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ON CERTAIN UNIFYING PRINCIPLES IN ECOLOGY

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Ecologists have been reluctant to place their observations and their findings in the frame of a general theory. Present day ecology is extremely poor in unifying and ordering principles. A certain effort should be made in constructing a general frame of reference, even though some of the speculation may be dangerous or misleading. This paper presents various points of view, some perhaps original, others not so. Certain of these viewpoints have been discussed previously but separately, in other papers published or in press.

In such an enterprise, discussion with students and colleagues has been essential, and the author has profited from the experience and criticism of many people. A special sense of indebtedness is felt towards Monte Lloyd, H. T. Odum, R. MacArthur, E. P. Odum, G. E. Hutchinson, and V. Tonolli.

STRUCTURE OF THE ECOSYSTEM

Ecosystems have a structure, in the sense that they are composed of different parts or elements, and these are arranged in a definite pattern. The interrelations between the constituent elements are the basis of the structure. Of course, it is possible to recognize and measure different degrees of structure. One measure would be the number of parameters needed for describing a certain situation.

More specifically, ecosystems formed by a greater number of species allow for a higher number of specific relations in food webs, parasitism, etc. These require a longer description, to express an equivalent degree of knowledge. Considering the ecosystem in terms of individuals distributed in different species is only one of several possibilities; we can think of it also in relation to chemical compounds or biochemical systems. For example, assimilatory pigments provide a very concrete and useful botanical approach. A similar concept of structure can be applied even to the environment. Consider, for instance, the kinds and proportions of organic substances produced by organisms and present in aquatic ecosystems.

The main point is that the "real" structure of an ecosystem is a property that remains out of reach, but this complete structure is reflected in many aspects of the ecosystem that can be subjected to observation: in the distribution of individuals into species, in the pattern of the food net, in the distribution of total assimilatory pigments in kinds of pigments, and so on.

Structure, in general, becomes more complex, more rich, as time passes; structure is linked to history. For a quantitative measure of structure it seems convenient to select a name that suggests this historical character, for instance, maturity. In general, we may speak of a more complex ecosystem as a more mature ecosystem. The term maturity suggests a trend, and moreover maintains a contact with the traditional dynamic approach in the study of natural communities, which has always been a source of inspiration.

Maturity, then, is a quality that increases with time in any undisturbed ecosystem. Field ecologists use many criteria to estimate the maturity of an ecosystem, without the need of assessing its precise place in an actual succession. Empirical knowledge of succession leads one to consider as more mature the ecosystems that are more complex; that is, composed of a great number of elements, with long food chains, and with relations between species well defined or more specialized. Strictly stenophagous animals, parasites, all sorts of very precise symbiotic or defensive relations, are commoner in mature ecosystems. Furthermore, situations are more predictable, the average life of individuals is longer, the number of produced offspring lower, and internal organization of the ecosystem turns random disturbances into quasiregular rhythms. Leaving aside for the moment the aspects of turnover and rhythms to be dealt with later, we can focus now on the structure and how it can be expressed quantitatively.

Practical situations impose severe limitations on theoretical possibilities. Theoretically, it would be possible to compute a diversity index, expressing the distributions of individuals into species in the whole ecosystem. This is most conveniently done by determining the average number of bits per individual (Margalef, 1957), but under conditions that are common in natural communities any other diversity index will be applicable. Unfortunately, nobody has even attempted to undertake a complete census of the whole community. Thus, we are forced to compute our diversity through samples of the community, selected by the use of certain technical implements (plankton nets, traps, light to attract insects) or by taxonomical criteria (diversity of birds, of insects, of copepods, of dinoflagellates). Nevertheless, there is evidence that the more inclusive structure is reflected in the composition of these selected parts, arbitrarily chosen by the taxonomic relation of components or by mechanical procedure, but always measured in the same way. Sampling has to be organized very critically. One has to remember, for instance, that samples including small organisms taken at random usually show a lower degree of organization and maturity than samples of bigger animals with definite spatial pattern of distribution, and with forms of behavior utilized by man in their capture. Samples that include organisms belonging to superior trophic levels may represent a higher maturity than samples with a more predominant representation of primary producers.

On the other hand, one can rely on the congruence between estimates of maturity obtained at different levels. There is a good correlation between the diversity in the distribution of individuals into species, and in the diversity of plant pigments in the plankton (Margalef, 1961b). MacArthur (1961) has found a good correlation between bird species diversity, plant species diversity and diversity in the mass distribution of foliage of plants in different strata. A glimpse at the fish market in any place of the world gives an idea of species diversity in the exploited fishery, and in general, biotic diversity of plankton in the same places varies accordingly.

There is no doubt that we can get numbers expressing the structure of ecosystems. If used properly, these numbers permit comparisons. We can tell which system, of two being confronted, is more complex and mature. This can be done either with neighboring ecosystems or with completely independent and distant ecosystems. The handling of diversity data poses certain problems, mostly concerned with the spectrum of diversity in relation to space, but these questions have been discussed elsewhere (Margalef, 1957, 1961a, 1961b) and moreover are not relevant to the present discussion.

THE ECOSYSTEM IN RELATION TO ENERGY AND MASS

The ecosystem has different complementary aspects: If we consider the elements and the relations between the elements, we have the structure, whereas in considering matter and energy, we have to deal with metric properties which are perhaps easier to express. The ecosystem is formed by a certain amount of matter (biomass) and there is a budget of matter and energy.

For the moment, let us consider an ecosystem in a steady state, with a material output equal to the material input. Here we need to consider only two quantities: the matter present, or biomass, in the ecosystem, always to be expressed in the same form (total weight, dry weight); and the potential energy necessary for maintenance in the ecosystem, amounting to total respiration and other losses. Both quantities can be considered in every ecosystem and simply equated to primary production (P) and biomass (B); both concepts are of common usage in ecology. Their relation (P/B) can be stated as flow of energy per unit biomass; it is the turnover rate of Cushing, Humphrey, Banse and Laevastu (1958) and the productivity index under natural light conditions of Strickland (1960). Note that it is convenient always to take the total biomass including that of the animals. The dimensions of the ratio P/B are $L^2 T^{-3}$, when P is expressed as power; and T^{-1} as simple turnover. The dimensional quotient $L^{-2}T^2$ represents the amount of biomass necessary to carry a given quantity of potential energy and may change from ecosystem to ecosystem.

What is important is the empirical relation between structure and energy flow per unit biomass. More mature ecosystems, with a richer structure, have a lower primary production per unit biomass. This has been observed in laboratory cultures and all the scattered data found in the literature that seem relevant in this connection, mostly on pelagic communities, point towards the same conclusion or, at least, do not contradict it. The ratio P/B is taken as the ratio expressed by *primary production/total biomass*, including all elements of the ecosystem, such as the consumers, etc. In ecosystems of higher maturity there is a more complete use of food, there is a greater proportion of animals, and energy cascades through a more considerable number of steps. This is true in aquatic ecosystems, but in terrestrial ecosystems a somewhat paradoxical situation arises owing to a certain exaggerated dominance of vegetation. On the other hand, the great number of possible kinds of relations in a mature ecosystem allows a higher efficiency in every relation. If these relations are considered as communication channels, less noise comes into them.

There is another way to look at the relations between energy flow per unit biomass and structure, based on an experiment that can be introduced in every ecology course. We start with an old aquarium harboring a mixed population. We can measure diversity in the distribution of individuals into species, and in the distribution of pigments; also we measure total biomass and primary production. The results are criteria for attributing to the system, a certain quantitative expression of rather high maturity. Then we lead the ecosystem to a state of lower maturity; the more effective way of doing this is to stir the contents of the aquarium and pour into it some nutritive solution. We get a bloom of plankton and the state of lower maturity is reflected both in a decreased diversity at all the levels, and in an increased ratio—*primary production/biomass*. Of course, the relation—*biomass of plants/biomass of animals*—changes to the benefit of plants. This simple experiment has a counterpart in terrestrial ecology: plowing a field and putting manure into it, and this is one of the oldest experiments in ecology.

If we want to follow the experiment, we leave the aquarium containing our "rejuvenated" population alone. As time goes on the ratio expressed by *primary production/total biomass* drops, both by increase of biomass and by reduction of primary production. Diversity increases at every level. Maturity increases. This is succession.

Perhaps the most instructive period in the experiment is when maturity decreases rapidly. Why does diversity decrease, as energy flow per unit biomass becomes higher and higher? At this moment, the system is suddenly able to produce a great power output, but only if there is not too much concern for efficiency (Odum and Pinkerton, 1955). Certain pigments capable of rapid synthesis and occupying a key position in photosynthesis (for example, chlorophyll A) increase much more than others. Pigment diversity drops. Similarly, species with the highest maximal rate of potential increase become advantageously dominant, and diversity drops. We are always confronted with a fall in species diversity in similar situations involving utilization of a sudden burst of potential productivity, for example, in a plankton bloom, in a polluted river, or in a cultivated field.

It seems safe to assume that maturity has a double measure: In its structural aspect, it can be measured in terms of diversity or of complexity over a certain number of levels. In the aspects relating to matter and energy, it can be measured as primary production per unit of total biomass. The connections between complementary aspects and measures require theoretical consideration.

The ratio—*primary production/total biomass* has not been selected for theoretical considerations, but simply because it is easily at hand. But the true meaning of biomass, if we think over this expression, has to be construed as something that is the keeper of organization, something that is proportional to the influence that an actual ecosystem can exert on future events. If this influence over the future is simply equated with dry weight or any other usual expression of biomass, one foresees inaccuracies. In fact, the same amount of dry weight may have a different influence on future developments according to how it is organized. Moreover, elements that actually are not counted as parts of biomass, such as dead wood, burrows, and the like, are elements of organization, since they exert a certain influence on the future development of the ecosystem. From a general theoretical standpoint, it would be advisable to replace the ratio *primary production/total biomass* by a more sophisticated ratio; turning to the converse (B/P), it could be defined as the amount of information that can be maintained with a definite spending of potential energy. Here information is taken in the sense of something at which life has arrived through a series of decisions, and that influences, in one or another sense, future events. The ratio P/B may be considered also as metabolism per unit biomass. The rate of change of average community metabolism is always negative along succession.

The ideas developed so far can be summarized as follows. An ecosystem that has a complex structure, rich in information, needs a lower amount of energy for maintaining such structure. If we consider the interrelations between the elements of an ecosystem as communication channels, we can state that such channels function on the average more effectively, with a lower noise level, if they are multiple and diverse, linking elements not subjected to great changes. Then, loss of energy is lower, and the energy necessary for preventing decay of the whole ecosystem amounts relatively to less. This seems to be one of the basic principles of ecology, probably recognized tacitly by most writers, although rarely put in an explicit way.

SUCCESSION AND FLUCTUATIONS

Any ecosystem not subjected to strong disturbances coming from outside, changes in a progressive and directional way. We say that the ecosystem becomes more mature. The two most noticeable changes accompanying this process are the increase of complexity of structure and the decrease of the energy flow per unit biomass. This theoretical background leads us to accept a sort of natural selection in the possible rearrangements of the ecosystem: Links between the elements of an ecosystem can be substituted by other links that work with a higher efficiency, requiring a change in the elements and often an increase in the number of elements and connections. The new situation now has an excess of potential energy. This can be used in developing the ecosystem further, for instance, by adding biomass after driving more matter into the system. A more complex state, with a reduced waste of energy, allows maintenance of the same biomass with a lower supply of energy — or a higher biomass with the same supply of energy — and replaces automatically any previous state.

The only limit set to this progressive change is interference from the physical environment. Succession can build history only when the environment is stable. In the case of a changing environment, the selected ecosystem will be composed of species with a high reproductive rate and lower special requirements. Such an ecosystem is less diverse and less complex; the energy flow per unit biomass remains relatively high. There is another situation where an ecosystem cannot increase maturity: when there is a constant loss of individuals by diffusion, sedimentation or exploitation by the action of external agents. In such situations, something is exported which otherwise could be used in increasing organization.

The study of succession does not include all relations of ecosystems with time. In a more refined consideration of concepts, diversity may be represented as the width of a communication channel, apt to carry along time a certain amount of organization or of information at the selected level. This sets limitations, of course. An ecosystem with a low biotic diversity cannot carry a high degree of true organization. But a highly diversified community has the capacity for carrying a high amount of organization or information. This does not signify that the potential amount is always actually carried. The difference can be illustrated by comparing a planktonic community with a bottom community over rocky substratum. Both communities may have similar diversities, but the organization based on such diversity can be carried more effectively along time in the benthic community. Here, spatial distribution of individuals belonging to different species (pattern) is preserved, and with it most of the relations existing between such individuals. If we determine the pattern of such a community at a time *a*, and then at a subsequent time *b*, and so on, we discover that transitions from one state to the next follow a notable regularity; the pattern's deterministic component is more important than its random component. In other words, diversity effectively measures information that is carried along with time. In the case of the plankton community, the matrix describing the transition probabilities between successive states can be recognized as possessing a deterministic part and a random part; but here the second part is more important than in the benthos: think only of the turbulence of water, carrying organisms and influencing contacts between organisms of different species. In this situation, the channel width is not effectively used because of turbulence — a random element of the environment.

Perhaps the following analogy may clarify the difference under discussion: Let us imagine the structure of a community in terms of a message, written in a language with a number of symbols equal to the number of species, and where individual symbols stand for individuals. A benthic community would be more like a real text written with this language; a planktonic community would be rather comparable with an imaginary text in which letters were not fixed, but are subjected to a certain sort of thermic agitation that makes them change places over and over again, so that the amount of information actually carried would be reduced. The conclusion is that in any estimate of maturity, not only diversity, but also predictability of change with time has to be considered. Ordinarily both characters are correlated. Less mature ecosystems not only have a lower diversity, but in them transition between successive states includes a higher amount of uncertainty. And more diverse ecosystems have, in general, more predictable future states. In other words, in more mature ecosystems the future situation is more dependent on the present than it is on inputs coming from outside. Homeostatis is higher. On the other hand, future states in less mature ecosystems are heavily influenced by external inputs, by changes in the physical environment.

Let us consider any structure formed by interconnected elements, like a nervous net, an automaton, or an ecosystem, and subjected to inputs (changes in the physical environment, as stimuli) and giving off outputs (reaction on the environment, population waves, migrations, rhythms of activity and so on). Internal organization of such a system can turn random inputs or disturbances into much more regular outputs or rhythms. Cole (1951) and Palmgren (1949), among other ecologists, have discussed the possibility that "regular" cycles in populations may originate by the interaction of random inputs, for example, relative strength of year classes, as related to random changes in climatic factors or to alteration in the structure of the existing unispecific population and of the whole ecosystem in which the population is integrated. The properties associated with the structure of the ecosystem define the operations to do with the random inputs, and give more or less regular output patterns. Analogously, a crystalline body converts a random x-ray input into a regular diffraction pattern. It may be pertinent for the ecologists to remember here the importance of general theories on automata and nerve nets, and the theory of storage (Moran, 1959), and the recent developments on random theory (Wiener, 1958; see also Barlow, 1961).

In general, the expected differences in the character of fluctuations in less mature and more mature communities would be as follows. In less mature communities, environmental fluctuations are strong and able to stop the trend to increase maturity at a certain level. Maturity does not increase because abiotic fluctuations are too strong, and homeostatis is difficult to attain in a poorly organized, often a pioneer community. In a more stable environment, succession proceeds and maturity increases; now we have to expect rhythms that are more regular, more independent of environment and often endogenous. Anticipatory power has survival value and is the expression of a complex system, able to produce very efficient homeostatic mechanisms. Up to a certain level, these homeostatic mechanisms can protect the system from disruption due to external agents. Maturity is self-preserving.

Fluctuations of unispecific populations can be considered on the same background. Large fluctuations in populations are to be expected in less mature ecosystems: a rapid increase of numbers of a plant or an animal is possible only in a system that works with low efficiency, the subsequent drop in the number of individuals means either a great mortality and consumption by other organisms, or dispersal or migration out of the ecosystem, in any case a strong flow or export of potential energy. In this sense strong fluctuations in plankton populations represent a heavy export towards other communities, for instance, towards the benthos. Planktonic communities retain always a less mature character than benthic communities, and it is to be expected, in good agreement with observation, that fluctuations in planktonic populations are of shorter period and wider ranges.

Fluctuations of an ecosystem often may be considered as fluctuations in the degree of maturity around an average maturity. At certain periods of the year the ecosystem is less mature than at other times. Such changes could be considered as true successions, starting again and again. In the plankton, for instance, the period of vertical mixing of water corresponds to a less mature aspect of the whole ecosystem and can be taken as the starting point of a succession of phytoplankton. In other elements of pelagic life, changes are simple fluctuations, rather than true successions.

The necessary energy to disrupt an ecosystem probably maintains certain relations with the attained maturity. Anything that keeps an ecosystem oscillating, retains it in a state of low maturity. Often it is the environment, as in the case of successions of phytoplankton. At other times it is an active exploitation from outside that forces a repeated reconstruction and an output of work reconcilable only with less mature states. Because it is of practical value, I want to state again that fluctuations in less mature systems are more related to environmental changes, to abiotic factors; but fluctuations in more mature ecosystems are more dependent on internal conditions of equilibrium, that is, on biotic factors.

Fluctuations in the populations are, of course, accompanied by fluctuations in the biotically controlled properties of environment. For instance, strong yearly fluctuations in the phosphate content of water are linked to less mature and strongly fluctuating plankton populations. They are related also to essentially exploitable fish populations, as Cushing remarked, that is, to fish populations capable of great changes in numbers and, thus, capable of supporting human extraction. In the more mature ecosystems, with damped fluctuations, the supply of nutrients in the environment is kept constantly at a low level, as in tropical forests.

EXTENSIVE SYSTEMS WITH LOCAL DIFFERENCES IN THE VALUE OF MATURITY

We can measure a global property of ecosystems — named maturity for convenience — in different ways: in terms of structure and in terms of energy flow per unit biomass. Applying these criteria in the analysis of the parts of any extensive system, it is possible to estimate maturity in the different points, and map the values, say, of species diversity, of pigment diversity, of primary production per unit of total biomass. As is to be expected, the different maps so prepared are congruent (Margalef, 1961b; Herrera, Margalef and Vives, in press) and, in general, it is possible to trace surfaces linking all the points that have a similar degree of maturity. Every one of such surfaces is a boundary between a subsystem of lower maturity and a subsystem of higher maturity. We can repeat such maps at different times, in order to study succession and changes in the general pattern of distribution of maturity.

As is well known, succession and spatial heterogeneity are strongly linked (Margalef, 1958). Heterogeneity often originates because succession proceeds at different speeds according to the location, and it is a common experience of ecologists that enclaves or spots with a lower maturity — immersed in more mature systems — are related to some local disturbance (strong mixing by underwater springs in the sea, presence of bare rock in terrestrial vegetation, etc.). These exclude, at least for the moment, a further progress in the succession. Every reader will remember sketches in treatises on ecology depicting the vegetation girdles around a senescent lake and showing differences in maturity, that is, in the stage reached in succession if we assume a general trend towards increasing maturity. Maps depicting the distribution of biotic diversity, and of the ratio D_{430}/D_{665} (optical densities at the stated wavelengths of acetone extracts) in plankton populations, are of the same kind. This ratio is a simplified expression of the diversity of pigments. The distribution of the values of the ratio *primary production/respiration*, used by H. T. Odum, may have a similar meaning.

Let us explore what happens along a surface of equal maturity. Remember that at one side we have a subsystem of lower maturity, with a high production per unit biomass, with less strong links between species, subject to wider fluctuations and to an easy dispersal of the elements. At the other side we find a subsystem with a greater biomass for the same energy flow, with well organized relations over elements more strongly localized.

If maturity increases in the less mature system, especially at the proximity of the boundary (which is to be expected from succession) the surface of equal maturity moves towards the less mature subsystem. This is probably accompanied by a flow of energy going the converse way. This means that matter (biomass and non-living matter) goes in both directions, since both coupled subsystems are actually open, but the content of potential energy of such matter is, on the average, higher in the matter going the way of increasing maturity than in the matter going the way of decreasing maturity. The subsystem with a lower maturity maintains a higher ratio between primary production and total present biomass, because it actually loses biomass, in going across the border to the more mature coupled subsystems.

Let us remember that succession is simply the exchange of an excess available energy in the present, for a future increase of biomass. An ecosystem in its present state is less mature and has an excess production that goes to the future and helps reorganize the ecosystem in a more mature form. If there is no available excess production or it is drained out of the system, succession proceeds no further. We will find no difficulty in applying the same type of relation, not to successive states of the same system, but to adjoining systems. What the one does in excess (production) is put in use by the other. There is a transfer, or an exchange, between energy and what can be called an "organizing influence."

It seems important to stress that the different degrees of maturity of two coupled subsystems can be, and have to be, estimated through the study of structure and turnover of every subsystem, with total independence of the eventual existence and direction of any exchange between both subsystems. In other words, it is not necessary to find out that there is a certain exchange between subsystems, in order to label automatically as the less mature the subsystem that exports, and as the more mature the importing subsystem.

The discussion of some concrete examples will permit the development of these ideas, and the proper consideration of changing properties along the boundary. Intensity of exchange between subsystems of different maturity may be quite different.

Plankton, in general, is a less mature system than the benthos. All the required qualifications are there: lower species diversity, lower pigment diversity (lower ratio D_{430}/D_{665}), more uncertainty in defining the relations between successive states and higher primary production per unit of total biomass. In the coupling of plankton and benthos, a net transfer of energy exists from plankton to benthos; it can be said that the plankton, in part, feeds the benthos. Such exchange is due to the combination of several effects. There is a major passive factor: sedimentation of plankton. There are other, biotic, factors, such as the existence of benthonic filter-feeders that actively attract the plankton, pumping production from plankton to benthos. There are also benthonic animals that produce planktonic larvae. Later these larvae become adults and return to the benthonic environment. In general, potential energy going towards the benthos in the form of the settling larvae is higher than potential energy going the opposite way in the form of reproductive cells or hatched larvae.

It is worthwhile to discuss further the relative and the combined importance of these effects. An active exploitation by the more mature system may prevent the progressive development of a coupled subsystem, keeping it in a state of low maturity. As an example, we may cite the heavy passive loss resulting from the sedimentation of plankton. The fact is that the presence of bottom filter-feeding animals in an aquarium drives the free-floating population into a state of lower maturity. Also, animals harboring symbiotic algae probably maintain them in a state of lower maturity, through active absorption of organic compounds. Looking for an analogy in human affairs we may compare such a coupling to colonialism: a master country, taking out the product of an underdeveloped country, impedes its economic progress; that is, its maturity.

The steepness of the gradient between a more mature and a less mature subsystem depends not only on active exploitation, but also on other characteristics. Light is a basic factor in plankton production and is more intense above. Furthermore, sedimentation leads a part of the produced biomass down. It is thus natural to expect that surface planktonic populations will be, in general, less mature than populations living at greater depths. The contrast may be enhanced at the level of pycnoclines; the steepness of gradients is particularly sharp where there is a reduced rate of diffusion or exchange. In such a case, the intensity of exchange between coupled subsystems is clearly related to environmental variables.

The ideas developed in the present section are easily testable by coupling two culture vessels containing populations of different maturity. One culture can be maintained in a situation of lower maturity by being continuously stirred. In this one we will have a bloom of small cells. In the other container, we observe, in most replications of the experience, a notable development of swimming organisms, a heavy growth over the walls and a more important proportion of animal life. This is a simple school experiment, but it illustrates how net energy-flow goes from the less towards the more mature, that is, towards the unstirred subsystem. This experiment can be performed by placing the containers side by side, at the same level, with a connecting tube; also in tall, stratified vessels, where it proves that sedimentation in plankton is one of the multiple mechanisms of transfer.

If we want to consider a comparable example in terrestrial ecology, perhaps we could take the boundary between a forest and a place with open and low vegetation. The boundary should have a tendency to be displaced towards the open land; it is expected that there will be more animals in the forest getting food from grassland, than animals in the grassland getting food in the forest.

CONTRACTION AND EXPANSION OF THE ECOSYSTEM

In vagrant communities, like plankton, subsidiary problems appear. Here we must choose, as reference, between a system of coordinates fixed in space or a set of coordinates moving with the populations or with the water masses. When transport is accompanied by deformation, if trajectories are not parallel and have different speeds, problems become increasingly complex. There is a possibility that some of these problems are not without analogies in physics.

Expansion of ecosystems in space is frequently associated with individual trajectories at random, and means a reduction in maturity. In contracting communities, movements are often organized and lead to an increase of maturity, or at least of diversity per unit space.

These processes are perhaps not absolutely general, but may be followed easily in laboratory cultures placed in appropriate experimental conditions. Take, for instance, cultures in a liquid medium placed in containers separated by a glass filter-barrier, with the possibility of pumping medium across the porous wall. We can obtain, at will, the usual drop of diversity and increase in the primary production per unit biomass in the subculture towards which we pump the fluid. Another good example, this one in nature, is afforded by the behavior and distribution of plankton in a system formed by alternating convergences and divergences, or convection cells. The divergences harbor less mature and expanding populations, with many diatoms, low diversity, etc., while in the convergences are found communities of a more mature character; they are contracting because flagellates keep moving or swimming upwards to become concentrated above. The whole structure behaves as the coupling of less mature (divergence) with more mature (convergence) subsystems, with the expected net transfer of production from the divergences to the convergences.

Sedimentation of passive plankton is another illustration of the same general model, where transport is directed downwards. In the upper layers, plankton becomes diluted or dispersed and in the lower levels it is concentrated. The continuous drain of a part of the surface plankton needs to be countered by an excess production and does not allow a great increase in organization. For this reason, plankton remains less mature in the upper levels and other effects (exploitation, active movements) may make this vertical difference more conspicuous, or change it otherwise.

Other similar models, where the horizontal dimensions are more important, can be constructed to represent populations in estuaries (both normal or positive, and hypersaline or negative) and also to represent running waters in general, in which the increase in maturity is always downstream (Margalef, 1960).

One need is for the mathematical tools necessary to compute the movements, or the relative displacements, of elements in an ecosystem in terms of any suitable measure of structure. If this is achieved, the way is open for adding the effects of transport and succession, expressing the results as changes in maturity. Such a possibility would be useful in dealing with planktonic communities.

THE PARTITION OF UNISPECIFIC POPULATIONS MOVING FREELY ACROSS ECOSYSTEMS WITH LOCAL DIFFERENCES IN MATURITY

Any unispecific population that expands over a wide range has local differences in the demographic structure, even when internal flow of individuals is important. Any portion of the population with a higher proportion of young individuals (suggesting a lower average life span, and a higher mortality) means a higher energy-flow per unit of biomass. By an obvious analogy, the population can be said to have a less mature demographic structure. In the places where such populations exist, fluctuations are shorter and the range in change of biomass is wider.

Broadly speaking, there is a spatial correspondence between the localization of the less mature portion of a unispecific population and the less mature parts of the whole system. Good examples are furnished by benthic animals that send larvae and young to the less mature and superficial waters, and by migrating birds breeding in the less mature ecosystems of temperate latitudes. Animals tend to spend their adult lives in the more mature systems, but to reproduce in the less mature ones and send larvae or reproductive elements into them.

Monte Lloyd, in a personal communication discussing this point, expressed its meaning very clearly: "I tend to see this as a reflection of a previous evolutionary history: it has always been an advantage to reproduce on less mature ecosystems, since these are maintaining themselves less efficiently, and energy needed for growth is more readily available. Competition for it is less severe. Those individuals that developed behavior patterns which led them to reproduce in less mature systems have left behind more offspring. They have been selected for. The adults, which live in more mature ecosystems send their young outside to less mature systems to gather energy (growth) and bring it back. Here, certainly is a 'directive influence' emanating from the more mature ecosystems."

In the Mediterranean coasts of East Spain a very good example has been worked out. From the mouth of the Ebro River towards the South, there is a gradient of increasing maturity in the planktonic ecosystem. It is well reflected in diversity indices, pigment composition and other properties. There is an important breeding area of sardine in the less mature part of the system, and the demographical structure of the fish populations changes gradually as maturity of the ecosystem in which they are incorporated increases (data of M. Gomez Larraneta and coworkers). Human exploitation, if restricted geographically, leads to a local decrease of maturity, both of the general ecosystem and in the demographical structure of the selectively exploited species.

Many other examples could be found in insects that breed in aquatic environments but have adult forms that are integrated into terrestrial ecosystems, or in fish that breed in inundation waters.

The fish that migrate between sea water and fresh water offer a special subject for meditation. Eels breed in the sea and spend their adult life in fresh water; in salmon the converse is true. How can this be made consistent with our theory that requires animals to breed always in the less mature part of the available systems? Eels develop in the marine pelagic environment, one of the least mature of marine ecosystems. Adult eels belong to the bottom of lowland fresh water, a relatively mature system. Salmon breed in the upper stretches of streams, one of the less mature fresh-water ecosystems. Adult salmon, on the contrary, belong to a more mature system in the marine littoral.

A similar parallelism or adjustment between demographic or age structure and general maturity of the ecosystem is observed not only across space, but also along time. Planktonic animals with a regular reproductive cycle breed when the whole mixed population is in a less mature state, after a pulse of primary production, and when an important surplus of food is available. In this moment the demographic structure of the species under consideration is in a state of very low "maturity."

TEMPERATURE AND MATURITY

A higher temperature induces a higher flow of energy (increased respiration) per unit biomass; organisms are also smaller and have a shorter life span. These changes, observed in the populations of a species at different temperatures, leads us to predict a certain relation between high temperature and low maturity. This parallelism seems to be reinforced by other coincidences.

An ecosystem has chances of survival with different degrees of organization, that is, with higher or with lower maturity. But the general trend is towards an increase of maturity. The reasons for this may have to do with certain principles of thermodynamics. Something similar happens in temperature relationships. There are organisms well adapted to high temperature and to low temperature, but the more common trend in evolution seems to be towards the production of organisms better fit for a lower temperature — bigger size, longer life, and so on (Margalef, 1955). Here is a suggestion, also, of the operation of very general physical principles.

But the ecological picture is rather diverse. At present and in our planet, the most mature ecosystems, the coral reef in the sea, the tropical forest on land, are restricted to warmer environments. In my opinion this is not related to temperature, but to stability of environment. A stable environment, warm or cold, allows the increase of maturity up to a level much higher than a fluctuating environment, cold or warm. Coral reefs are a good example of very mature ecosystems limited to areas of great stability, rather than to areas of a definite temperature as is generally believed. They are lacking in many tropical waters where yearly fluctuations in phosphate content, for instance, are important. Indeed, in such areas with fluctuating conditions (north-east of Venezuela, for instance), we have important pulses of phytoplankton, accompanied by a heavy development of clupeids, all indicators of much less mature ecosystems.

MATURITY AND EVOLUTION

A related problem that I have discussed elsewhere (Margalef, 1958, 1959) is the relation between pattern (rhythm and mode) of evolution and maturity of the ecosystem in which the species evolves.

In less mature ecosystems or in less mature trophic levels of any ecosystem, we expect species to be short-lived, easily dispersed, able to colonize with rapidity virgin areas, able to leave numerous offspring and, of course, characterized by high ratio *energy flow/biomass*. Phenotypes may be plastic, cyclomorphosis or temporary variation is common, and genetic compatibility between separate and distant populations is rarely lost. They are euryoic, competition is for dominance and evolution may be rapid. They are opportunistic species, subjected to a dynamic type of selection, often for prolificness.

In more mature ecosystems or in more mature areas of their structure, the selected species are of rather long life, with limited but well protected offspring, and with more restricted possibilities of dispersion accompanied by isolation in small breeding units. The species are very well integrated in the respective ecosystems from the standpoint of biochemistry, nutritional needs, behavior, and so on. They have well developed territorial instincts, endogenous rhythms, etc. Development is often canalized and morphological stability is high, but genetic differences between the diverse breeding units are common. Competition between closely related forms may become limited. Success is linked to efficiency and manifested in a stabilizing type of selection.

No wonder evolution in less mature ecosystems, implying a higher flow of energy per unit biomass, is more expensive and by this very fact can be more creative or, at least, go faster.

Another point in the relation between maturity and evolution is worth to recall. By the fact of succession, conditions of equilibrium in every ecosystem are slowly shifting towards characteristics of increased maturity, and the evolution of species is "sucked" towards a better adjustment to conditions of ever-increasing maturity. In the slow process of evolution, so well manifested in the fossil record of phylogenetic series, we can expect many series demonstrating an adjustment to conditions of increasing maturity of ecosystems.

UTILITY OF A SYNTHETIC APPROACH

Most of what has been discussed can be summarized in two very simple principles:

(1) The relative amount of energy necessary for maintaining an ecosystem is related to the degree of structure or organization of this ecosystem. Less energy is necessary for a more complex ecosystem, and the natural trend in succession is towards a decreasing flow of energy per unit of biomass and towards increasing organization. Briefly stated the trend is towards increasing maturity.

(2) When two systems of different maturity meet along a boundary that allows an exchange, energy (production) flows towards the more mature subsystem, and the boundary or surface of equal maturity shows a trend to move in an opposite direction to such energy flow.

These general principles clarify many ecological interactions and processes and allow quantitative formulation. They can be used or tested in predicting changes induced by human action. Exploitation is like inflicting a wound upon a heterogeneous organic structure: some tissues or subsystems (more mature) do not regenerate; other (less mature) do and these supply the basis for a further eventual increase of maturity. Maintained exploitation keeps the maturity of the exploited system constantly low. Exploited natural communities come to have a higher primary production per unit biomass, a lower species diversity and, presumably, a lower ratio D_{430}/D_{665}. More energy goes into fluctuations such as those represented by exploited populations or by populations that are integrated into exploited ecosystems. For example, pests have fluctuations with a wider range and shorter periodicity than similar populations that are integrated into more mature, eventually unexploited, ecosystems. Extremely mature ecosystems, such as tropical forests, are unable to go back and are totally disrupted by human exploitation. The examples furnished by fisheries are illustrative:

very productive fisheries belong to ecosystems of low maturity, with a fluctuating supply of inorganic nutrients and with notable pulses in plankton production. The less the maturity, the more important the "abiotic" control of populations. Human activity decreases maturity and can enhance fluctuations. The notable exclusion between coral reefs and a heavy production of clupeids in tropical waters has been cited and it is possible to hypothesize that pollution and other alterations along tropical coasts may destroy very mature ecosystems, and then fisheries can become more important than at present. Radiation increase can be expected to act destructively to accumulated information (that is, to biomass) but with no effect on potential energy flow; radiation, then, must reduce the maturity of ecosystems, in part by selective destruction of the more mature elements of the ecosystem. Thus, a great increase in radiation may mean a new push given to an already lagging evolution.

Most of the same principles can be applied to human organizations. Taking as criteria the diversification of skills and jobs (diversity), or the relative flow of potential energy, it is possible to map the "maturity" of states and continents in the ecological sense of organization. Energy flow goes from less mature (rural) areas to more mature (urban) areas. The urban centers represent localized elements that have accumulated high amounts of information, fed on the production of neighboring subsystems, and have exerted a directive action. Very old systems can survive with a small flow of energy, and like their ecological counterparts can break down as a consequence of a minor environmental change. It is possible to deal objectively and quantitatively with big and complex structures, if one never forgets the complementary aspects of energy as related to matter, and structure.

SUMMARY

An attempt is made to provide some unifying principles in ecology. The structure of ecosystems is considered in relation to various components, with emphasis on the characteristics of maturity as measured by diversity data and other determinable features, including primary production (P) and biomass (B). Ecosystems with complex structure and containing a high amount of information can be maintained with a relatively lower expenditure of energy. Oscillations, introduced for example by environmental changes or outside exploration, tend to retain an ecosystem in a state of lower maturity. Where succession is occurring, involving exchange of an excess of available energy for a future increase in biomass, the relations encountered may be applied not only to successive states in the same system, but to adjoining or coupled subsystems. Steepness of the gradient between subsystems is shown to depend on several factors subject to quantitative determination and the relation between these subsystems can be imitated by simple experiment. When ecosystems contract or expand there are corresponding increase or decreases of maturity.

Factors affecting the maturity of ecosystems and of special interest are the movement of species. These suggest a spatial correspondence between

the juvenile or immature portion of an unspecific population and the less mature parts of ecosystems available for habitation.

Maturity is related to evolution in a way that permits generalization concerning the type of organisms to be found in ecosystems of more or less maturity and stability. As evolution proceeds, there is a trend toward adjustment to maturity.

The concepts that emerge may be applied to human social systems. Two principles become evident: The energy required to maintain an ecosystem is inversely related to complexity, with the natural trend toward decreasing flow of energy per unit biomass; that is, increased maturity. Secondly, in adjacent systems there is a flow of energy toward the more mature system and an opposite movement in the boundary or surface of equal maturity.

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