consequently, one will find that the quantities:

$$n_s = \lim_{t \to \infty} \frac{1}{t - t_0} \int_{t_0}^{t} N_s(\tau) d\tau$$

satisfy equations (2) of equilibrium. Since the determinant is non-zero, one must have that $n_s = q_r$; i.e., *the asymptotic mean of N_s will be q_r* . One will call that *asymptotic mean* simply the *mean*.

If N_1 , N_2 , … N_n have limits for t infinite then those limits will be their asymptotic means, and as a result, they will correspond to a stationary state. The constant C will therefore have the value $\sum_{s=1}^{n} p_s$, and consequently, the values N_1 , N_2 , … N_n will correspond to an equilibrium state and will be kept constant. One infers from this that if the initial state is not an equilibrium state then the N_1 , N_2 , … N_n will not tend to limits, and in turn, *the fluctuations will not die out.*

The first law is thus proved completely. It bears the name of *the law of conservation of fluctuations.*

From what we found previously, *the means of the populations are equal to the equilibrium populations*. That is the second law.

That law is called *the law of the conservation of means*.

Indeed, since they are equal to the equilibrium populations, they will be independent of the initial conditions, and therefore they will not change when one varies the initial conditions.

6. We now arrive at the third law, which is called *the law of variation of the means*.

It refers to the change in the asymptotic means when one modifies the growth coefficients – i.e., when one simultaneously augments or diminishes all of the numbers ε_1, ε_2, …, ε_n, which corresponds to supposing that one increases or destroys the species in proportion to their populations. For example, the destruction can be realized by fish when the biological association is comprised of several species of fish that cohabitate in the same medium.

We calculate the variations of the asymptotic means that correspond to the $\Delta\varepsilon_r$ that all have the same sign.

One infers from paragraph 4 that if the $\Delta\varepsilon_r$ are all positive or all negative then the Δq_r cannot be either all zero or all of the same sign. That is why *the means of certain species must be augmented, and the means of other species must be diminished*; that is, upon simultaneously augmenting or diminishing the growth coefficients of the species, some of them will be at an advantage, while other ones will be at a disadvantage.

However, the species can be classified into three categories:

1. The ones that eat other ones without being eaten by anything.
2. The ones that are eaten by others without eating anything.
3. The ones that are eaten by others and also eat other ones.

It is obvious that the first category cannot exist in isolation, and likewise for the second category, but it can happen that the three categories exist simultaneously or that there exist two of them, or that the third exists by itself.

Suppose that the $\Delta\varepsilon_1$, $\Delta\varepsilon_2$, …, $\Delta\varepsilon_n$ are negative and the first species is comprised of the ones that are at an advantage for destruction – i.e., that Δq_1 is positive.

Two cases can then present themselves: Either one of the numbers a_{21}, a_{31}, …, a_{n1} is negative, or these numbers are all positive or zero. Consequently, by virtue of the first of equations (3), there will be some positive values among the Δq_1, Δq_2, …, Δq_n , and in turn, there will be some species 2, 3, …, *n* that are eaten by the species 1 that will be at an advantage.

Therefore, there will always exist a species that is eaten and favored – i.e., among the species that are at an advantage, there will be at least one of them that belongs to category 2 or 3.

However, if the species 1 is at an advantage for the destruction (which corresponds to the diminution of the quantities ε_r) then there must exist a species that is at a disadvantage. Thus, if one argues in this case by analogy with the argument that we just made for species 1 then one will find that there must exist at least one species in category 1 or 3 – i.e., a disadvantaged species that is harmed.

7. The third law – i.e., the law of the variation of the means – can thus be stated in the following manner:

If one destroys all of the species uniformly and in proportion to their populations then the mean of at least one of the disadvantaged species (i.e., the species that belong to

categories 2 *and* 3) *will be augmented, and the mean of at least one of the disadvantaged species (i.e., ones that belong to categories* 1 *and* 3) *will diminish.*

That corresponds to the fact that at least of the species that belong to categories 2 and 3 will be at an advantage, and at least one of the species that belong to categories 1 and 3 will be harmed.

In the case for which there exist only species of categories 1 and 2, the destruction will favor at least one of the species 2 and disfavor at least one of the species 1.

My preceding work envisioned only that case. I called species *eaters* only when they belonged to category 1 and *eaten* when they belonged to category 2. I suppressed the existence of species that belonged to category 3, which greatly limited the scope of the third law and estranged me from the real conditions that are presented in nature.

I shall leave aside the exposition of the experimental verifications that the three laws have led to, because we are getting further away from the mathematical viewpoint that we would not like to abandon.

III.

8. Rather, we shall pass on to the exposition of the reciprocity principles that emerge from the laws and formulas that we have envisioned.

Suppose that we have two equilibrium states. The first one corresponds to the growth coefficients ε_1, ε_2, …, ε_n and to the equilibrium populations q_1, q_2, …, q_n.

The other one corresponds to the coefficients ε_1', ε_2', …, ε_n' and to the equilibrium populations q_1', q_2', …, q_n'. In addition, we make the hypothesis (which we also shall also maintain in what follows) that the β_r and a_{rs} do not change.

By virtue of equations (3), one will have:

$$(2') \qquad \begin{cases} \varepsilon_r \beta_r + \sum_{s=1}^{n} a_{sr} q_s = 0, \\[2mm] \varepsilon_r' \beta_r' + \sum_{s=1}^{n} a_{sr} q_s' = 0, \end{cases}$$

so

$$\sum_{r=1}^{n} \varepsilon_r \beta_r q_r' = \sum_{r=1}^{n} \sum_{s=1}^{n} a_{rs} q_s q_r',$$

$$\sum_{r=1}^{n} \varepsilon_r' \beta_r q_r = \sum_{r=1}^{n} \sum_{s=1}^{n} a_{rs} q_s' q_r.$$

However:

$$\sum_{r=1}^{n} \sum_{s=1}^{n} a_{rs} q_s' q_r = \sum_{r=1}^{n} \sum_{s=1}^{n} a_{sr} q_s' q_r = - \sum_{r=1}^{n} \sum_{s=1}^{n} a_{rs} q_s q_r',$$

so:

$$\sum_{r=1}^{n} \varepsilon_r \beta_r q_r' = - \sum_{r=1}^{n} \varepsilon_r' \beta_r q_r.$$

That is the *first reciprocity principle*.

9. We remark that the quantities q_r and q_r' must be positive, but that limitation does not extend to their variations. In addition, observe that equations (3), which one obtains by varying equations (2′), have the same form since they are linear.

Now, neither the ε_r nor the q_r appear in equations (3); therefore, the Δq_r will always be the same for any q_1, q_2, …, q_n, provided that one preserves the values of the $\Delta \varepsilon_r$. One can then state the theorem:

The variations of the equilibrium populations depend upon variations of the growth coefficients, but they are independent of the growth coefficients and the original equilibrium populations.

It is obvious that this proposition is subordinate to the condition that the equilibrium populations will remain positive after their variation.

10. By virtue of equations (2) and (3), one will get:

$$\sum_{r=1}^{n} \varepsilon_r \beta_r \Delta q_r = \sum_{r=1}^{n} \sum_{s=1}^{n} a_{rs} q_s \Delta q_r \,,$$

$$\sum_{r=1}^{n} \Delta \varepsilon_r \beta_r q_r = \sum_{r=1}^{n} \sum_{s=1}^{n} a_{rs} \Delta q_s q_r \,,$$

and by a process that is analogous to the one that was followed in paragraph 8, one will have:

$$\sum_{r=1}^{n} \varepsilon_r \beta_r \Delta q_r = - \sum_{r=1}^{n} \Delta \varepsilon_r \beta_r q_r \,.$$

This is *the second reciprocity principle.*

11. One infers from equations (4) that if $\Delta \varepsilon_i$ is non-zero, while $\Delta \varepsilon_1$, …, $\Delta \varepsilon_{i-1}$, $\Delta \varepsilon_{i+1}$, …, $\Delta \varepsilon_n$ are zero, then one must have $\Delta q_i = 0$. The theorem then results:

The equilibrium population of a species will be preserved when one changes its growth coefficient, provided that one does not change the coefficients of the other species.

However, we have found in paragraph 5 that the mean of the population of a species coincides with its equilibrium population; therefore, one can state the preceding proposition in the following manner:

If one preserves the growth coefficients of the species without alteration, except for one of them, then the mean of the population of that species will not change, while the means of the other species will change.

The statement of this theorem seems *paradoxical*, which is why one calls it the *demographic paradox*. It is nonetheless easy to persuade oneself of its exactitude.

In order to do that, it will suffice to envision a particular example, namely, that of the two species that we considered in paragraph 2.

In the case of equilibrium, equations (*A*) will become:

$$\varepsilon_1 - \gamma_1 N_2 = 0, \qquad -\varepsilon_2 + \gamma_2 N_1 = 0,$$

which is why the equilibrium populations will be:

$$q_1 = \frac{\varepsilon_2}{\gamma_2}, \qquad q_2 = \frac{\varepsilon_1}{\gamma_1},$$

and we will have:

$$\Delta q_1 = \frac{\Delta \varepsilon_2}{\gamma_2}, \qquad \Delta q_2 = \frac{\Delta \varepsilon_1}{\gamma_1}.$$

For example, if $\Delta \varepsilon_1 > -\varepsilon_1$ is negative and $\Delta \varepsilon_2 = 0$ then Δq_2 will be negative and $\Delta q_1 = 0$. Therefore, a reduction of the growth in the species 1 (viz., the eaten species) without there being any variation in the growth coefficient of species 2 will produce a diminution of the equilibrium population, and in turn, of the mean of the species 2 (viz., the eating species), but it will not modify the equilibrium population of species 1, and in turn, its mean. It is easy to imagine the truth of this conclusion, since there will be one kind of compensation between the negative variation of growth of the eaten species and the diminution of the destruction that is due to the reduction of the population of the eating species. That is why the mean of the first species will not change, while that of the second species will diminish.

All of the other cases that can be presented can be interpreted in an analogous fashion.

12. Suppose that one is first given the variations $\Delta \varepsilon_1$, $\Delta \varepsilon_2$, …, $\Delta \varepsilon_n$ of the growth coefficients and then the variation $\Delta' \varepsilon_1$, $\Delta' \varepsilon_2$, …, $\Delta' \varepsilon_n$, and that one first obtains the variations of the equilibrium populations Δq_1, Δq_2, …, Δq_n and then $\Delta' q_1$, $\Delta' q_2$, …, $\Delta' q_n$, respectively.

Due to equations (3), one will have:

$$\beta_r \Delta \varepsilon_r + \sum_{s=1}^{n} a_{sr} \Delta q_s = 0,$$

$$\beta_r \Delta' \varepsilon_r + \sum_{s=1}^{n} a_{sr} \Delta' q_s = 0,$$

so

$$\sum_{r=1}^{n} \beta_r \Delta\varepsilon_r \Delta'q_r = \sum_{r=1}^{n}\sum_{s=1}^{n} a_{rs}\Delta q_s \Delta'q_r ,$$

$$\sum_{r=1}^{n} \beta_r \Delta'\varepsilon_r \Delta q_r = \sum_{r=1}^{n}\sum_{s=1}^{n} a_{rs}\Delta'q_s \Delta q_r .$$

However:

$$\sum_{r=1}^{n}\sum_{s=1}^{n} a_{rs}\Delta q_s \Delta'q_r = \sum_{r=1}^{n}\sum_{s=1}^{n} a_{sr}\Delta q_r \Delta'q_s = -\sum_{r=1}^{n}\sum_{s=1}^{n} a_{rs}\Delta'q_s \Delta q_r .$$

Therefore:

$$\sum_{r=1}^{n} \beta_r \Delta\varepsilon_r \Delta'q_r = -\sum_{r=1}^{n} \beta_r \Delta'\varepsilon_r \Delta q_r .$$

This is *third reciprocity principle.*

We have called (§ 2) β_1, β_2, …, β_n the values of the individuals of the different species. That is why $V_r = \beta_r N_r$ will be the value of the species r and:

$$V = \sum_{r=1}^{n} \beta_r q_r$$

will be the mean value of the association.

Since $a_{sr} = -a_{rs}$, one will have:

$$\frac{dV}{dt} = \sum_{r=1}^{n} \frac{\beta_r dN_r}{dt} = \sum_{r=1}^{n} \varepsilon_r \beta_r N_r + \sum_{r=1}^{n}\sum_{s=1}^{n} a_{sr} N_s N_r = \sum_{r=1}^{n} \varepsilon_r \beta_r N_r ,$$

and consequently:

$$dV = \sum_{r=1}^{n} \varepsilon_r \beta_r N_r \ dt.$$

Therefore, at each instant, the augmentation of the value of the association will depend upon only the growth coefficients, because it will not depend upon the reciprocal action that the different species exert upon each other. An association of that sort will be called *conservative*.

Suppose that:

$$\Delta\varepsilon_1 = \Delta\varepsilon_2 = \ldots = \Delta\varepsilon_{r-1} = \Delta\varepsilon_{r+1} = \ldots = \Delta\varepsilon_n = 0,$$
$$\Delta'\varepsilon_1 = \Delta'\varepsilon_2 = \ldots = \Delta'\varepsilon_{r-1} = \Delta'\varepsilon_{r+1} = \ldots = \Delta'\varepsilon_n = 0,$$

while $\Delta\varepsilon_r$ and $\Delta'\varepsilon_r$ are non-zero.

Due to the third reciprocity principle, one will have:

$$\beta_r \ \Delta\varepsilon_r \ \Delta'q_r = -\beta_s \ \Delta'\varepsilon_s \ \Delta q_s ,$$

and in turn, if:

$$\Delta \varepsilon_r = \Delta' \varepsilon_s,$$

then one will get:

$$\beta_r \, \Delta' q_r = - \, \beta_s \, \Delta q_s \, ;$$

i.e.:

$$\Delta' v_r = - \, \Delta v_s \, .$$

One will then have the proposition:

The variation of the mean value of the species r (i.e., the variation of the value of the equilibrium population) *that is produced by a variation of the growth coefficient in the species s is equal and of opposite sign to the variation of the mean value of the species s* (i.e., the variation of the value of the equilibrium population) *that is due to an equal variation of the growth coefficient in the species r.*

This theorem presents an analogy with the known reciprocity theorems of the theories of elasticity and electrostatics, but it differs by a change of sign. Indeed, these latter theorems depend upon a symmetric determinant, while the preceding theorem that one has in biology follows from the existence of a hemi-symmetrical determinant.

15. I will conclude with an elegant extension of the preceding propositions that was given H. Freda.

Take a group of species that belong to the association and, consider its mean value $\sum \beta_r \, q_r$, which one obtains by adding the mean values of the species that comprise it. The variation of that value that is due to a change in the growth coefficients will be $\sum \beta_r \, \Delta q_r$.

If one varies only the growth coefficients of the species of the group, and *by the same quantity* $\Delta \varepsilon$ (i.e., uniform variation) then due to equation (4), one will get:

$$\sum \beta_n \, \Delta \varepsilon \, \Delta q_n = 0,$$

and in turn:

$$\sum \beta_n \, \Delta q_n = 0;$$

the mean value of the group does not change.

Imagine a second group of different species. If we combine them with the first group then we will obtain an ensemble whose value does not change when we give the same variation to all of the growth coefficients of the species that comprise it.

However, the variation of the mean value of the ensemble is composed of variations of the mean values of the two groups; in each of them, one can combine the terms that result from the uniform variation of just one growth coefficient of the species of one or the other group. If we distinguish the two groups by the indices 1 and 2 then we will have:

$$\Delta V_{11} + \Delta V_{22} + \Delta V_{12} + \Delta V_{21} = 0,$$

in which ΔV_{ik} denotes the variation of the mean value of the group *i* when the uniform modification of the growth coefficients applies to only the species of the group *k*.

Since the first two terms in the preceding equality are zero, the other two must compensate – i.e., they must be equal and of opposite sign.

One can thus state the following theorems:

If one gives the growth coefficient of one group of species a uniform variation then the mean value of that group will not change.

The variation of the mean value of a group that is due to a uniform variation of the growth coefficients of another group is equal and of opposite sign to the variation of the mean value of the second group for the same uniform variation of the coefficients of the first one.

These theorems generalize the ones in paragraphs 11 and 14.

One can add that the first of these theorems will remain valid when the group includes the entire association.

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