productivity, diversity, etc. These features of communities will usually increase through the succession to the climax, but there is no reason why, in a given case, the usual direction should not be reversed. In general, climax status should be determined not by abstract or generalized conceptions of what should be ultimate, but by what populations actually replace other populations and then maintain themselves. . . .

Kormondy, E.J. 1965. Readings in Ecology. Prentice-Hall, Inc. NJ. 219 pp.

THE CONCEPT OF THE ECOSYSTEM

One of the ends to which science directs itself is the development of an encompassing theory. In ecology, the principle of the ecosystem provides such a unifying framework within which specialized study at the individual, population and community level can be meaningfully conducted.

The concept of the ecosystem as an ecological unit comprising living and nonliving components interacting to produce a stable system is not new. Those who have read more or less consecutively in this anthology have recognized that many ecologists discussed the interrelations of a particular biotic assemblage with its environment and the interrelations of biotic units within the assemblage. However, the theoretical development of the concept and the implementing of studies oriented to its clarification are largely products of the period since 1940, *the major impetus occurring in the 1950's.*

ECOSYSTEM AS THE BASIC UNIT IN ECOLOGY

Francis C. Evans—1956

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Although the term ecosystem *was first proposed by Tansley in* 1935, *the context in which it is used today is much broader in scope. Systematic treatment and development of the concept in its current sense is largely associated with Eugene Odum beginning with his 1953 text Fundamentals of ecology. However, the following succinct statement by Professor Evans, of the University of Michigan, provides an excellent introduction to this section.*

The term *ecosystem* was proposed by Tansley as a name for the interaction system comprising living things together with their nonliving habitat. Tansley regarded the ecosystem as including "not only the organism-complex, but also the whole complex of physical factors forming what we call the environment." He thus applied the term specifically to that level of biological organization represented by such units as the community and the biome. I here suggest that it is logically appropriate and desirable to extend the application of the concept and the term to include organization levels other than that of the community.

In its fundamental aspects, an ecosystem involves the circulation, transformation, and accumulation of energy and matter through the medium of living things and their activities. Photosynthesis, decomposition, herbivory, predation, parasitism, and other symbiotic activities are among the principal biological processes responsible for the transport and storage of materials and energy, and the interactions of the organisms engaged in these activities provide the pathways of distribution. The food-chain is an example of such a pathway. In the nonliving part of the ecosystem, circulation of energy and matter is completed by such physical processes as evaporation and precipitation, erosion and deposition. The ecologist, then, is primarily concerned with the quantities of matter and energy that pass through a given ecosystem and with the rates at which they do so. Of almost equal importance, however, are the kinds of organisms that are present in any particular ecosystem and the roles that they occupy in its structure and organization. Thus, both quantitative and qualitative aspects need to be considered in the description and comparison of ecosystems.

Ecosystems are further characterized by a multiplicity of regulatory mechanisms, which, in limiting the numbers of organisms present and in influencing their physiology and behavior, control the quantities and rates of movement of both matter and energy. Processes of growth and reproduction, agencies of mortality (physical as well as biological), patterns of immigration and emigration, and habits of adaptive significance are among the more important groups of regulatory mechanisms. In the absence of such mechanisms, no ecosystem could continue to persist and maintain its identity.

The assemblage of plants and animals visualized by Tansley as an integral part of the ecosystem usually consists of numerous species, each represented by a population of individual organisms. However, each population can be

regarded as an entity in its own right, interacting with its environment (which may include other organisms as well as physical features of the habitat) to form a system of lower rank that likewise involves the distribution of matter and energy. In turn, each individual animal or plant, together with its particular microenvironment, constitutes a system of still lower rank. Or we may wish to take a world view of life and look upon the biosphere with its total environment as a gigantic ecosystem. Regardless of the level on which life is examined, the ecosystem concept can appropriately be applied. The ecosystem thus stands as a basic unit of ecology, a unit that is as important to this field of natural science as the species is to taxonomy and systematics. In any given case, the particular level on which the ecosystem is being studied can be specified with a qualifying adjective—for example, community ecosystem, population ecosystem, and so forth.

All ranks of ecosystems are open systems, not closed ones. Energy and matter continually escape from them in the course of the processes of life, and they must be replaced if the system is to continue to function. The pathways of loss and replacement of matter and energy frequently connect one ecosystem with another, and therefore it is often difficult to determine the limits of a given ecosystem. This has led some ecologists to reject the ecosystem concept as unrealistic and of little use in description or analysis. One is reminded, however, of the fact that it is also difficult, if not impossible, to delimit a species from its ancestral or derivative species or from both; yet this does not destroy the value of the concept. The ecosystem concept may indeed be more useful when it is employed in relation to the community than to the population or individual, for its limits may be more easily determined on that level. Nevertheless, its application to all levels seems fully justified.

The concept of the ecosystem has been described under many names, among them those of *microcosm*, *naturkomplex*, *holocoen* and *biosystem*. Tansley's term seems most successfully to convey its meaning and has in fact been accepted by a large number of present-day ecologists. I hope that it will eventually be adopted universally and that its application will be expanded beyond its original use to include other levels of biological organization. Recognition of the ecosystem as the basic unit in ecology would be helpful in focussing attention upon the truly fundamental aspects of this rapidly developing science.

THE LAKE AS A MICROCOSM

Stephen A. Forbes—1887

Reprinted by permission of the publisher from Illinois Natural History Survey Bulletin No. 15, pp. 537–550, 1925, a reprinting of an article which first appeared in the Bulletin of the Peoria Scientific Association, pp. 77–87, 1887.

In the tradition of Mobius' biocoenosis (see p. 121), Forbes showed considerable insight into the dynamic interrelationships between the living and nonliving components of stable systems. In some few respects, his microcosm *is but semantically different from today's* ecosystem. *In addition to careful observations, and perceptive insights, Forbes was a gifted writer; part of the classic quality of this essay is its literary charm. The breadth of viewpoint belies Forbes' narrow speciality as an applied entomologist with the Illinois Natural History Survey.*

A lake . . . forms a little world within itself—a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp.

Nowhere can one see more clearly illustrated what may be called the *sensibility* of such an organic complex, expressed by the fact that whatever affects any species belonging to it, must have its influence of some sort upon the whole assemblage. He will thus be made to see the impossibility of studying completely any form out of relation to the other forms; the necessity for taking a comprehensive survey of the whole as a condition to a satisfactory understanding of any part. If one wishes to become acquainted with the black bass, for example, he will learn but little if he limits himself to that species. He must evidently study also the species upon which it depends for its existence, and the various conditions upon which *these* depend. He must likewise study the species with which it comes in competition, and the entire system of conditions affecting their prosperity; and by the time he has studied all these sufficiently he will find that he has run through the whole complicated mechanism of the aquatic life of the locality, both animal and vegetable, of which his species forms but a single element. . . .

The amount and variety of animal life contained in them as well as in the streams related to them is extremely variable, depending chiefly on the frequency, extent, and duration of the spring and summer overflows. This is, in fact, the characteristic and peculiar feature of life in these waters. There is perhaps no better illustration of the methods by which the flexible system of organic life adapts itself, without injury, to widely and rapidly fluctuating conditions. Whenever the waters of the river remain for a long time far beyond their banks, the breeding grounds of fishes and other animals are immensely extended, and their food supplies increased to a corresponding degree. The slow or stagnant backwaters of such an overflow afford the best situations possible for the development of myriads of Entomostraca, which furnish, in turn, abundant food for young fishes of all descriptions. There thus results an outpouring of life—an extraordinary multiplication of nearly every species, most prompt and rapid, generally speaking, in such as have the highest reproductive rate, that is to say, in those which produce the largest average number of eggs and young for each adult.

The first to feel this tremendous impulse are the protophytes and Protozoa, upon which most of the Entomostraca and certain minute insect larvæ depend for food. This sudden development of their food resources causes, of course, a corresponding increase in the numbers of the latter classes, and, through them, of all sorts of fishes. The first fishes to feel the force of this tidal wave of life are the rapidly-breeding, non-predaceous kinds; and the last, the game fishes, which derive from the others their principal food supplies. Evidently each of these classes must act as a check upon the one preceding it. The development of animalcules is arrested and soon sent back below its highest point by the consequent development of Entomostraca; the latter, again, are met, checked, and reduced in number by the innumerable shoals of fishes with which the water speedily swarms. In this way a general adjustment of numbers to the new conditions would finally be reached spontaneously; but long before any such settled balance can be established, often of course before the full effect of this upward influence has been exhibited, a new cause of disturbance intervenes in the *disappearance of the overflow*. As the waters retire, the lakes are again defined; the teeming life which they contain is restricted within daily narrower bounds, and a fearful slaughter follows; the lower and more defenceless animals are penned up more and more closely with their predaceous enemies, and these thrive for a time to an extraordinary degree. To trace the further consequences of this oscillation would take me too far. Enough has been said to illustrate the general idea that the life of waters subject to periodical expansions of considerable duration, is peculiarly unstable and fluctuating; that each species swings, pendulum-like but irregularly, between a highest and a lowest point, and that this fluctuation affects the different classes successively, in the order of their dependence upon each other for food. . . .

It would be quite impossible within reasonable limits, to go into details respecting the organic relations of the animals of these waters, and I will content myself with two or three illustrations. As one example of the varied and far-reaching relations into which the animals of a lake are brought in the general struggle for life, I take the common black bass. In the dietary of this fish I find, at different ages of the individual, fishes of great variety, representing all the important orders of that class; insects in considerable number, especially the various water-bugs and larvæ of day-flies; fresh-water shrimps; and a great multitude of Entomostraca of many species and genera. The fish is therefore directly dependent upon all these classes for its existence. Next, looking to the food of the species which the bass has eaten, and upon which it is therefore indirectly dependent, I find that one kind of the fishes taken feeds upon mud, algæ, and Entomostraca, and another upon nearly every animal substance in the water, including mollusks and decomposing organic matter. The insects taken by the bass, themselves take other insects and small Crustacea. The crawfishes are nearly omnivorous, and of the other crustaceans some eat Entomostraca and some algæ and Protoza. At only the second step, therefore, we find our bass brought into dependence upon nearly every class of animals in the water.

And now, if we search for its competitors we shall find these also extremely numerous. In the first place, I have found that all our young fishes except the Catostomidæ feed at first almost wholly on Entomostraca, so that the little bass finds himself at the very beginning of his life engaged in a scramble for food with all the other little fishes in the lake. In fact, not only young fishes but a multitude of other animals as well, especially insects and the larger Crustacea, feed upon these Entomostraca, so that the competitors of the bass are not confined to members of its own class. Even mollusks, while they do not directly compete with it do so indirectly, for they appropriate myriads of the microscopic forms upon which the Entomostraca largely depend for food. But the enemies of the bass do not all attack it by appropriating its food supplies, for many devour the little fish itself. A great variety of predaceous fishes, turtles, water-snakes, wading and diving birds, and even bugs of gigantic dimensions destroy it on the slightest opportunity. It is in fact hardly too much to say that fishes which reach maturity are relatively as rare as centenarians among human kind.

As an illustration of the remote and unsuspected rivalries which reveal themselves on a careful study of such a situation, we may take the relations of fishes to the bladderwort[1]—a flowering plant which fills many acres of the water in the shallow lakes of northern Illinois. Upon the leaves of this species are found little bladders—several hundred to each plant—which when closely examined are seen to be tiny traps for the capture of Entomostraca and other minute animals. The plant usually has no roots, but lives entirely upon the animal food obtained through these little bladders. Ten of these sacs which I took at random from a mature plant contained no less than ninety-three animals (more than nine to a bladder), belonging to twenty-eight different species. Seventy-six of these were Entomostraca, and eight others were minute insect larvæ. When we estimate the myriads of small insects and Crustacea which these plants must appropriate during a year to their own support, and consider the fact that these are of the kinds most useful as food for young fishes of nearly all descriptions, we must conclude that the bladderworts compete with fishes for food, and tend to keep down their number by diminishing the food resources of the young. The plants even have a certain advantage in this competition, since they are not strictly dependent on Entomostraca, as the fishes are, but sometimes take root, developing then but very few leaves and bladders. This probably happens under conditions unfavorable to their support by the other method. These simple instances will suffice to illustrate the intimate way in which the living forms of a lake are united.

Perhaps no phenomenon of life in such a situation is more remarkable than the steady balance of organic nature, which holds each species within the limits of a uniform average number, year after year, although each one is always doing its best to break across boundaries on every side. The reproductive rate is usually enormous and the struggle for existence is correspondingly severe. . . .

It is a self-evident proposition that a species can not maintain itself continuously, year after year, unless its birth-rate at least equals its death-rate. If it is preyed upon by another species, it must produce regularly an excess of individuals for destruction, or else it must certainly dwindle and disappear. On the other hand, the dependent species evidently must not appropriate, on an average, any more than the surplus and excess of individuals upon which it preys, for if it does so it will continuously diminish its own food supply, and thus indirectly but surely exterminate itself. The interests of both parties will therefore be best served by an adjustment of their respective rates of multiplication such that the species devoured shall furnish an excess of numbers to supply the wants of the devourer, and that the latter shall confine its appropriations to the excess thus furnished. We thus see that there is really a close *community of interest* between these two seemingly deadly foes.

And next we note that this common interest is promoted by the process of natural selection; for it is the great office of this process to eliminate the unfit. If two species standing to each other in the relation of hunter and prey are or become badly adjusted in respect to their rates of increase, so that the one preyed upon is kept very far below the normal number which might find food, even if they do not presently obliterate each other the pair are placed at a disadvantage in the battle for life, and must suffer accordingly. Just as certainly as the thrifty business man who lives within his income will finally dispossess his shiftless competitor who can never pay his debts, the well-adjusted aquatic animal will in time crowd out its poorly-adjusted competitors for food and for the various goods of life. Consequently we may believe that in the long run and as a general rule those species which have survived, are those which have reached a fairly close adjustment in this particular.

Two ideas are thus seen to be sufficient to explain the order evolved from this seeming chaos; the first that of a general community of interests among all the classes of organic beings here assembled, and the second that of the beneficent power of natural selection which compels such adjustments of the rates of destruction and of multiplication of the various species as shall best promote this common interest.

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[1] Utricularia.

THE ACCUMULATION OF ENERGY BY PLANTS

Edgar Nelson Transeau—1926

Reprinted by permission of the publisher from the Ohio Journal of Science 26: 1-10, 1926.

If he is to study energy flow in an ecosystem, the ecologist needs information about the energy relations of the only group of organisms that can transform radiant energy into a form useable by other organisms. Transeau's study of the energy budget of a cornfield was considerably in advance of its time and provided the basis for what has subsequently become a highly active area of research—primary production.

. . . Let us now examine the energy budget of a hypothetical acre of corn in the heart of the corn belt in north central Illinois where corn attains yields as great as anywhere, and not far from Madison, Wisconsin, one of the stations at which solar radiation has been studied. The growing season is from June 1 to September 8, one hundred days. The best yields have been with 10,000 plants to the acre. One hundred bushels, with a dry weight of

2160 kg. per acre, is the yield assumed although it is not a maximum crop for the corn belt. How well an acre of corn covers the area is shown by the fact that during the latter half of the season nearly two acres of leaves are exposed to the light.

At maturity the average corn plant contains about 20 per cent of dry matter and about 80 per cent of water. Of the dry matter, carbon makes up about 44.58 per cent. This is the most important figure for our calculations derived from the chemical analyses of the corn plants. We must also know the total amounts of mineral elements present which is 5.37 per cent from which we can derive the fact that 94.63 per cent of the plant's dry weight is organic matter. The dry weight of an average corn plant growing under these circumstances is 600 g., of which 216 g. makes up the grain 200 g. the stalk, 140 g. the leaves, and 44 g. the roots. The total weight of the 10,000 plants is 6000 kg. Subtracting from this the 322 kg. of mineral elements in the ash we have left 5678 kg. of organic matter, of which 2675 kg. is carbon.

To estimate the amount of photosynthesis we must determine the amount of carbon, because carbon enters the plant only by photosynthetic reduction of CO_2. The total carbon is 2675 kilograms and the glucose equivalent of this carbon is 6687 kilograms. This is the amount of primary sugar equivalent to the carbon accumulated in the mature plant.

TABLE 3. *Glucose equivalent of respiration*

Estimated rate of CO_2 release = 1% of the dry wt per day	
Average dry weight for season (½ total wt.)	= 3000 kg.
Average rate of CO_2 release (.01 × 3200) per day	= 30 kg.
Total CO_2 release during season	= 3000 kg.
Carbon equivalent: C:CO_2 = 12:44	= 818 kg.
Glucose equivalent $C_6H_{12}O_6$:C_6 = 180·72	= 2045 kg.

At maturity however, only a part of the carbon remains, for some has been lost as CO_2 in respiration (Table 3). The average rate of CO_2 loss is not far from one per cent of the dry weight per day. This would cause a daily loss of 30 kilograms of CO_2, and during the entire season a loss of 3000 kilograms. The glucose equivalent to this amount of carbon dioxide is 2045 kilograms.

Adding the amount of this lost glucose to the glucose equivalent of the carbon in the plant, gives the total glucose manufactured as 8732 kilograms. It requires energy equivalent to 3760 calories to produce one kilogram of glucose. Hence it required not far from 33 million calories to produce the entire photosynthetic product. (Table 4).

TABLE 4. *Energy consumed in photosynthesis*

Glucose equivalent of accumulated carbon	6687 kg.
Glucose equivalent of carbon oxidized	2045 kg.
Total glucose manufactured	8732 kg.
Energy required to produce 1 kg. glucose	3760 Cal.
Total energy consumed in photosynthesis	33 million Cal.

We are now in a position to estimate the efficiency of the corn plant as a photosynthetic agent: (Table 5).

TABLE 5. *Efficiency of photosynthesis*

Total energy available on acre during the growing season	2043 million Cal.
Total energy used in photosynthesis	33 million Cal.
Per cent of available energy used by the corn plant in photosynthesis, (efficiency of corn plant)	1.6%
Of the total light spectrum measured, however, only about 20% is used in photosynthesis, hence the efficiency of the photosynthetic process is.	8%

The total energy available according to the Smithsonian figures is 2043 million Calories. The energy utilized is 33 million, or 1.6 per cent. In photosynthesis however, only certain rays are effective, and these furnish about 20 per cent of the energy measured by the pyrheliometer. Consequently the efficiency of photosynthesis in 100-bushel corn is 8 per cent.

Another source of energy loss to the plant is transpiration. From the water requirement studies of corn it is probable that in Illinois not far from 276 kilograms of water are evaporated during the growing season for every kilogram of its dry weight. The total weight of water lost in this way therefore is one and a half million kilograms. This is equal to 408,000 gallons or sufficient water to cover the acre to a depth of fifteen inches.

The energy necessary to evaporate one kilogram of water at the average temperature of the growing season is 593 calories. Consequently 910 million Calories are expended in this way. This is equivalent to 44.5 per cent of the available energy.

TABLE 7. *Energy released in respiration*

Glucose consumed in respiration	2045 kg.
One kilogram of glucose releases	3760 Cal.
Total energy released in Respiration	7.7 million Cal.
Of the energy made potential in photosynthesis, Respiration releases	23.4%

Assuming that photosynthesis goes on 12 hours each day and respiration 24 hours each day, the average daily rate of photosynthesis is about 8 times the rate of respiration.

Respiration again releases a part of the energy rendered potential in photosynthesis. As we have seen 2045 kilograms of glucose are thus oxidized, and in consequence 7.7 million Calories are released within the plant. This energy raises the temperature of the plant and escapes to the environment, or it is used in synthesis of fats, proteins and other reduced organic substances.

The energy released in respiration amounts to 23.4 per cent—almost one-fourth of the energy absorbed in photosynthesis. This is far more than is needed to account for the endothermic reactions associated with food transformations within the plant.

Assuming that photosynthesis goes on 12 hours and respiration 24 hours each day, the average rate of photosynthesis must be about 8 times the rate of respiration.

We may now summarize the energy budget [Table 8]:

TABLE 8. *Summary of budget*

Total energy available	2043 million Cal.
Used in photosynthesis	33 million Cal.
Used in transpiration	910 million Cal.
Total energy consumed	943 million Cal.
Energy not directly used by the plants	1100 million Cal.
Energy released by respiration	8 million Cal.
Of the available energy, 100-bushel-corn uses about	46%
The environment takes up about	54%

As a result we are in a position to make a number of generalizations regarding the metabolism and growth of plants, both as to materials and energy. (1) An acre of 100-bushel corn uses during the growing season about 408,000 gallons of water or 15 acre-inches. (2) The evaporation of this water consumes about 45 per cent of the available light energy. (3) In photosynthesis the corn plant utilizes about 1.6 per cent of the energy available; its effieiency is about 8 per cent. (4) An acre of 100-bushel corn manufactures on the average 200 pounds of sugar a day. (5) Of the energy rendered potential in photosynthesis, 23.4 per cent is again released in respiration. (6) Of the sugar manufactured nearly one-fourth is oxidized in respiration. (7) Respiration releases several times as much energy as is needed to account for the reductions in the synthesis of fats, proteins and other compounds. (8) At maturity the grain contains about one-fourth of the total energy utilized in photosynthesis, or about .5 per cent of the energy available. (9) The average rate of photosynthesis is about eight times the rate of respiration. (10) Since the young corn seedling weighs .3 grams and the mature plant weighs 600 grams, on the basis of the compound interest law of growth the average daily increment in dry weight is 7.9 per cent. . . .

THE ANNUAL ENERGY BUDGET OF AN INLAND LAKE

Chancey Juday—1940

Reprinted by permission of the publisher from Ecology 21: 438–450, 1940.

Transeau's energy budget calculations (see p. 171) were limited to one growing season of a single crop. Juday's study not only covers an entire year but considers the totality of energy relations of a system. The complexity of studying community metabolism is obvious in this paper which represented a major forward step in ecosystem analysis. Its influence on Lindeman's research and formulation of his trophic-dynamics concept is also apparent (see p. 179). Juday, with E. H. Birge, pioneered limnological studies in the United States and established the University of Wisconsin as the center of such studies.

The variation in the quantity of solar radiation delivered to the surface of an inland lake during the course of the year is the principal factor in determining the physical, chemical and biological cycle of changes that take place within the water. This is true especially of lakes which are situated in temperate latitudes where there are considerable differences between summer and winter temperatures of the air and of the water. . . .

The annual energy budget of a lake may be regarded as comprising the energy received from sun and sky each year and the expenditures or uses which the lake makes of this annual income of radiation. In general the annual income and outgo substantially balance each other. This is true more particularly of the physical energy budget. Considerable biological material produced in one energy year lives over into the next, but this overlapping crop of organisms is much the same in quantity from year to year so that it plays approximately the same annual role. For this reason it does not require any special consideration. There is a certain amount of organic material contributed to the bottom deposits in the deeper water and to peat formation in the shallow water which lasts for long periods of time, but the annual energy value of these materials is so small in most cases that they may be neglected. . . .

. . . the monthly means of solar and sky radiation delivered to the surface of Lake Mendota during the 28 year period ranged from a minimum of 3,568 calories in December to a maximum of 16,392 calories in July. The annual means for the 28 years varied from a minimum of 108,597 calories in 1935 to a maximum of 129,659 calories in 1937. . . . the annual mean for the 28 years is 118,872 calories. . . .

The respective amounts of energy included in the four items of the physical energy budget which have been considered so far are indicated in table III.

TABLE III. *Quantity of solar and sky radiation used by Lake Mendota in various physical and biological processes*

The results are indicated in gram calories per square centimeter of surface.

Melting of ice in spring	3,500
Annual heat budget of water	24,200
Annual heat budget of bottom	2,000
Energy lost by evaporation	29,300
Annual surface loss	28,500
Loss by conduction, convection and radiation	30,324
Biological energy budget (maximum)	1,048

The sum of these four items is 71,000 calories, which is approximately 60 per cent of the mean quantity of energy delivered to the surface of Lake Mendota annually by sun and sky. . . .

BIOLOGICAL ENERGY BUDGET

A certain amount of the solar radiation that passes into the water of Lake Mendota is utilized by the aquatic plants in the process of photosynthesis. The products of this assimilation, namely, proteins, fats and carbohydrates, thus constitute the primary accumulation or storage of the energy derived from the sub-surface illumination. Since this organic material manufactured by the plants serves, either directly or indirectly, as a source of food for all of the non-chlorophyllaceous organisms that inhabit the lake, these latter forms, therefore, constitute a secondary stage in the storage of the energy accumulated by the aquatic plants. The original amount of energy represented by these secondary organisms varies with the different forms, depending upon the number of links in their respective food chains; in general they represent a comparatively small proportion of the primary organic material manufactured by the plants.

Chemical analyses of the various aquatic organisms have now progressed far enough to enable one to compute their energy values from the standards that have been established by food chemists. The standard values are 5,650 calories per gram of protein, 9,450 calories per gram of fat and 4,100 calories per gram of carbohydrate, on a dry weight basis. These values do not represent the total quantity of energy utilized by the aquatic organisms, however, because a part of the synthesized material is oxidized in the metabolic processes of the living organisms. These metabolic oxidations result in the production of heat which is transmitted to the water, but the quantity of heat derived from this source is extremely small in comparison with that which comes from direct insolation.

The amount of organic matter consumed in the metabolism of plants is much smaller than that in animals because several grams of plant material may be consumed in the production of one gram of animal tissue even in animals that feed directly on plants; the predaceous animals represent a still larger quantity of the original photosynthesized material.

Plankton. . . In view of all of these complexities, it may be estimated that the average turnover in the organic matter of the mean standing crop of plankton takes place about every two weeks throughout the year. It would be more frequent than this in spring and summer, and less frequent in winter. A turnover of 26 times per year would give an annual yield of 6,240 kilograms of dry organic matter per hectare of surface as indicated in table IV. This material would consist of 2,704 kilograms of protein, 431 kilograms of fat and 3,105 kilograms of carbohydrate. Approximately 94 per cent of the organic matter comes from the phytoplankton and 6 per cent from the zooplankton.

TABLE IV. *Annual production of plankton, bottom flora, bottom fauna and fish, as well as crude protein, ether extract (fat), and carbohydrate constituents of the organic matter*

The results are stated in kilograms per hectare on a dry, ash-free basis. The plankton yield is based on a turnover every two weeks during the year. The average quantity of dissolved organic matter is included also.

	Dry organic matter	Crude protein	Ether extract	Carbohydrate
Total plankton	6240	2704	431	3105
Phytoplankton	5850	2501	383	2966
Zooplankton	390	203	48	139
Bottom flora	512	64	6	442
Bottom fauna	45	33	4	8
Fish	5	3.4	1	0.6
Dissolved organic matter	1523	334	68	1121
Total organic matter	8325	3138.4	510	4676.6

Bottom flora. . . . the annual crop of large aquatics amounted to 2,000 kilograms per hectare, dry weight. If evenly distributed over the entire lake, this crop would give a yield of 628 kilograms per hectare. A little more than 18 per cent of this material consisted of ash, so that the organic matter was equivalent to 512 kilograms per hectare. . . .

. . . the energy values. . . are given in table IV. The 512 kilograms of dry organic matter per hectare consisted of 64 kilograms of protein, 6 kilograms of ether extract or fat and 442 kilograms of carbohydrate.

The bottom deposits, especially in the deeper water, contain a rather large population of bacteria. . . . While these organisms are present in considerable numbers, they are so small in size that they add very little to the crop of organic matter in the lake; so they have been disregarded. Likewise fungi are fairly abundant in the bottom deposits, but no quantitative study of them has yet been made; it seems probable that their contribution to the organic content of the lake is negligible from an energy standpoint.

Bottom fauna. . . The macroscopic bottom fauna yielded 45 kilograms of dry organic matter per hectare; of this amount 33 kilograms consisted of protein, 4 kilograms of ether extract or fat and 8 kilograms of carbohydrate. While some of these organisms live more than one year, others pass through two or three generations in a year; the two groups of organisms are generally considered as balancing each other, so that the above quantities may be taken as the annual crop of this material as shown in table IV.

Considerable numbers of protozoa and other microscopic animals have been found in the bottom deposits, but no quantitative study of them has been made. It seems probable, however, that these minute forms would not add an appreciable amount of organic matter to the total weight of the bottom fauna.

Fish. No accurate census of the fish caught by anglers in Lake Mendota each year has ever been made so that the assessment of this part of the biological crop can be estimated only roughly. . . . adding the carp crop to that of the game and pan fish gives an annual fish yield of 22 kilograms per hectare, live weight. On a dry, ashfree basis, the total yield amounts to a little more than 5 kilograms per hectare as indicated in table IV. By far the greater part of this material consists of protein and fat.

Energy value of annual crop. Table IV shows that the total quantity of stored and accumulated energy in the form of dry organic matter in the annual crop of plants and animals amounts to 6,802 kilograms per hectare; of this quantity protein constitutes a little more than 2,804 kilograms, ether extract or fat 442 kilograms and carbohydrates 3,556 kilograms. On the basis of the energy equivalents of these three classes of organic matter, as indicated in a previous paragraph, the total energy value of the annual crop amounts to 346 gram calories per square centimeter of lake surface (table V).

TABLE V. *Energy values of the organic matter in the organisms, together with the estimated amounts of energy represented in their metabolism, and in the dissolved organic matter*

The values are stated in gram calories per square centimeter of lake surface. The results for phytoplankton and zooplankton are based on a turnover every two weeks during the year.

Phytoplankton	299
Metabolism	100
Zooplankton	22
Metabolism	110
Bottom flora	22
Metabolism	7
Bottom fauna and fish	3
Metabolism	15
Dissolved organic matter	71
Total	649

In addition to the organic material in the plants and animals, the water contains a certain amount of organic matter which cannot be recovered with a high speed centrifuge. It is either in true solution or is in such a finely divided state that it cannot be obtained with a centrifuge; for lack of a better term it has been called "dissolved organic matter" as compared with the "particulate organic matter" which can be recovered from the water with a centrifuge. The water of Lake Mendota contains 10 to 14 milligrams per liter, dry weight, of this dissolved organic matter; the mean of some 60 determinations is 12 milligrams per liter. When computed to an area basis, the average weight of this material is 1,523 kilograms per hectare, dry weight, of which 334 kilograms are protein, 68 kilograms fat and 1,121 kilograms carbohydrate. The energy value of this dissolved organic matter is about 71 gram calories per square centimeter.

Utilization of solar energy. The chlorophyll-bearing aquatic plants are responsible for the utilization of the subsurface radiation; that is, the sun furnishes the power and the chlorophyll and associated pigments of the plants serve as the machines for the manufacture of the fundamental organic matter of the lake. Table IV shows that the phytoplankton and the large aquatic plants constitute the major item in the annual yield of biological material. Together they contribute 6,362 kilograms of dry organic matter per hectare as compared with 440 kilograms of zooplankton, bottom fauna and fish; that is, the plant contribution is 93 per cent and the animal part is 7 per cent of the total organic matter.

Table V gives the energy value of the various constituents of the annual biological crop. The two groups of plants, namely phytoplankton and large aquatics, have an energy value of 321 gram calories as compared with 25 gram calories per square centimeter in the animals. The 321 gram calories represented in the organic matter of the plants is only 0.27 of one per cent of the mean annual radiation delivered to the surface of the lake, namely 118,872 calories. Two corrections need to be made in this result, however. (1) As already indicated some 28,500 calories of solar energy are lost at the surface of the water and thus do not reach the aquatic vegetation. Deducting this amount leaves 90,372 calories which pass into the water and thus become available for the plants. On this basis the percentage of utilization is increased to a little more than 0.35 of one per cent of the available radiation. (2) A certain amount of the organic matter synthesized by the plants is used in their metabolism and this does not appear in the percentage of utilization given above. Experiments show that some of the algae utilize in their metabolic processes about one-third of the organic matter that they synthesize. No data are available for the large aquatics, but assuming that they also utilize a similar proportion in their metabolism, the two groups of plants would represent a utilization of 428 calories which is equivalent to 0.47 of one per cent of the annual quantity of solar energy that actually enters the water.

This percentage is based on an average turnover in the phytoplankton every two weeks throughout the year, but there is some evidence that the turnover takes place more frequently, especially from April to October. With an average turnover once a week in the organic matter of the phytoplankton during the year, the energy value of this crop would be 798 calories, including metabolism; adding to this amount the 29 calories in the annual crop of bottom flora gives a total of 827 calories which is utilized by the plants. This is 0.91 of one per cent of the 90,372 calories of energy that penetrate the water and become available to the plants; in round numbers this may be regarded as a utilization of one per cent.

This small percentage of utilization of solar energy by aquatic plants shows that Lake Mendota is not a very efficient manufacturer of biological products in so far as utilizing the annual supply of solar and sky radiation is concerned; on the other hand it belongs to the group of highly productive lakes.

While the aquatic plant crop appears

to be inefficient in its utilization of solar energy, it compares very favorably with some of the more important land crops in this respect. Transeau states that only 1.6 per cent of the total available energy is used by the corn plant in photosynthesis during a growing period of 100 days, or from June 1 to September 8. . . . These computations for cultivated crops, however, take into account only the quantity of solar radiation available during comparatively brief growing periods and thus do not cover the entire year as indicated for the aquatic plants.

Energy value of animals. The organic content of the animal population of the lake represents a conversion and further storage of the material manufactured by the plants, but no direct utilization of solar energy is involved in the transformation. It may be regarded as an expensive method of prolonging the existence of a certain portion of the original plant material. As previously indicated, it may take five grams of plant food to produce one gram of animal tissue, so that the plant equivalent of the animal crop may be reckoned as five times as large as the organic content of the animals; in the predatory animals, however it would be much larger.

Table V shows that the energy value of the bottom and fish population is 25 gram calories per square centimeter; on the fivefold basis, this would represent the conversion of at least 125 gram calories of original plant organic matter. This utilization is approximately 40 per cent of the potential energy stored in the annual plant crop of 321 gram calories which is based on a turnover in the phytoplankton every two weeks during the year. A turnover in the phytoplankton every week would give a plant crop of 620 calories and an animal utilization of a little more than 20 per cent.

Dissolved organic matter. The energy value of the dissolved organic matter is indicated as 71 gram calories per square centimeter in table V. This material is constantly being supplied to the water by the various organisms and the standing crop of it remains fairly uniform in quantity during the different seasons of the year as well as in different years. While there is a regular turnover in this organic matter, it needs to be taken into account only once in computing the organic crop of the lake because it has its source in the plants and animals for which an annual yield has already been computed. . . .

THE TROPHIC-DYNAMIC ASPECT OF ECOLOGY

Raymond L. Lindeman—1942

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This paper incorporates the most significant formulation in the development of modern ecology. It provided not only a conceptual framework within which to work but also stimulated a great profusion of effort because of the basic questions it posed. Hutchinson stated the case well in a postscript to the paper, ". . . here for the first time, we have the interrelated dynamics of a biocoenosis presented in a form that is amenable to a productive abstract analysis." Lindeman's potentially productive career which began at the University of Wisconsin and ended at Yale was foreshortened at age 27 while the following paper was in press.

The trophic-dynamic viewpoint, as adopted in this paper, emphasizes the relationship of trophic or "energy-availing" relationships within the community-unit to the process of succession. From this viewpoint, which is closely allied to Vernadsky's "biogeochemical" approach and to the "oekologische Sicht" of Friederichs, a lake is considered as a primary ecological unit in its own right, since all the lesser "communities" are dependent upon other components of the lacustrine food cycle for their very existence. Upon further consideration of the trophic cycle, the discrimination between living organisms as parts of the "biotic community" and dead organisms and inorganic nutritives as parts of the "environment" seems arbitrary and unnatural. The difficulty of drawing clear-cut lines between the living *community* and the nonliving *environment* is illustrated by the difficulty of determining the status of a slowly dying pondweed covered with periphytes, some of which are also continually dying. . . . much of the nonliving nascent ooze is rapidly reincorporated through "dissolved nutrients" back into the living "biotic community." This constant organic-inorganic cycle of nutritive substance is so completely integrated that to consider even such a unit as a lake primarily as a biotic community appears to force a "biological" emphasis upon a more basic functional organization.

This concept . . . is inherent in the term *ecosystem*, proposed by Tansley for the fundamental ecological unit. . . . The *ecosystem* may be formally defined as the system composed of physical-chemical-biological processes active within a space-time unit of any magnitude, i.e., the biotic community *plus* its abiotic environment. . . .

TROPHIC DYNAMICS

Qualitative food-cycle relationships. Although certain aspects of food relations have been known for centuries, many processes within ecosystems are still very incompletely understood. The basic process in trophic dynamics is the transfer of energy from one part of the ecosystem to another. All function, and indeed all life, within an ecosystem depends upon the utilization of an external source of energy, solar radiation. A portion of this incident energy is transformed by the process of photosynthesis into the structure of living organisms. In the language of community economics introduced by Thienemann, autotrophic plants are *producer* organisms, employing the energy obtained by photosynthesis to synthesize complex organic substances from simple inorganic substances. Although plants again release a portion of this potential energy in catabolic processes, a great surplus of organic substance is accumulated. Animals and heterotrophic plants, as *consumer* organisms, feed upon this surplus of potential energy, oxidizing a considerable portion of the consumed substance to release kinetic energy for metabolism, but transforming the remainder into the complex chemical substances of their own bodies. Following death, every organism is a potential source of energy for saprophagous organisms (feeding directly on dead tissues), which again may act as energy sources for successive categories of consumers. Heterotrophic bacteria and fungi, representing the most important saprophagous consumption of energy, may be conveniently differentiated from animal consumers as specialized *decomposers* of organic substance. Waksman has suggested that certain of these bacteria be further differentiated as *transformers* of organic and inorganic compounds. The combined action of animal consumers and bacterial decomposers tends to dissipate the potential energy of organic substances, again transforming them to the inorganic state. From this inorganic state the autotrophic plants may utilize the dissolved nutrients once more in resynthesizing complex organic substance, thus completing the food cycle. . . .

Productivity. DEFINITIONS. The quantitative aspects of trophic ecology have been commonly expressed in terms of the productivity of the food groups concerned. Productivity has been rather broadly defined as the general rate of production, a term which may be applied to any or every food group in a given ecosystem. . . .

In the following pages we shall consider the quantitative relationships of the following productivities: λ_0 (rate of incident solar radiation), λ_1 (rate of photosynthetic production), λ_2 (rate of primary or herbivorous consumption), λ_3 (rate of secondary consumption or primary predation), and λ_4 (rate of tertiary consumption). The total amount of organic structure formed per year for any level Λ_n, which is commonly expressed as the annual "yield," actually represents a value uncorrected for dissipation of energy by (1) respiration, (2) predation, and (3) post-mortem decomposition. Let us now consider the quantitative aspects of these losses.

RESPIRATORY CORRECTIONS. The amount of energy lost from food levels by catabolic processes (respiration) varies considerably for the different stages in the life histories of individuals, for different levels in the food cycle and for different seasonal temperatures. In terms of annual production, however, individual deviates cancel out and respiratory differences between food groups may be observed. . . .

Considering that predators are usually more active than their herbivorous prey, which are in turn more active than the plants upon which they feed, it is not surprising to find that respiration with respect to growth in producers (33 per cent), in primary consumers (62 per cent) and in secondary consumers ($>$100 per cent) increases progressively. These differences probably reflect a trophic principle of wide application: the percentage loss of energy due to respiration is progressively greater for higher levels in the food cycle.

PREDATION CORRECTIONS. In considering the predation losses from each level, it is most convenient to begin with the highest level, Λ_n. In a mechanically perfect food cycle composed of organically discrete levels, this loss by predation obviously would be zero. Since no natural food cycle is so mechanically constituted, some "cannibalism" within such an arbitrary level can be expected, so that the actual value for predation loss from Λ_n probably will be somewhat above zero. The predation loss from level Λ_{n-1} will represent the total amount of assimilable energy passed on into the higher level (i.e., the true productivity, λ_n), plus a quantity representing the average content of substance killed but not assimilated by the predator. . . . The predation loss from level Λ_{n-2} will likewise represent the total amount of assimilable energy passed on to the next level (i.e., λ_{n-1}), plus a similar factor for unassimilated material, as illustrated by the data of tables II and III. The various categories of parasites are somewhat comparable to those of predators, but the details of their energy relationships have not yet been clarified.

DECOMPOSITION CORRECTIONS. In conformity with the principle of Le Chatelier, the energy of no food level can be completely extracted by the organisms which feed upon it. In addition to the energy represented by organisms which survive to be included in the "annual yield," much energy is contained in "killed" tissues which the predators are unable to digest and assimilate. . . . Although the data are insufficient to warrant a generalization, these values suggest increasing digestibility of the higher food levels, particularly for the benthic components of aquatic cycles.

The loss of energy due to premature death from non-predatory causes usually must be neglected, since such losses are exceedingly difficult to evaluate and under normal conditions probably represent relatively small components of the annual production. . . .

Following non-predated death, every organism is a potential source of energy for myriads of bacterial and fungal saprophages, whose metabolic products provide simple inorganic and organic solutes reavailable to photosynthetic producers. These saprophages may also serve as energy sources for successive levels of consumers, often considerably supplementing the normal diet of herbivores. . . .

APPLICATION. The value of these theoretical energy relationships can be illustrated by analyzing data of the three ecosystems for which relatively comprehensive productivity values have been published (table I). . . . The calorific values in table I, representing annual production of organic matter, are uncorrected for energy losses.

TABLE I. *Productivities of food-groups in three aquatic ecosystems, as g-cal/cm²/year, uncorrected for losses due to respiration, predation and decomposition. Data from Brujewicz ('39), Juday ('40) and Lindeman ('41b)*

	Caspian Sea	Lake Mendota	Cedar Bog Lake
Phytoplankters: Λ_1	59.5	299	25.8
Phytobenthos: Λ_1	0.3	22	44.6
Zooplankters: Λ_2	20.0	22	6.1
Benthic browsers: Λ_2	20.6	1.8*	0.8
Benthic predators: Λ_3		0.9*	0.2
Plankton predators: Λ_3 . . .			0.8
"Forage" fishes: $\Lambda_3(+\Lambda_2?)$.	0.6	?	0.3
Carp: $\Lambda_3(+\Lambda_2?)$.	0.0	0.2	0.0
"Game" fishes: $\Lambda_4(+\Lambda_3?)$.	0.6	0.1	0.0
Seals: Λ_5	0.01	0.0	0.0

*Roughly assuming that $\frac{2}{3}$ of the bottom fauna is herbivorous.

Correcting for the energy losses due to respiration, predation and decomposition, as discussed in the preceding sections, casts a very different light on the relative productivities of food levels. The calculation of corrections for the Cedar Bog Lake values for producers, primary consumers and secondary consumers are given in table II. The application of similar corrections to the energy values for the food levels of the Lake Mendota food cycle given by Juday, as shown in table III, indicates that Lake Mendota is much more productive of producers and primary consumers than is Cedar Bog Lake, while the production of secondary consumers is of the same order of magnitude in the two lakes.

TABLE II. *Productivity values for the Cedar Bog Lake food cycle, in g-cal/cm²/year, as corrected by using the coefficients derived in the preceding sections*

Trophic level	Uncorrected productivity	Respiration	Predation	Decomposition	Corrected productivity
Producers: Λ_1	70.4 ± 10.14	23.4	14.8	2.8	111.3
Primary consumers: Λ_2	7.0 ± 1.07	4.4	3.1	0.3	14.8
Secondary consumers: Λ_3	1.3 ± 0.43*	1.8	0.0	0.0	3.1

*This value includes the productivity of the small cyprinoid fishes found in the lake.

TABLE III. *Productivity values for the Lake Mendota food cycle, in g-cal/cm²/year, as corrected by using coefficients derived in the preceding sections, and as given by Juday ('40)*

Trophic Level	Uncorrected productivity	Respiration	Predation	Decomposition	Corrected productivity	Juday's corrected productivity
Producers: Λ_1	321*	107	42	10	480	428
Primary consumers: Λ_2	24	15	2.3	0.3	41.6	144
Secondary consumers: Λ_3	1†	1	0.3	0.0	2.3	6
Tertiary consumers: Λ_4	0.12	0.2	0.0	0.0	0.3	0.7

*Hutchinson gives evidence that this value is probably too high and may actually be as low as 250.

†Apparently such organisms as small "forage" fishes are not included in any part of Juday's balance sheet. The inclusion of these forms might be expected to increase considerably the productivity of secondary consumption.

Biological efficiency. The quantitative relationships of any food-cycle level may be expressed in terms of its efficiency with respect to lower levels. Quoting Hutchinson's definition, "the efficiency of the productivity of any level (Λ_n) relative to the productivity of any previous level (Λ_m) is defined as (λ_n/λ_m) 100. If the rate of solar energy entering the ecosystem is denoted as λ_0, the efficiencies of all levels may be referred back to this quantity λ_0." In general, however, the most interesting efficiencies are those referred to the previous level's productivity (λ_{n-1}), or those expressed as (λ_n/λ_{n-1}) 100. These latter may be termed the *progressive efficiencies* of the various food-cycle levels, indicating for each level the degree of utilization of its potential food supply or energy source. All efficiencies discussed in the following pages are progressive efficiencies, expressed in terms of relative productivities ((λ_n/λ_{n-1}) 100). It is important to remember that efficiency and productivity are not synonymous. Productivity is a rate (i.e., in the units here used, cal/cm²/year), while efficiency, being a ratio, is a dimensionless number. The points of reference for any efficiency value shoud always be clearly stated.

The progressive efficiencies ((λ_n/λ_{n-1}) 100) for the trophic levels of Cedar Bog Lake and Lake Mendota, as obtained from the productivities derived in tables II and III, are presented in table IV. In view of the uncertainties concerning some of the Lake Mendota productivities, no definite conclusions can be drawn from their relative efficiencies. The Cedar Bog Lake ratios, however, indicate that the progressive efficiencies increase from about 0.10 per cent for production, to 13.3 per cent for primary consumption, and to 22.3 per cent for secondary consumption. . . . These progressively increasing efficiencies may well represent a fundamental trophic principle, namely, that the consumers at progressively higher levels in the food cycle are progressively more efficient in the use of their food supply.

TABLE IV. *Productivities and progressive efficiencies in the Cedar Bog Lake and Lake Mendota food cycles, as g-cal/cm²/year*

	Cedar Bog Lake		Lake Mendota	
	Productivity	Efficiency	Productivity	Efficiency
Radiation	≤118,872		118,872	
Producers: Λ_1 . .	111.3	0.10%	480*	0.40%
Primary consumers: Λ_2	14.8	13.3%	41.6	8.7%
Secondary consumers: Λ_3	3.1	22.3%	2.3†	5.5%
Tertiary consumers: Λ_4	—	—	0.3	13.0%

*Probably too high; see footnote of table III.

†Probably too low; see footnote of table III.

At first sight, this generalization of increasing efficiency in higher consumer groups would appear to contradict the previous generalization that the loss of energy due to respiration is progressively greater for higher levels in the food cycle. These can be reconciled by remembering that increased activity of predators considerably increases the chances of encountering suitable prey. The ultimate effect of such antagonistic principles would present a picture of a predator completely wearing itself out in the process of completely exterminating its prey, a very improbable situation. However, Elton pointed out that food-cycles rarely have more than five trophic levels. Among the several factors involved, increasing respiration of successive levels of predators contrasted with their successively increasing efficiency of predation appears to be important in restricting the number of trophic levels in a food cycle. . . .

TROPHIC-DYNAMICS IN SUCCESSION

Dynamic processes within an ecosystem, over a period of time, tend to produce certain obvious changes in its species-composition, soil characteristics and productivity. Change, according to Cooper, is the essential criterion of succession. From the trophic-dynamic viewpoint, succession is the process of development in an ecosystem, brought about primarily by the effects of the organisms on the environment and upon each other, towards a relatively stable condition of equilibrium.

It is well known that in the initial phases of hydrarch succession (oligotrophy→eutrophy) productivity increases rapidly; it is equally apparent that the colonization of a bare terrestrial area represents a similar acceleration in productivity. In the later phases of succession, productivity increases much more slowly. . . .

SUCCESSIONAL PRODUCTIVITY CURVES

In recapitulating the probable photosynthetic productivity relationships in hydrarch succession, we shall venture. . . a hypothetical hydrosere, developing from a moderately deep lake in a fertile cold temperate region under relatively constant climatic conditions. The initial period of oligotrophy is believed to be relatively short. . . . with productivity rapidly increasing until eutrophic stage-equilibrium is attained. The duration of high eutrophic productivity depends upon the mean depth of the basin and upon the rate of sedimentation, and productivity fluctuates about a high eutrophic mean until the lake becomes too shallow for maximum growth of phytoplankton or regeneration of nutrients from the ooze. As the lake becomes shallower and more senescent, productivity is increasingly influenced by climatic fluctuations and gradually declines to a minimum as the lake is completely filled with sediments. . . .

Efficiency relationships in succession. The successional changes of photosynthetic efficiency in natural areas (with respect to solar radiation, i.e., (λ_1/λ_0) 100) have not been intensively studied. In lake succession, photosynthetic efficiency would be expected to follow the same course deduced for productivity, rising to a more or less constant value during eutrophic stage-equilibrium, and declining during senescence, as suggested by a photosynthetic efficiency of at least 0.27 per cent for eutrophic Lake Mendota and of 0.10 per cent for senescent Cedar Bog Lake. For the terrestrial hydrosere, efficiency would likewise follow a curve similar to that postulated for productivity. . . .

DYNAMICS OF PRODUCTION IN A MARINE AREA

George L. Clarke—1946

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Problems and confusion in the description and measurement of the energy relations within ecosystems, and concomitantly in the attempt to compare the energetics of ecosystems, were considerably clarified by Clarke. In this clear-cut discussion of concepts of production, he indicates the limitations of traditionally used measurements and suggests a basis for meaningful comparison which is now widely followed. (See p. 27 for another paper by Clarke.)

CONCEPTS OF PRODUCTION

All the ideas and measurements of productivity which have an ecological application, may be grouped under the following three fundamental concepts:

Standing crop—the amount of organisms *existing* in the area at the time of observation.

Material removed—the amount of organisms *removed* from the area per unit time by man, or in other ways.

Production rate—the amount of organisms *formed* within the area per unit time.

All three of these major concepts of productivity are important, and are essential for a complete understanding of the operation of the area as an ecological complex. In addition, the quantities involved are to a certain extent mutually dependent. To avoid ambiguity in discussing the ecological relationships of the area, it is suggested that the terms "productivity" and "production" be not used in referring to the standing crop or to the material removed unless a phrase is added to make the meaning clear. Measurements made under any of the three categories may be stated in terms of number of individuals, weight or "biomass," energy content, or any other characteristic (such as chlorophyll content) which may be adequate for the given situation. Evaluation on the basis of energy content has the advantage that the efficiency of the utilization of the incident solar radiation may be calculated directly.

Standing crop. Measurements of the standing crop, and hence of the concentration, of the various species inhabiting the area are essential in judging the harmful or beneficial effect of crowding within the species, and the effectiveness with which dependent species can feed upon forage species. When applied to the exploitation of a natural population by man, the magnitude of the standing crop similarly influences the size of the catch per unit effort. However, a knowledge of the standing crop does not give any information as to the time which has been required to produce the crop, or its replaceability.

To illustrate these points, the changes of population size with time for three hypothetical situations are represented diagrammatically in Figure 2. In the first situation the growth rate of the population is much more rapid than in the second, but conditions are such that the same size of standing crop is attained provided that the season is sufficiently long for the maximum value to be reached. In this case, the final size of the standing crop gives no information as to the rate of net increase. If, however, the standing crop is measured before the asymptotic level is approached, the situation with the more rapid increase will have the larger standing crop. The size of the standing crop at any time is the result of the summation of the excess of production over destruction from the beginning of the growth of the population to the moment of observation.

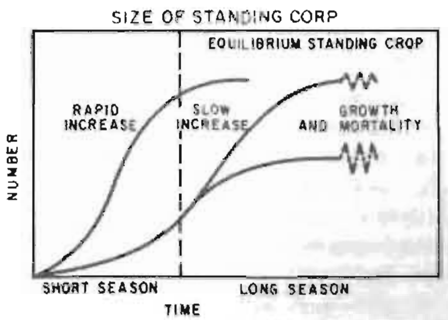

FIG. 2. *Changes of population size with time in three hypothetical situations (for full explanation see text).*

In the third hypothetical situation, the same length of time is required for the population to reach a maximum size as in the second situation, but the maximum level reached is lower. In both situations, the population may fluctuate above and below the average limiting value (broken lines at right of curves), and since equilibrium is being maintained, at least temporarily, the average rate of production must be exactly balanced by the average rate of destruction. . . .

Material removed. The material removed from an area may fall into several categories. In the first place, the amount of organisms harvested by man during a certain period may be measured and designated as the *yield.* In addition, other organisms may be permanently removed from the area by wind or currents, or by emigration accomplished by the organisms' own locomotion. Organisms which grow in the area but which are consumed, or die in other ways, and decompose so as to enter the ecological cycle again within the same area are not considered to be a yield in the sense recommended here. However, dead organic matter which has become permanently inaccessible, as for example, if buried under bottom deposits, is an irrevocable loss to the system, and hence forms another subdivision of the material removed.

These different subdivisions have in common the fact that in each instance the particular material which is removed from the area does not return again to that area. . . . Because of the inevitable loss of materials (and energy) at each level in the food chain, the yield will ordinarily be much smaller than the supply. Measurement of the ratio of yield to supply, and hence the efficiency of the formation of the yield, is therefore of great importance to . . . ascertain whether the actual yield represents a needlessly low utilization or an over-exploitation of the area.

Production rate. The concept of the production rate as the amount of organisms formed per unit time (per unit area or volume) is complicated by the fact that in most natural areas organic matter is being formed or transformed at several trophic levels simultaneously, i.e., by the plants and animals of the food chain which depend upon one another. In order for measurements of production rate to be useful it is necessary to keep separate the values for the various trophic levels and in each case to distinguish between gross and net rates of formation.

These trophic relations among the components of the production pyramid may be . . . [considered] first, for a situation in which the constructive and destructive processes are equal so that there is no gain or loss in the amounts of organisms present at the end of the period over that at the beginning. . . .

In tracing the energy and material

through the production pyramid we may start with the incident light which falls upon the area. A portion of this light (small, in the aquatic environment) reaches the plant cells and is absorbed by them. A small portion of the absorbed energy appears as the carbohydrate which has been formed by photosynthesis (P_1). The amount of material produced by this anabolic process (or of the energy represented) is termed the *gross plant production*. It has also been called the *primary production* because the animal substances which result from consuming the plants, and each other, are transformations of the original plant material, and thus represent alternative forms of the same material (and energy). . . . A large part of the gross production is lost as the result of catabolic processes. This loss may be measured by the amount of respiration. The remaining fraction of the gross production accounts for the new plant growth (P_2) and this is termed the *net plant production*, or simply, the *plant production*, for unit area and time.

Since in the case considered there is no permanent increase or decrease in plant material, all of this new plant growth is destroyed and the energy transformed before the end of the period. Part of the plant material produced is consumed by herbivores and the remainder dies in some other manner and decomposes. In many situations a large proportion of the plant material consumed is not assimilated by the herbivores, but is passed through the gut undigested. This fraction (U) may be added to that which has decomposed following destruction in other ways.

A similar analysis may be made of the material which enters into each of the successive trophic levels represented by the animals and colorless plants. . . .

At the end of the period for this hypothetical case of complete equilibrium the standing crop is of exactly the same magnitude as at the beginning and there has obviously been no yield. Production has been going on, however, at definite rates at the various levels, and in this case destruction of the materials has exactly balanced their formation during the period. . . .

Let us consider now a second case, in which smaller amounts of organisms are destroyed than are formed during the period. Under these circumstances the growth (P_2) of any one of the categories of organisms would be accounted for at the end of the period in three ways: one portion consumed, one portion decomposed, and one portion remaining in existence and representing an increment which may be termed the *net increase* (P_3). The standing crop at the end of the period is consequently larger than at the beginning of the period by the amount of the net increase. In a situation in which the amount of destruction during the period was greater than the amount of production, the net increase (P_3) would be negative, and the standing crop would be reduced.

If this surplus material is permanently removed from the system by man, it will constitute a yield. Obviously these organisms could not continue to be removed from the system in succeeding periods unless an equal amount of material, as nutrients or in some other form, were added each period. If the organisms representing the net increase are not removed from the system, and if circumstances are such that they can continue in existence in the area, there will be a permanent increase in the size of the standing crop. Again, this can take place only to the extent to which an equivalent supply of nutrients or other materials are added to the area. The standing crops of lakes are frequently seen to increase in this way with the result that the lakes become more eutrophic and the process is known as *eutrophication*.

In the discussion of production rate thus far nothing has been said about the length of the period considered. The time required for each type of organism to complete its growth, to die and decompose, and to start the cycle over again is known as its period of *turnover*. The length of the turnover period usually differs widely for the organisms at the different trophic levels of the production pyramid, and may differ for the same level in different situations and at different seasons of the year. The green plants of a terrestrial area may have essentially only one turnover per year, whereas the phytoplankton of an aquatic area may turnover within short periods varying widely from a few days to several weeks. In the latter case the same material may be used over again several times during the year, and it would thus have little meaning to add up the increments of growth for the whole year in an attempt to reach a "total" annual value. If the growth of the plants is measured as energy, it is permissible to summate the amount of energy which has been transformed during the year since the energy can be used by the plants only once. A comparison may thus be made between the annual incident radiation and the energy content of the plants produced.

In the case of the organisms at successively higher trophic levels, both the materials and the energy are used over again one or more times. A summation of amounts of production at all trophic levels for a long period, such as a year, therefore similarly has little meaning. . .

. . . Production is therefore best measured as a set of rates applying to the gross production, net production, and net increase for each category of organisms or each trophic level. . . .

TROPHIC STRUCTURE AND PRODUCTIVITY OF SILVER SPRINGS, FLORIDA

Howard T. Odum—1957

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The significance of this paper lies in its extensive application of Lindeman's trophic-dynamics concept. It has been a model for subsequent studies on different ecosystems. It also introduced an energy flow model which has had successful instructional value in incorporating the various energy relations of an ecosystem into a readily comprehensible pattern. Following a productive career as Director of the Institute of Marine Science, of the University of Texas, Odum recently assumed the directorship of the terrestrial ecology program of the Puerto Rico Nuclear Center.

The study of Silver Springs reported here has been made with the purpose of determining the basic structure and workings of flowing water ecosystems by the careful study of one stream under some unusually favorable conditions provided. In recent years such holistic consideration of the energy flux and biomass have provided a fruitful approach to the understanding of many types of ecological communities. . . . Diagrammatically, the object of the energy approach may be said to be the complete quantitative determination of the states and flow in Figure 7 as well as the control mechanisms by which such a picture is sustained. The story in this paper concerns the details and workings previewed in Figure 7. . . .

Energy flow diagram. In Figure 7 the flow of energy through the community in Silver Springs was shown according to trophic levels. The use of the diagram is applicable in general form to any system. It shows distinctly the workings of the first two laws of thermodynamics. According to the first law the total influx of energy equals the total flux out. According to the second law, especially as interpreted with the optimum efficiency maximum power hypothesis. . ., wherever an energy transformation occurs most of the energy is dispersed into heat that is unavailable for further use by the organisms in the community.

Since the overall metabolism has now been estimated. . . it is now possible to make some rough estimates of the component flow rates. Where estimates are complete, the diagram may be used as a check since the parts must agree with the whole. Where estimates are incomplete the diagram may be used to fill in the part from the total. The figure must be regarded as extremely tentative because of the many possible errors and incomplete data.

As discussed in the animal growth rate section, there are several procedures required to work out the flow rates of production at the various trophic levels. To obtain the respiration of a trophic level one determines the standing crops, estimates the respiratory metabolism per gram, and multiplies to obtain the total respiratory metabolism in each trophic level. The net production of the trophic level follows from the determination of the growth rates (output) directly using varied means depending on the organisms. As described in sections on animal growth rate above, this has been done in some cases and reported as turnover. The best estimates from this table are used in the energy flow diagram in Figure 7. The input of energy into a trophic level is mainly the sum of the respiration and net production if one neglects egested unassimilated matter. The flow picture in Figure 7 shows the relationship of growth, utilization, assimilation, and heat loss for each trophic level. From these concepts one may also derive the several types of efficiencies (ratios × 100) useful in describing ecological systems. These are defined as follows using symbols from the flow diagram:

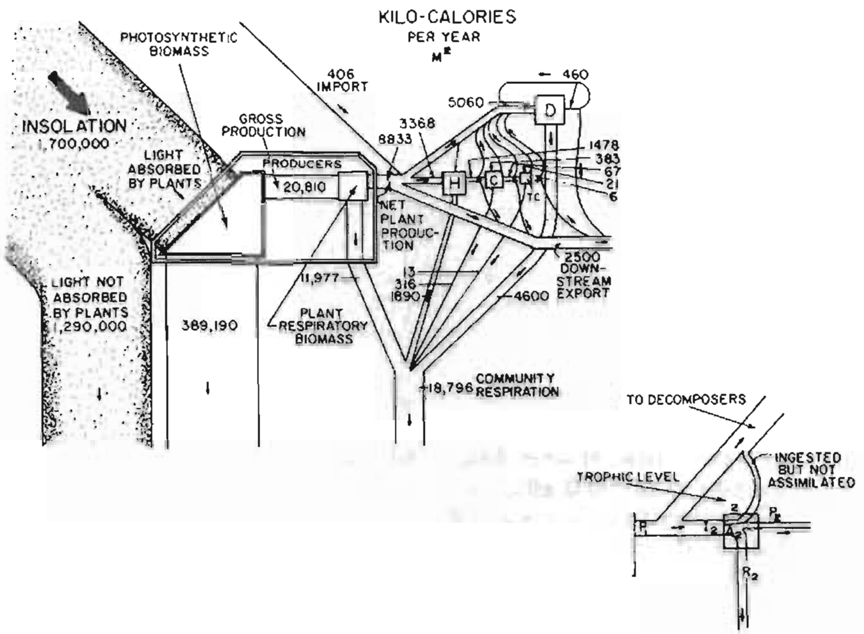

FIG. 7. *Energy flow diagram with estimates of energy flows in kilo-colories per square meter per year in the Silver Springs community. The small diagram contains symbols used in text discussion (P, production; I, energy intake; A, consumer assimilation; R, respiration).*

P = production rate (rate of net organic synthesis in the form of the species of the trophic level or in storage products)
A = rate of assimilation
I = rate of ingestion (consumption) or energy intake
R = rate of respiration
E_u = utilization efficiency

$$= \frac{I_2}{P_1} = \frac{I_3}{P_2} = \frac{I_4}{P_3} = \frac{I_5}{P_4}$$

E_a = assimilation efficiency

$$= \frac{A_2}{I_2} = \frac{A_3}{I_3} = \frac{A_4}{I_4} = \frac{A_5}{I_5}$$

E_t = tissue growth efficiency

$$= \frac{P_2}{A_2} = \frac{P_3}{A_3} = \frac{P_4}{A_4} = \frac{P_5}{A_5}$$

E_e = ecological growth efficiency

$$= \frac{P_2}{I_2} = (E_t)\ (E_a)$$

E_l = Lindeman efficiency (ratio of intakes of trophic levels)

$$= \frac{I_2}{I_1} = (E_e)\ (E_u)$$

E_p = trophic level production ratios

$$= \frac{P_2}{P_1} = (E_u)\ (E_e) = (E_u)\ (E_t)\ (E_a)$$

The data in Figure 7 permit the calculation of the ecological growth efficiencies (E_e) and the trophic level production ratios (E_p, synonomous with Lindeman's usage of trophic level efficiencies only in the first trophic level). The ecological growth efficiencies E_e and the trophic level production ratios are given as follows:

	E_e	E_p	E_1
Plant Net Production	$\frac{8{,}833}{20{,}810} = 42\%$	$\frac{8{,}833}{20{,}810} = 42\%$	$\frac{20{,}810}{410{,}000} = 5\%$
Herbivores	$\frac{1{,}478}{3{,}368} = 44\%$	$\frac{1{,}478}{8{,}833^*} = 17\%^*$	$\frac{3{,}368^*}{20{,}810} = 16\%^*$
Carnivores	$\frac{67}{383} = 17\%$	$\frac{67}{1{,}478^*} = 5\%^*$	$\frac{383}{3{,}368^*} = 11\%^*$
Top Carnivores	$\frac{6}{21} = 29\%$	$\frac{6}{67} = 9\%$	$\frac{21}{383} = 6\%$

Great confusion often results from misunderstanding as to which efficiency is meant. The energy flow diagram is a help in this clarification. In another communication some current uses of the term production as synonomous with assimilation are questioned.

The general principle from Lindeman and Dineen that trophic level efficiency (E_1 or E_p) increased along the food chain was not entirely confirmed for Silver Springs although the estimates of rates at the higher trophic levels are probably not accurate enough to test the relationship definitely.

Turnover, climax and steady state. With a gross primary production during a year of 6390 gms/m^2 and with a standing crop biomass of all components of 819 gms/m^2 it is clear from the ratio that the community turnover is 8 times/year. As discussed elsewhere, the smaller the component organism, the more rapid the turnover. Thus the overall community turnover has meaning only in that it expresses the relationship of the size of the community and the total productivity.

Where all of the components of a community turn over several times a year there would be ample opportunity for changes to occur if there were no self regulative mechanisms. In Silver Springs there is apparently a fairly high degree of stability. Shelford & Eddy presented evidence that the climax concept was applicable to streams. The Silver Springs community is strong evidence that where the hydrographic climate is constant the community may develop a steady state. The possible relationship to the balanced aquarium idea is discussed elsewhere.

It is suggested that the stability of a system be measured by the number of times it turns over without change. Thus communities of small organism which persist for a year with a daily turnover may be considered as stable in this sense as a community of large organisms which lasts 300 years while turning over once per year.

The summer pulse of primary production due to the greater influx of light mainly leads to an increase in reproduction in the consumers rather than to pulses, blooms, and changes in populations. The increases in rates at any one trophic level are accompanied apparently by increases in utilization at other trophic levels so that the standing crops do not change markedly. . . .

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*These figures have been corrected from the original publication at the request of the author [Ed.].

NITRATE IN THE SEA

H. W. Harvey—1926

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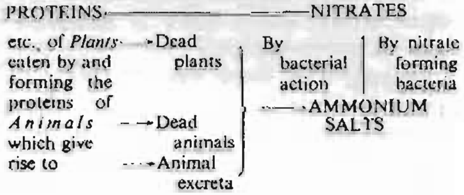
H. W. Harvey, a pioneer in marine biological chemistry, describes here not only the inverse relationship between the size of diatom populations and nitrogen availability but also the regulation of environment by organisms. In the nitrogen cycle, utilizable nitrogen is returned to the system by organisms acting on the bound nitrogen in the excreta and remains of other organisms; the major function of the environment in the process is in physically distributing the requisite materials.

THE NITROGEN CYCLE

Denitrifying bacteria have been found in water near the shore and in mud of the Baltic, but as pointed out by Gran they are not likely to play a part in the economy of the open oceans, since the water almost invariably contains a sufficiency of oxygen for these bacteria, without their having recourse to attack the small quantities of nitrates present.

Azotobacter, fixing dissolved nitrogen has been found in the slime of Baltic algæ and in bottom deposits from near the land. There is no evidence as yet that they are general in occurrence or that they add more than a minute fraction to the combined nitrogen in the sea.

As far as we know the inorganic salts necessary for plant life are always present in sea-water in ample amount except phosphates and nitrates. Iron is a possible exception. The nitrates are converted by the algæ into proteins, etc. Some of these algæ die, and from the decay of their corpses ammonium salts are produced. Others nourish marine animals which in turn are fed upon by other animals. These excrete the products of their metabolism and in due course die; ammonium salts are produced from their corpses and excreta by bacterial action. Thus we have in the sea a closed cycle.



Phosphate is regenerated in a similar manner, and the evidence so far obtained shows that in both cases the cycle is practically a closed one, the increment due to land washings not being very great compared with the amount continually being regenerated from dead marine organisms.

A deficiency of nutrient salts limits both the rate of multiplication of vegetable plankton, and in all probability the rate of carbon assimilation as well. All the energy expended in the vital processes of plants and animals in the sea is derived from the energy of light absorbed during the course of carbon assimilation by phytoplankton—the fixed algæ being but a small proportion of the plant life.

Hence a quantitative knowledge of those factors, which control and limit the multiplication of vegetable plankton and which affect its efficiency as an energy absorber, is the first step in any fundamental inquiry concerning the fertility of the sea.

The consideration of this cycle indicates that the fertility of any area of the open oceans, not subject to considerable inflows of water from other areas, depends upon three main factors. (*a*) The length of time protein formed by phytoplankton remains part of the plant or nourished animal's body. (*b*) The time which elapses during the decay and formation of ammonium salts and phosphate from corpses and excreta. To this must be added the time taken for nitrate forming bacteria to convert the ammonium into nitrates. (*c*) The time which elapses before the reformed nitrate and phosphate again reaches the upper layers where there is sufficient light for photosynthesis.

Dealing with these three factors in turn, the first is controlled by the natural length of life of the plants and animals, and by the proportion of the plants which are eaten. This decides the proportion of total living matter to the rate of loss by natural death. The proportion of total living matter to its rate of loss by respiration and excretion is controlled by *temperature*. In a warm sea the loss will be in excess of that taking place under colder conditions, since the rate of metabolism roughly doubles for a rise of 10°C., and more food will be required by animals to provide for their irreducible metabolism necessary to maintain life.

Of the second factor (*b*) there is little information. Presumably the breakdown products of proteins and phosphoproteins produced in the course of metabolism are excreted mostly as urea and phosphates, and the decay of corpses is largely brought about by bacterial agency. From the analyses of water collected in the Atlantic during the expedition of the *Planet* it appears that there is rarely less than 25 milligrams per cubic metre of ammonium nitrogen in the waters of the open ocean. The distribution of nitrate forming bacteria, possibly identical with the *nitrobacter* of the land in the open ocean is quite unknown.

The third factor (*c*), being the length of time that the reformed nitrate lies unusable below the illuminated upper layers, is of great magnitude. . . . [there is] an enormous store of nitrate below the upper 100-metre layer. A rough calculation indicates an amount somewhere in the order of 250 thousand million metric tons of nitrate-nitrogen in the deeper layers of the great oceans, lying dormant until such time as currents bring the deep water into the upper sunlit layers. There is every reason to suppose that this third factor regulates the speed at which nitrogen and phosphorus pass through the complete cycle in the sea *as a whole*, being the slowest in the series of changes.

In particular shallow areas, however, such as where tidal streams and sufficient surface cooling to set up convection currents reaching to the bottom cause vertical circulation, during the whole or part of the year, the regenerated nitrate is subject to no delay before again becoming available. These areas, usually coastal, are very fertile. The North Sea, English Channel, and the Shallow Shelf between the Grand Banks and Cape Cod are such. Here the conditions are somewhat complicated by a certain amount of inflow of oceanic water, and by the fact that the rate of regeneration of nitrate, and phosphate, from dead organisms overtakes the rate at which plant life utilises it during the autumn and short days of winter. A store of available nitrate and phosphate is thus formed which is rapidly used up as soon as some three hours of sunshine per day occur in the spring in the English Channel. Insufficient illumination becomes the limiting factor during the winter months, delaying for a period the rate at which combined nitrogen and phosphorus passes through the complete cycle.

In the deep open oceans the winter cooling of the surface layers in temperated and arctic regions will set up convection currents. By lessening the density gradient, the convection currents will be assisted by wave motion in bringing about more effectual mixing with the layers below. Hence in such latitudes, as opposed to the subtropical regions, a small store of nutrient salts may be expected in the spring, and in general a richer plankton particularly in the early summer. In the tropical regions of the Atlantic the heated surface water streams away to form the Gulf Stream, etc., to be replaced by water upwelling from below. Hence in these regions richer plankton may be expected than in the subtropical. These expectations are born out by the results of Hensen's Plankton Expedition.

It is a remarkable fact that plant growth should be able to strip seawater of both nitrates and phosphates, and that in the English Channel the store of these nutrient salts formed during autumn and winter should be used up at about the same time. . . .

HYDROGEN ION CONCENTRATION, SOIL PROPERTIES AND GROWTH OF HIGHER PLANTS

O. Arrhenius—1922

Reprinted by permission of the publisher from Arkiv für Botanik **18**: 1–54, 1922.

There are two major ecological principles developed in this paper: (1) the principle of interaction of factors, namely of substrate, climate and organisms in soil formation and reaction, and (2) the principle of regulation, namely the regulatory role of soil in determining plant associations and the modifying influence of plants on the nature and properties of soil.

We may therefore say, that in every soil there exists a certain concentration of hydrogen ions, and by measuring this, we also measure the actual acidity of the soil.

The question of the origin of this acidity has caused a vivid discussion. It has been shown, that not only humus but also sterilized cotton and other substances quite free from acids are able to "absorb" alkali. There are also pretty many acid mineral soils known, where it is impossible to identify any particular acid, but still they are giving an acid reaction.

This has been explained by so called selective adsorption, but there remained still some very essential points unexplained.

Also with the conceptions of the colloid chemists it has been quite impossible to find any satisfactory solution of the question. But there are many facts speaking for, that we must take a new point of view in the soil-science. . . .

Also several authors have shown that soils are acting as buffers (and it is not the inorganic salts in the soils which are the main factors) so that humus soils are very strong buffers, clays medium and sand weak, but even the buffer action of pure sand is greater than that of e. g. hydrochloric acid or SÖRENSEN's phosphate solutions.

On the other hand clay behaves as gelatine and this behaviour is independent of orgin or original reaction.

It is very probable, that all substances behave in the same manner, i.e., that they are real salt formers. We can thus say that the same laws hold for particles not visible in the ultramicroscope up to stones big as the fist or more.

These ampholytes give a certain hydrogen ion concentration to the solution due to their very low dissociation and this is the chief source of the hydrogen ion concentration of the soil.

After what is said above one may say that the soil is a system of ampholytes, partly dissociated, partly undissociated, water, air and small amounts of salts. . .

The first loose earth crust was probably nearly neutral. This assumption is founded on the fact, that on one hand most volcanic ashes investigated are neutral or nearly neutral, on the other hand that when digging into the soil and penetrating deeper than the uppermost region of great fluctuations one mostly reaches strata, which are practically neutral.

It also seems very probable that the earth came out of its smelting stage in a rather neutral and homogeneous condition.

The factors influencing the development of alkaline and acid soils are chiefly the relation between precipitate and evaporation, the vegetation and the rocks and their debris.

If we assume that the surface of the soil from the beginning had a neutral reaction and that it is acting as an ampholyte it is easily understood how the differences, now so great, have developed. During earlier geological periods the climate was much more moist and rainy and the atmosphere richer in carbonic dioxide. The washing out must then have gone on with a much higher rate than nowadays, and as this is not small it is easy to understand how immense areas have gained in salt content and thus alkalinity whereas others are so well washed out that the soils more or less have come to their isoelectric point.

Through this washing out process and later climate changes new soil conditions have been developed which may be looked at as primary conditions, when we only take a short period into consideration.

The process is going on so that the rainwater loaded with carbon dioxide and acidified by the humus decomposes the alkali- and alkali earth silicates and carries away more readily soluble salts of these elements. In the low lands where the water is spreading over wide areas, e. g. as seepage in the soil or by irrigation, and the evaporation is strong, the solution becomes more and more concentrated and also the carbon dioxide of double carbonates is given off by stillstanding [*sic*], the salts therefore are more or less deposited and the soil made alkaline. . . .

It is only as long as the rocks nearly reach the soil surface that they have a great influence. As soon as covered with debris they loose their direct influence. Also the mineral-soil looses a great deal of its importance as former of the surface soil reaction, when the plants have taken the ground. But indirectly the mineral soil and the rocks are always influencing the soil reaction through the soil water. . . .

Within a very short time, 50 years or less, the ground is covered with a layer of decomposing plant substances, mould or peat, and then this covering layer will play the greatest rôle for the soil acidity as influencing the vegetation, because the plants always first come in contact and grow a greater part of their life in this soil.

Therefore it is impossible to predict the soil reaction with aid of geological maps, neither using the rocks nor the mineral soils as indicators. One only very generally can state, that one may expect alkaline, neutral or slightly acid soils, where there is much lime in the subsoil, whereas in siliceous regions the soils may be more or less acid. . . .

The most important factor in the formation of the soil reaction, however, are the plants and their humus forming action.

From long ago it has been well known that under certain associations one finds a special soil. The best and most close study of these things is delivered by P. E. MÜLLER in his book on the humus formation in the Danish forests, where he shows that there is a correlation between the two types: Oxalis-Fagus-Wood and Trientalis-Fagus-Wood and the mild and raw humus. But he and many following authors saw in the soil the primary, and the vegetation was looked at as a secondary factor.

Some years ago the author showed, that the soil type, the soil reaction and the vegetation type are dependent of each other, so that the soil reaction is the primary factor but in many and essential ways influenced by the vegetation. . . .

The process may be regarded as follows: The pioneer-plants move in on the mineral soil, and within a short time a rather thick humus layer is formed. In northern countries as southern Sweden there can be formed a layer of up to half a meter or more in 100 years. The rate of humus formation is very different in different places but is at least of the same order of degree in temperate and tropic parts of the world when the climate is humid. The author observed by visiting Verlaten Eiland, one of the islands in the Krakatoa-archipelago destroyed by eruption in 1883, how in the Casuarina vegetation a layer of humus of about 10 cm thickness was formed. In other vegetation types there was found less, down to 5 cm. Also on volcanoes which recently have been in action there were observed rather thick humus deposits, up to 0.5 m., which must have been formed during the last 20—30 years.

As soon as this humus layer is formed the plants are more or less independent of underlying strata and the properties of the humus play the great rôle.

The humus deposits also influence the further developement of the soil profile through their more or less acidifying influence on the percolating water. . . . the saps of different plants have widely different acidity and also plant debris of different plants have a reaction which seems to lie very near to that of the pre-sap from the living plant.

Now it seems . . . as if those plants forming a certain stabilized association, and thus also forming the humus and the reaction, also have their optimal growth at that reaction, but in all unstabilized associations the reaction forming power plays a great rôle in the competition.

But also in stabilized associations there will occur changes. For instance the trees fall or fire devastates the forest and then one gets a natural clearing. It has been shown by OLSEN that on such wind clearings the reaction may change rather much, for instance from 5.2—6.6.

A very great influence is caused by man who sometimes incidentally sometimes consciously changes the soil reaction.

By deforestation, thus preventing a good deal of humus formation, the acidifying action of the soil is decreased. The cattle, when grazing, are also taking away an enormous amount of organic matter which otherwise would have taken a part in the humus formation. . .

More conscious [*sic*] has a change in the reaction been made for agricultural purposes. The first used method was probably the denshiring of woods thus forming alkaline ash and clearing the wood, both actions which change the soil reaction. Later on, when agriculture was more developed the farmers have been using lime, marle and clay to a great extent, trying to improve the soil condition. . . .

THE BIOLOGICAL CONTROL OF CHEMICAL FACTORS IN THE ENVIRONMENT

Alfred C. Redfield—1958

Reprinted by permission of the author and publisher from American Scientist **46**: 205–221, 1958.

Redfield's essay has as its central theme that the nitrate in the sea and the oxygen in the atmosphere are controlled by the biochemical cycle. This is environment regulated by organism. However, the biochemical cycle is ultimately determined by the solubility of phosphate. This is organism regulated by environment. Operationally, both types of regulatory mechanisms function to promote stability. Dr. Redfield has been a staff member of Harvard University and the Woods Hole Oceanographic Institution for over thirty five years.

It is a recognized principle of ecology that the interactions of organisms and environment are reciprocal. The environment not only determines the conditions under which life exists, but the organisms influence the conditions prevailing in their environment. . . .

The purpose of this essay is to discuss the relations between the statistical proportions in which certain elements enter into the biochemical cycle in the sea, and their relative availability in the water. These relations suggest not only that the nitrate present in sea water and the oxygen of the atmosphere have been produced in large part by organic activity, but also that their quantities are determined by the requirements of the biochemical cycle. . . .

THE BIOCHEMICAL CYCLE

The production of organic matter in the sea is due to the photosynthetic activity of microscopic floating plants, the phytoplankton, and is limited to the surface layers where sufficient light is available. The formation of organic matter in the autotrophic zone requires all the elements in protoplasm, of which carbon, nitrogen, and phosphorus are of particular concern. These are drawn from the carbonate, nitrate, and phosphate of the water. Following the death of the plants the organic matter is destroyed, either by the metabolism of animals or the action of microorganisms. Normally, decomposition is completed by oxidation so that carbon, nitrogen, and phosphorus are returned to the sea water as carbonate, nitrate, and phosphate, while requisite quantities of free oxygen are withdrawn from the water.

The autotrophic zone has a depth of 200 meters at most and includes less than five per cent of the volume of the

ocean. Below this zone, life depends on organic matter carried down by organisms sinking from above or by the vertical migrations of animals back and forth between the depths. Although the greater part of the nutrient chemicals absorbed in the autotrophic zone complete the cycle in this layer, the portion which sinks as organic matter tends to deplete the surface layers of these chemicals and, with the decomposition of the organic matter in the depths, to enrich this heterotrophic zone with the products of decomposition.

The existence of the vast reservoir of deep water in which organic matter may accumulate and decay out of reach of autotrophic resynthesis is a distinctive feature of the oceanic environment which enables one to separate, in observation and thinking, the constructive and destructive phases of the biochemical cycle. . . .

CORRESPONDENCE BETWEEN REQUIREMENT AND AVAILABILITY OF PHOSPHORUS, NITROGEN, AND OXYGEN

The stoichiometric relations . . . indicate that phosphorus, nitrogen, and oxygen are available in ocean water in very nearly the same proportions as those in which they enter the biochemical cycle. In discussing the remarkable coincidence in the supply and demand for nitrogen and phosphorus it has been pointed out that it might arise from: (1) a coincidence dependent on the accidents of geochemical history; (2) adaptation on the part of the organisms; or (3) organic processes which tend in some way to control the proportions of these elements in the water.

Of the first alternative not much can be said except that the probability that the ratio in the sea be what it is rather than any other is obviously small. That the coincidence applies to the oxygen as well as to the nutrient elements compounds the improbability.

For the second alternative, it may be said that the phytoplankton do have some ability to vary their elementary composition when one element or another is deficient in the medium in which they grow. Such physiology might account for the coincidence in the nitrogen-phosphorus ratios. However, it is not evident how adaptation could determine the oxygen relation since this depends more on the quantity than the quality of the organic matter formed, and the oxygen requirement is felt only after the death of the living plant.

For these reasons the third alternative deserves serious consideration. Mechanisms should be examined by which organic processes may have tended to control the proportions of phosphorus, nitrogen, and oxygen available for life in the sea. . . .

THE PHOSPHORUS-OXYGEN RATIO

. . . It is widely held among geochemists that the primitive atmosphere was devoid of oxygen, or at least contained very much less oxygen than at present. During the course of geological history atmospheric oxygen is thought to have been produced by the photochemical dissociation of water in the upper atmosphere and by the photosynthetic reduction of carbon dioxide, previously present in much greater quantities. . . . Estimates of the quantity of reduced carbon present in the earth's crust as coal and petroleum indicate that photosynthetic processes have been much more than adequate to produce the present oxygen content of the atmosphere. It has not been suggested, to my knowledge, why this process has proceeded just so far as it has; that is, why there is 21 per cent of oxygen in the atmosphere at present, no more or no less. It is, however, on this fact that the quantity of oxygen dissolved in the sea depends.

My supposition is that the actual quantities of oxygen present in the sea may have been regulated by the activities of sulfate-reducing bacteria. This group of bacteria are known to have the ability to use sulfates as a source of oxygen when free oxygen is absent and organic compounds are present to supply a source of energy. The over-all reaction is $SO_4^= \longrightarrow S^= + 2\,O_2$.

The process should be broken down into two steps, each of which takes place in the sea under different environmental conditions, (1) Sulfate Reduction, $SO_4^= + 2\,C \rightarrow 2\,CO_2 + S^=$ which occurs at depth under anaerobic conditions, and (2) Photosynthesis $2\,CO_2 \rightarrow 2\,C + O_2$ which occurs near the surface in the presence of light.

In these equations C represents the reduced carbon present in organic matter. The decomposition of this material by sulfate-reducing bacteria according to the first step also liberates a corresponding quantity of nitrogen and phosphorus, which permit the CO_2 formed to re-enter the biological cycle when the second step comes into play. The CO_2 produced in this way can thus contribute to the production of oxygen in a way in which the excess carbonate normally present in sea water cannot.

The first step, which depends upon the presence of organic matter in excess of the free oxygen required to complete its decomposition, will initiate a mechanism which will tend to increase the oxygen when, and only when, the quantity of available free oxygen is deficient. If the total mechanism has operated on a large enough scale in the course of geochemical history, it may have kept the supply of oxygen available in the sea adjusted to the requirements of the biochemical cycle.

There is very good evidence that sulfate reduction does operate on a large scale in the sea wherever anaerobic conditions exist. . . .

GEOCHEMICAL CONSIDERATIONS

As a final check on these speculations, we can look at the relative availability of the principal materials of the biochemical cycle on the earth's surface, to see if they conform to the postulates...

. . . the numbers of atoms relative to the atoms of phosphorus in the ocean. . . are indicated in Figure 3 which presents in diagrammatic form the biochemical cycle as described.

The diagram shows phosphate, nitrate, and carbonate entering the organic phase of the biochemical cycle near the sea surface, through the process of photosynthesis. Phosphorus, nitrogen, and carbon are selected by the synthetic process in the proportions of 1:15:105. This is the step which coordinates the cycles of the several elements in a unique way and gives meaning to the comparisons. The elements are carried in these proportions to the point of decomposition where they are oxidized to their original state as phosphate, nitrate, and carbonate. The oxygen required is just that set free by photosynthesis. Such a cycle could run indefinitely in an otherwise closed system so long as light is supplied.

To account for the correspondence in the ratios of phosphorus and nitrogen in the organic phase of the cycle and in the inorganic environment, bacterial processes of nitrogen fixation and denitrification are indicated at the upper right and, similarly, the sulfate reduction process is shown at the lower left. This latter is assumed to operate effectively only when the environment becomes anaerobic. Finally, the exchanges with the atmosphere and the sediments of the sea bottom are shown. If these processes are operative it is necessary that supplies are adequate and that their products exist in suitable quantities.

Considering first nitrogen, there exist in sea water for each atom of phosphorus 15 atoms of nitrogen available as NO_3 and a reserve of 510 atoms of nitrogen as dissolved N_2 which may be drawn on by nitrogen-fixing bacteria. In addition, there is a reserve of nitrogen in the atmosphere equivalent to 86,000 atoms of phosphorus, which is available to replace that dissolved in the sea were it to be drawn on. The nitrogen of the sedimentary rocks is about one-sixth that in the atmosphere and twenty times that in the ocean. More than four-fifths of this is fossil nitrogen which may be assumed to be derived from organic matter. Consequently, large quantities of nitrogen have passed through the biochemical cycle in its passage from the atmospheric reserves to be deposited in sediments at the sea bottom. The quantity withdrawn in this way is small, however, in comparison to the reserve in the atmosphere. Clearly, the nitrogen supply is adequate.

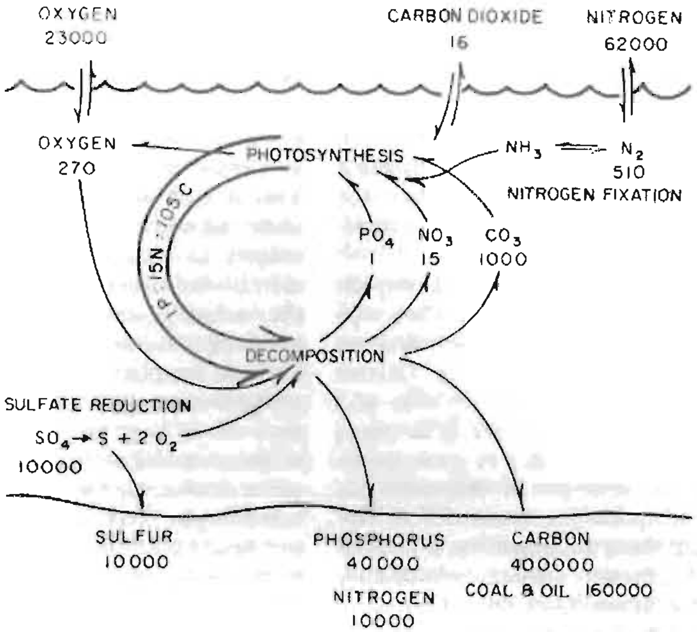


FIG. 3. *The Biochemical Cycle. Numbers represent quantities of respective elements present in the atmosphere, the ocean, and the sedimentary rocks, relative to the number of atoms of phosphorus in the ocean.*

Sulfate is one of the most abundant ions in sea water. In this form there is present sulfur equivalent to 10,000 atoms of phosphorus. It would be capable of supplying oxygen equivalent to 40,000 atoms of phosphorus on reduction. Clearly, the sulfate reduction mechanism could continue to operate for a long time. If it has operated as postulated in the past much sulfide may have been removed from the sea. Sedimentary rocks are estimated to contain sulfur equivalent to 10,000 atoms of oceanic phosphorus. If this were all the product of sulfate reduction, this would have produced oxygen equivalent to 40,000 atoms of oceanic phosphorus, which is almost twice that present in the atmosphere. It is not clear how much of the sulfur in sedimentary rocks is present as sulfides, but much of it is. Clearly, much oxygen can have been produced in the past by sulfate reduction and possibly this process has contributed to an important degree in producing the oxygen of the atmosphere.

Carbon is present in the sea, chiefly as carbonate ions, in about ten times the quantity required for the biochemical cycle. Much of the large deposits of carbon in the sedimentary rocks is present as carbonates and cannot have contributed to the production of free oxygen. The estimated carbon present as coal and petroleum, equivalent to 160,000 atoms of oceanic phosphorus, is sufficient to yield oxygen on reduction equivalent to 320,000 atoms of oceanic phosphorus, which is more than ten times the present content of the atmosphere.

The known facts of geochemistry do not appear to contradict the suppositions presented on the mechanism which may have controlled the relative availability of phosphate, nitrate, and oxygen in the sea. Sources of nitrogen and sulfate are available in great excess and the by-products of the reactions can be adequately accounted for. According to these suppositions, phosphorus is the master element which controls the availability of the others. . . .

If the argument presented is sound it may be concluded that the quantity of nitrate in the sea, and the partial pressure of oxygen in the atmosphere are determined through the requirements of the biochemical cycle, by the solubility of phosphate in the ocean. This is a physical property of a unique chemical compound and as such is not subject to change except in so far as alterations in conditions may influence the activity coefficients of the ions involved. It follows then that the nutrient supplies in sea water, and the oxygen content of the atmosphere have been about as at present for a long time in the past and will remain at much the same level into the future. This argument may then be added to those reviewed by Rubey that the composition of sea water and atmosphere has varied surprisingly little at least since early geologic time. . . .

LAKES IN RELATION TO TERRESTRIAL LIFE PATTERNS

Aldo Leopold—1941

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This essay by an outstanding conservationist not only reflects his attitude regarding man's intervention in "our biotic constitution," but also focuses on another aspect of organism-environment regulation. The issue here is the role of organisms in the dynamics of energy exchange between two major environments as one of many interrelations between them.

FOOD CIRCUITS IN SOIL AND WATER

Soil and water are not two organic systems, but one. Both are organs of a single landscape; a derangement in either affects the health of both. We acknowledge this interaction between water and land after erosion or pollution makes them sick, but we lack a "language" for describing their normal interactions. Such a language must deal, for one thing, with their exchanges of nutrient materials.

All land represents a downhill flow of nutrients from the hills to the sea. This flow has a rolling motion. Plants and animals suck nutrients out of the soil and air and pump them upward through the food chains; the gravity of death spills them back into the soil and air. Mineral nutrients, between their successive trips through this circuit, tend to be washed downhill. Lakes retard this downhill wash, and so do soils. Without the impounding action of soils and lakes, plants and animals would have to follow their salts to the coast line.

The rate of retardation depends, for one thing, on the length and the termini of the food chains. A nutrient salt impounded in an oak may take a century to pass through an acorn, a squirrel, a redtail, and parasite before it re-enters the soil for another upward roll. The same particle may take only a year to pass through a corn plant and a fieldmouse to the soil. Again it may pass through a grass, a cow, a pig, and a member of the Townsend Club, emerging not into the soil, but into a sewer and thence into a lake. Civilization shortens food chains, and routes them into lakes and rivers instead of fields and pastures.

The rate of retardation depends also on the fertility of soils. Fertile soils wash slowly. They support long chains if we let them do so. Food circuits are intricately adjusted to maintain normal rates of retardation. A normal soil balances its intake from the decomposition of rocks against its loss from downhill wash. We now know, to our cost, the disturbing effects of too low a rate: erosion. A normal water balances its intake from the soil against its outwash to the sea. Pollution is an excess of intake arising from erosion, or from routing land wastes to water. Underfed soils thus mean overfed waters. Healthy land, by balancing the internal economy of each, balances the one against the other.

The food balance between soils and waters is accomplished not only by circuitous routes of flow, but also by eddies and back-currents. That is to say, some animals pump food back uphill. These local reversals of the downhill flow have not, to my knowledge, been described or measured. They may be important to science, and to land health, or conservation.

MOVEMENTS FROM WATER TO LAND AND FROM LAND TO WATER

Back-currents are likely to be clearly visible in areas inhabited by some animal requiring a larger supply of a particular nutrient than the soil supplies. The red deer on the Scottish highlands is a case in point. Here nutrients are scarce because the soil is derived from sterile rocks. The red deer's yearly production of new antlers calls for more calcium and phosphorus than his highland range can supply. Where and how does he get them?

Fraser Darling records the facts as a calcium-phosphorus food chain. The deer gets a little, but not enough, of these horn-building salts from the native herbs and grasses. His supply increases when fires concentrate in ashes the dilute supplies stored in the heather. Hence gamekeepers practice rotation burning on the moors. To make good his deficiency in horn-building salts, the deer taps the aquatic food chain of the lakes and tarns, where rich supplies are concentrated in aquatic animals. He eats frogs immobilized by frost. As his relative, the reindeer, is reported to do, he may eat duck eggs and dead fish. By acquiring such unusual or "depraved" food habits, the deer requisitions from lakes what his terrestrial range fails to provide.

That the stored salts are what the red

deer is after is shown by certain other extraordinary food habits which help balance his calcium-phosphorus economy. He eats the velvet from his own horns; the bones of dead deer left by hunters; his own cast antlers or those of other deer; the rabbit or vole which has extracted salts from these same materials and then chanced to die. Direct ingestion of lemmings and mice by wild reindeer has been recorded and may also be practiced by the red deer.

The ingestion of aquatic animals by deer is an uphill movement of nutrients; a back-current of the downhill stream. Food which has already "passed" the terrestrial deer but lies temporarily impounded in lakes is pulled back into the terrestrial circuit. On the other hand, the ingestion by deer of velvet, horns, bones, and dead rodents is not a back-current, but rather a short circuit in the usual roll of the food chain. The salts contained in these body parts would normally re-enter the soil and become (in part) available to the deer as plants, but by shorting this normal circuit he recovers them in less time and with less waste.

The quantity of minerals involved in these movements is small, but even small quantities may, on poor soils, be of critical importance. Range managers now realize that the continued "deportation" of phosphorus and calcium in the bones of cattle and sheep may eventually impoverish grazing ranges. Darling hints that deportation in sheep may have helped to impoverish the Scottish moors.

Many animals other than red deer tap aquatic food chains and restore food to terrestrial circuits. Many also move food in the opposite direction. The net retardation, or preponderance of uphill transport, varies from zero upward. The length of uphill transport also varies from short to long distances. Thus river ducks, geese, gulls, terns, rails, bitterns, frogs, snakes, and muskrats eat in or at the edge of water and die or defecate inland, but they likewise eat inland and die or defecate in water. There is no clear preponderance of uphill transport. The first three range far inland, the others not far. Eagles, crows, swallows, bears, deer, caribou, and moose carry food both to and from water, but they probably move more food uphill than downhill, and to a considerable distance inland. River-spawning salmon which die inland perform a large and long uphill transport. Guano birds, penguins, herons, otters, minks, skunks, bats, and certain water-hatching, land-dying insects perform a preponderance of uphill transport, but only to a short distance inland.

Probably no other food chain concentrates so much food on so small an area as that ending in guano birds. The whole aquatic garden of the south Pacific ships its produce, via the upwelling Humboldt current, to the coastal guanays, which deposit it on their rainless island rookeries as guano. Here then is a bottleneck where the oceanic food circuit achieves a "voltage" of extraordinary intensity. The guano deposits, however, lie so near the shore and in so dry a climate that until they are moved further inland by man they have little effect on terrestrial circuits. Antarctic penguins likewise carry oceanic foods inland, but their deposits are refrigerated and eventually slide back into the sea. As against the long list of higher animals which transport food in a prevalently uphill direction, I can think of only two, man and the beaver, which get most of their food on land and deposit most of it in the water. Marsh-roosting blackbirds also do this, but only in autumn.

Most animals merely circulate food within the terrestrial or aquatic circuit which is their habitat. Thus the diving ducks, except when caught by some land predator, feed from and die into the aquatic circuits. Gallinaceous birds, except when shot by a hunter with modern conveniences, feed from and die into the terrestrial circuits.

LONG-DISTANCE TRANSPLANTATIONS

Migratory birds and fish move food to a distance from its point of origin. Until man began to ship foods and fertilizer, the only long-distance movers were water, air, and migratory animals. Migratory birds must move a considerable volume of food, with more than transitory effects. Thus Hawkins points out that the plant community under passenger pigeon roosts was distinguishable for decades after the pigeons were gone.

Transplantations by migratory animals have no clear orientation uphill or downhill.

SUMMARY AND DISCUSSION

Soil health and water health are not two problems, but one. There is a circulatory system of food substances common to both, as well as a circulatory system within each. The downhill flow is carried by gravity, the uphill flow by animals.

There is a deficit in uphill transport, which is met by the decomposition of rocks. Long food chains, by retarding downhill flow, reduce this deficit. It is further reduced by storage in soils and lakes. The continuity and stability of inland communities probably depend on this retardation and storage.

These movements of food substances seem to constitute, collectively, the nutritional system of the biotic organism. It may be surmised, by analogy with individual plants and animals, that it has qualitative as well as quantitative aspects. The recent history of biology is largely a disclosure of the importance of qualitative nutrition within plants and animals, and within land and water communities. Is it also important as between land and water? Does the wild goose, reconnoitering the farmer's cornfield, bring something more than wild music from the lake, take something more than waste corn from his field?

Such questions are, for the moment, beyond the boundaries of precise knowledge, but not beyond the boundaries of intelligent speculation. We can at least foresee that the prevalent mutilations of soil and water systems, and wholesale simplification of native faunas and floras, may have unpredictable repercussions. Neither agriculturists nor aquiculturists have so far shown any consciousness of this possibility. A prudent technology should alter the natural order as little as possible.

HOMAGE TO SANTA ROSALIA OR WHY ARE THERE SO MANY KINDS OF ANIMALS?

G. Evelyn Hutchinson—1959

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Although he may be best recognized for his contributions to biogeochemistry, Hutchinson's publications in limnology and population ecology have been no less significant. In this essay, notwithstanding its chance homage to a saint of unknown history presumed for purposes of the essay to be the patroness of evolutionary studies, Hutchinson explores the diversity of species as a function of the complexities of trophic organization and niche diversification in achieving stability. Professor Hutchinson's succession of productive students from his "itinerant ivory tower" at Yale and his significant contributions to ecology led to his being recognized as Eminent Ecologist by the Ecological Society of America in 1962.

There are at the present time supposed to be about one million described species of animals. Of these about three-quarters are insects, of which a quite disproportionately large number are members of a single order, the Coleoptera.[1] The marine fauna although it has at its disposal a much greater area than has the terrestrial, lacks this astonishing diversity. If the insects are excluded, it would seem to be more diverse. The proper answer to my initial question [why there are such an enormous number of animal species] would be to develop a theory at least predicting an order of magnitude for the number of speeics of 10^6 rather than 10^8 or 10^4. This I certainly cannot do. At most it is merely possible to point out some of the factors which would have to be considered if such a theory was ever to be constructed. . . .

FOOD CHAINS

Animal ecologists frequently think in terms of food chains, of the form *individuals of species S_1 are eaten by those of S_2, of S_2 by S_3, of S_3 by S_4*, etc. In such a food chain S_1 will ordinarily be some holophylic organism or material derived from such organisms. The simplest case is that in which we have a true *predator chain* in Odum's convenient terminology, in which the lowest link is a green plant, the next a herbivorous animal, the next a primary carnivore, the next a secondary carnivore, etc. A specially important type of predator chain may be designated Eltonian, because in recent years C. S. Elton has emphasized its widespread significance, in which the predator at each level is larger and rarer than its prey. This phenomenon was recognized much earlier, notably by A. R. Wallace in his contribution to the 1858 communication to the Linnean Society of London.

In such a system we can make a theoretical guess of the order of magnitude of the diversity that a single food chain can introduce into a community. If we assume that in general 20 per cent of the energy passing through one link can enter the next link in the chain, which is overgenerous (Slobodkin in an unpublished study finds 13 per cent as a reasonable upper limit) and if we suppose that each predator has twice the mass, (or 1.26 the linear dimensions) of its prey, which is a very low estimate of the size difference between links, the fifth animal link will have a population of one ten thousandth (10^{-4}) of the first, and the fiftieth animal link, if there was one, a population of 10^{-40} the size of the first. Five animal links are certainly possible, a few fairly clear cut cases having been in fact recorded. If, however, we wanted 50 links, starting with a protozoan or rotifer feeding on algae with a density of 10^6 cells per ml, we should need a volume of 10^{26} cubic kilometers to accommodate on an average one specimen of the ultimate predator, and this is vastly greater than the volume of the world ocean. Clearly the Eltonian food-chain of itself cannot give any great diversity, and the same is almost certainly true of the other types of food chain, based on detritus feeding or on parasitism. . . .

Effect of size. A second important limitation of the length of a food chain is due to the fact that ordinarily animals change their size during free life. If the terminal member of a chain were a fish that grew from say one cm to 150 cms in the course of an ordinary life, this size change would set a limit by competition to the possible number of otherwise conceivable links in the 1–150 cm range. At least in fishes this type of process (metaphoetesis) may involve the smaller specimens belonging to links below the larger and the chain length is thus lengthened, though under strong limitations, by cannibalism. . . .

Effects of terrestrial plants. The extraordinary diversity of the terrestrial fauna, which is much greater than that of the marine fauna, is clearly due largely to the diversity provided by terrestrial plants. This diversity is actually two-fold. Firstly, since terrestrial plants compete for light, they have tended to evolve into structures growing into a gaseous medium of negligible buoyancy. This has led to the formation of specialized supporting, photosynthetic, and reproductive structures which inevitably differ in chemical and physical properties. . . . A major source of terrestrial diversity was thus introduced by the evolution of almost 200,000 species of flowering plants, and the three quarters of a million insects supposedly known today are in part a product of that diversity. But of itself merely providing five or ten kinds of food of different consistencies and compositions does not get us much further than the five or ten links of an Eltonian pyramid. On the whole the problem still remains, but in the new form: why are there so many kinds of plants? As a zoologist I do not want to attack that question directly, I want to stick with animals, but also to get the answer. Since, however, the plants are part of the general system of communities, any sufficiently abstract properties of such communities are likely to be relevant to plants as well as to herbivores and carnivores. . . .

INTERRELATIONS OF FOOD CHAINS

Biological communities do not consist of independent food chains, but of food webs, of such a kind that an individual at any level (corresponding to a link in a single chain) can use some but not all of the food provided by species in the levels below it. . . .

MacArthur concludes that in the evolution of a natural community two partly antagonistic processes are occurring. More efficient species will replace less efficient species, but more stable communities will outlast less stable communities. In the process of com-

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[1] There is a story, possibly apocryphal, of the distinguished British biologist, J. B. S. Haldane, who found himself in the company of a group of theologians. On being asked what one could conclude as to the nature of the Creator from a study of his creation, Haldane is said to have answered, "An inordinate fondness for beetles."

munity formation, the entry of a new species may involve one of three possibilities. It may completely displace an old species. This of itself does not necessarily change the stability, though it may do so if the new species inherently has a more stable population than the old. Secondly, it may occupy an unfilled niche, which may, by providing new partially independent links, increase stability. Thirdly, it may partition a niche with a pre-existing species. Elton in a fascinating work largely devoted to the fate of species accidentally or purposefully introduced by man, concludes that in very diverse communities such introductions are difficult. Early in the history of a community we may suppose many niches will be empty and invasion will proceed easily; as the community becomes more diversified, the process will be progressively more difficult. Sometimes an extremely successful invader may oust a species but add little or nothing to stability, at other times the invader by some specialization will be able to compete successfully for the marginal parts of a niche. In all cases it is probable that invasion is most likely when one or more species happen to be fluctuating and are underrepresented at a given moment. As the communities build up, these opportunities will get progressively rarer. In this way a complex community containing some highly specialized species is constructed asymptotically.

Modern ecological theory therefore appears to answer our initial question at least partially by saying that there is a great diversity of organisms because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms. Even though the entry of an invader which takes over part of a niche will lead to the reduction in the *average* population of the species originally present, it will also lead to an increase in stability reducing the risk of the original population being at times underrepresented to a dangerous degree In this way loss of some niche space may be compensated by reduction in the amplitude of fluctuations in a way that can be advantageous to both species. The process however appears likely to be asymptotic and we have now to consider what sets the asymptote, or in simpler words why are there not more different kinds of animals?

LIMITATION OF DIVERSITY

It is first obvious that the processes of evolution of communities must be under various sorts of external control, and that in some cases such control limits the possible diversity. Several investigators, notably Odum and MacArthur, have pointed out that the more or less cyclical oscillations observed in arctic and boreal fauna may be due in part to the communities not being sufficiently complex to damp out oscillations. It is certain that the fauna of any such region is qualitatively poorer than that of warm temperate and tropical areas of comparable effective precipitation. . . . It is reasonable to suppose that the total biomass may be involved. If the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favorable conditions, then the rarer species in a community may be so rare that they do not exist. It is also probable that certain absolute limitations on growth-forms of plants, such as those that make the development of forest impossible above a certain latitude, may in so acting, severely limit the number of niches. . . .

NICHE REQUIREMENTS

The various evolutionary tendencies, notably metaphoetesis, which operate on single food chains must operate equally on the food-web, but we also have a new, if comparable, problem as

to how much difference between two species at the same level is needed to prevent them from occupying the same niche. Where metric characters are involved we can gain some insight into this extremely important problem by the study of what Brown and Wilson have called *character displacement* or the divergence shown when two partly allopatric species of comparable niche requirements become sympatric in part of their range.

. . . In the case of the aquatic insects with which I began my address, we have over most of Europe three very closely allied species of Corixa, the largest *punctata*, being about 116 per cent longer than the middle sized species *macrocephala*, and 146 per cent longer than the small species *affinis*. In northwestern Europe there is a fourth species, *C. dentipes*, as large as *C. punctata* and very similar in appearance. A single observation (Brown) suggests that this is what I have elsewhere termed a fugitive species, maintaining itself in the face of competition mainly on account of greater mobility. According to Macan while both *affinis* and *macrocephala* may occur with *punctata* they never are found with each other, so that all three species never occur together. In the eastern part of the range, *macrocephala* drops out, and *punctata* appears to have a discontinuous distribution, being recorded as far east as Simla, but not in southern Persia or Kashmir, where *affinis* occurs. In these eastern localities, where it occurs by itself, *affinis* is larger and darker than in the west, and superficially looks like *macrocephala*.

This case is very interesting because it looks as though character displacement is occurring, but that the size differences between the three species are just not great enough to allow them all to co-occur. Other characters than size are in fact clearly involved in the separation, *macrocephala* preferring deeper water than *affinis* and the latter being more tolerant of brackish conditions. It is also interesting because it calls attention to a marked difference that must occur between hemimetabolous insects with annual life cycles involving relatively long growth periods, and birds or mammals in which the period of growth in length is short and of a very special nature compared with the total life span. In the latter, niche separation may be possible merely through genetic size differences, while in a pair of animals like *C. punctata* and *C. affinis* we need not only a size difference but a seasonal one in reproduction; this is likely to be a rather complicated matter. For the larger of two species always to be larger, it must never breed later than the smaller one. I do not doubt that this is what was happening in the pond on Monte Pellegrino, but have no idea how the difference is achieved. . . .

MOSAIC NATURE OF THE ENVIRONMENT

A final aspect of the limitation of possible diversity, and one that perhaps is of greatest importance, concerns what may be called the mosaic nature of the environment. Except perhaps in open water when only uniform quasi-horizontal surfaces are considered, every area colonized by organisms has some local diversity. The significance of such local diversity depends very largely on the size of the organisms under consideration. In another paper MacArthur and I have . . . pointed out that even if we consider only the herbivorous level or only one of the carnivorous levels, there are likely, above a certain lower limit of size, to be more species of small or medium sized organisms than of large organisms. It is difficult to go much beyond crude qualitative impressions in testing this hypothesis, but we find that for mammal faunas, which contain such diverse organisms that they may well be regarded as models of whole faunas, there is a definite hint of the kind of theoretical distribution that we deduce. In qualitative terms the phenomenon can be exemplified by any of the larger species of ungulates which may require a number of different kinds of terrain within their home ranges, any one of which types of terrain might be the habitat of some small species. Most of the genera or even subfamilies of very large terrestrial animals contain only one or two sympatric species. In this connection I cannot refrain from pointing out the immense scientific importance of obtaining a really full insight into the ecology of the large mammals of Africa while they can still be studied under natural conditions. It is indeed quite possible that the results of studies on these wonderful animals would in long-range though purely practical terms pay for the establishment of greater reservations and National Parks than at present exist. . . .

We may, therefore, conclude that the reason why there are so many species of animals is at least partly because a complex trophic organization of a community is more stable than a simple one, but that limits are set by the tendency of food chains to shorten or become blurred, by unfavorable physical factors, by space, by the fineness of possible subdivision of niches, and by those characters of the environmental mosaic which permit a greater diversity of small than of large allied species. . . .

ON BIRD SPECIES DIVERSITY

Robert H. MacArthur and John W. MacArthur—1961

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The recognition of the stabilizing role of diversity in ecosystems prompts investigation into the description and regulation of diversity. This paper is an excellent example of such an investigation and its relevance to the discussions by Hutchinson (see page 204), Eugene Odum (see page 211) and Margalef (see page 215) will be readily apparent.

It is common experience that more species of birds breed in a mixed wood than in a field of comparable size. It is also well known that tropical forests seem to support more species than their temperate counterparts. These facts are often explained in terms of the number of "niches" or "ways of life" which the habitat provides. In this paper, a somewhat more precise analysis is attempted.

The actual number of species is better replaced by a number called the "bird species diversity," calculated as follows: Let p_i be the proportion of all of the bird individuals which belong to the i^{th} species. Then the bird species diversity, is $-\sum_i p_i \log_e p_i$. This is a formula used by communication engineers to calculate the information generated, *e.g.*, by a typist who uses the different

keys with frequencies p_i. Thus, for instance, a one species community always has zero diversity; 2 species, one with 99 individuals and one with 1 individual, will have diversity of $-.99 \log_e .99 - .01 \log_e .01 = .046 + .010 = .056$ (close to zero), while 2 species each with 50 individuals will have diversity of $.347 + .347 = .694$. This illustrates why diversity is a better measure than actual number of species, for the community with 99 of one and 1 of the other seems closer to the community with one species. Margalef has frequently used a similar measure in his plankton studies. In terms of this, the question becomes: "What is it about the environment which controls the bird species diversity?"

The procedure of the research described here was to census a wide variety of habitats, differing in (1) plant species composition, (2) foliage height profiles, and (3) latitude, and to determine how much each of these factors influenced the bird diversity. . . .

RESULTS

. . . [When] the corresponding foliage height diversity and bird species diversities . . . are plotted as a graph . . . [they show] a close fit to the line: bird species diversity = 2.01 foliage height diversity + .46, calculated by least squares. Various other subdivisions of the profile into horizontal layers were tried, and the layers 0–2′, 2′–25′ and > 25′ were chosen as those layers which made the collection of points on the graph most orderly. . . . The linearity of the cluster of points indicates that the addition of a new layer of a given amount of foliage results in the same increase in bird species diversity, (not however the same increase in number of bird species) no matter which layer (0–2′, 2–25′ or >25′) is added, and no matter which other layers are present to begin with. Thus, we can say that the layers 0–2′, 2′–25′ and >25′ are roughly equally important to the birds. (The reasons for this will be discussed later.) Looked at from this point of view, we can see the trouble with the other subdivisions. For definiteness, consider 0–15′, 15′–30′, > 30′. Adding a 0–15′ layer to a habitat without it causes a much greater increase in bird species diversity than the addition of the layer > 30′. There is nothing biological about the number of layers chosen. Four or 5 layers in a roughly similar subdivision would be more cumbersome to analyse but would presumably be even more accurate. In particular, the layers 0–½′, ½′–6′, 6′–15′ and > 15′ suggested by Elton and Miller allow a rather good prediction of the bird species diversity.

The next question is: How much of the remaining scatter, *i.e.*, how much of the variability in bird species diversity not accounted for by the variation in foliage height diversity, can be accounted for in variations of plant species diversity and latitude? Remarkably enough, the answer is "None". . . . Thus, although plant species diversity alone is a good predictor of bird species diversity it is because plant species diversity is high when foliage height diversity is high, and, when this is taken account of, plant species diversity can contribute nothing further. In other words, habitats of the same profile have the same bird species diversity whether composed of few or many plant species. . . .

DISCUSSION

These results are rather statistical in nature. What is their meaning in terms of individual birds or species? The simplest explanation which seems to account for the observations, describes the "shape" of a bird's niche. Let us return to the picture of many territories distributed over an area and consider the following evolutionary argument. A large number of species can be accommodated in an environment in a variety of ways of which there are 2 extremes. Each species may have different habitat preference and feed throughout this habitat on all kinds of food, or, all species may share the entire habitat, each species feeding on a different variety of food or in a different situation within the habitat. The first extreme violates what might be called the "jack of all trades—master of none" principle that natural selection favors the increased efficiency resulting from a certain amount of specialization. In the other extreme, specialization has proceeded so far that time and energy are wasted in travelling between spots for which the specializations are adapted. It is hard to say just where the balance of these opposing requirements would be reached, but it is clear that greater specialization resulting in increased efficiency would always be favored as long as no time or energy are wasted. And no time or energy will be wasted if niches are "convex" in the sense that between any 2 fairly distant feeding places there will be a fairly natural route also consisting of feeding places. A specialization to a single tree species in a mixed forest would clearly violate this since, in passing from one suitable tree to another, the bird would go through many unsuitable ones. Thus, natural selection would tend to eliminate a situation in which bird species diversity depended upon tree species diversity, unless, as in some fruit eating species, a very remarkable improvement in efficiency is achieved along with the restriction in feeding position. Thus, one principal result of these censuses can be predicted on assuming that niches are convex.

Next, we may ask "why are the layers 0–2′, 2–25′, > 25′ equally important? Is it because birds respond to different heights, or is it because they respond to different configurations of vegetation in different layers?" In the latter case, herbs, bushes and trees presumably correspond to the layers 0–2′, 2–25′ and > 25′ respectively, although small trees count as bushes, etc. There is good evidence for this latter explanation. For, although deciduous forests vary principally with height above the ground and hence have a bird diversity predictable from the height profile, conifers (especially spruce) have a marked "inside" and "outside" for which species are specialized. Hence bird species diversity would be high in a mature spruce forest even if few layers were present. This is precisely what happens in the Maine white spruce wood mentioned earlier, with bird species diversity of 1.712 and foliage height diversity of .287 which is seriously off the graph of deciduous forests.

A different way of looking at the data gives additional insight. Watt has pointed out that plants are distributed in patches. Hutchinson and MacArthur attempted to explain the sizes of coexisting organisms in terms of an environment composed of a mosaic of kinds of patches. Different combinations of patches formed the habitats selected by different species. The present research can be easily interpreted in terms of this picture of the environment. In fact, our results suggest that the patches forming the birds' environmental mosaic are sections of canopy C (over 25′), patches of bushes B from 2–25′, and the herbaceous and other cover H less than 2′ from the ground. And the sequence of patches encountered in moving through the habitat (or in taking ever larger samples) is then represented by a sequence of letters, *e.g.*, C, B, H, H, B, C, . . . with certain random properties but also subject to the condition that the long term frequency of C's, B's, and H's should conform to their respective densities (p_i) in the particular habitat. If the sequence is ergodic, which defines what we call a homogeneous habitat, then it is well known that the uncertainty of the next letters in the sequence is appropriately measured by the formula $-\sum_i p_i \log_e p_i$ which we used. If, instead of considering the uncertainty of future single letters in the sequence, we ask for the uncertainty of future pairs of letters, the formula becomes $-2\sum_i p_i \log_e p_i$ which is 2 × foliage height diversity, which is essentially the predicted value of the bird species diversity. Thus we can say that bird species diversity is determined as if the birds recognized suitable habitats by pairs of foliage types (> 25′, 2–25′, 0–2′). The species area curve could then be predicted from this.

RELATIONSHIPS BETWEEN STRUCTURE AND FUNCTION IN ECOSYSTEMS

Eugene P. Odum—1962

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In defining ecology as the study of the structure and function of ecosystems, Odum brings into much closer alliance these two major traditional approaches in biology. There is intimation of causal relations between the two in line with current thinking on the molecular and subcellular levels of biological organization. By discussing aquatic and terrestrial systems in parallel, Odum strengthens his strongly espoused contention regarding the universality of applying the ecosystem approach. This view is the theme of both editions of his text, Fundamentals of ecology (1953, 1959. Philadelphia, W. B. Saunders, Inc.) which enjoys wide use.

. . . As you know ecology is often defined as: The study of interrelationships between organisms and environment. I feel that this conventional definition is not suitable; it is too vague and too broad. Personally, I prefer to define ecology as: The study of the structure and function of ecosystems. Or we might say in a less technical way: The study of structure and function of nature.

By structure we mean: (1) The composition of the biological community including species, numbers, biomass, life history and distribution in space of populations; (2) the quantity and distribution of the abiotic (non-living) materials such as nutrients, water, etc.; (3) the range, or gradient, of conditions of existence such as temperature, light, etc. Dividing ecological structure into these three divisions is, of course, arbitrary but I believe convenient for actual study of both aquatic and terrestrial situations.

By function we mean: (1) The rate of biological energy flow through the ecosystem, that is, the rates of production and the rates of respiration of the populations and the community; (2) the rate of material or nutrient cycling, that is, the biogeochemical cycles; (3) biological or ecological regulation including both regulation of organisms by environment (as, for example, in photoperiodism) and regulation of environment by organisms (as, for example, in nitrogen fixation by microorganisms). Again, dividing ecological function into these three divisions is arbitrary but convenient for study. . . .

Both aquatic and terrestrial community types have several structural features in common. Both must have the same three necessary biological components: (1) Producers or green plants capable of fixing light energy (i.e., autotrophs); (2) animals or macroconsumers which consume particulate organic matter (i.e., phagotrophs); and (3) microorganism decomposers which dissolve organic matter releasing nutrients (i.e., osmotrophs). Both ecosystems must be supplied with the same vital materials such as nitrogen, phosphorus, trace minerals, etc. Both ecosystems are regulated and limited by the same conditions of existence such as light and temperature. Finally, the arrangement of biological units in vertical space is basically the same in the two contrasting types of ecosystems. Both have two strata, an autotrophic stratum above and a heterotrophic stratum below. The photosynthetic machinery is concentrated in the upper stratum or photic zone where light is available, while the consumer-nutrient regenerating machinery is concentrated largely below the photic zone. It is important to emphasize that while the vertical extent or thickness of communities varies greatly (especially in water), light energy comes into the ecosystem on a horizontal surface basis which is everywhere the same. Thus, different ecosystems should be compared on a square meter basis, not on a cubic or volume basis.

On the other hand, aquatic and terrestrial ecosystems differ in structure in several important ways. Species composition is, of course, completely different; the roles of producers, consumers and decomposers are carried out by taxonomically different organisms which have become adapted through evolution. Trophic structure also differs in that land plants tend to be large in size but few in number while the autotrophs of open water ecosystems (i.e., phytoplankton) are small in size but very numerous. In general, autotrophic biomass is much greater than heterotrophic biomass on land, while the reverse is often true in the sea. Perhaps the most important difference is the following: The matrix, or supporting framework, of the community is largely physical in aquatic ecosystems, but more strongly biological on land. That is to say, the community itself is important as a habitat on land, but not so important in water.

Now, we may ask: How do these similarities and differences in structure affect ecological function?

One important aspect of function is . . . the energy flow through the ecosystems beginning with the incoming solar energy and passing through the successive trophic levels. At each transfer a large part of the energy is dissipated in respiration and passes out of the system as heat. The amount of energy remaining after three steps is so small that it can be ignored in so far as the energetics of the community are concerned. However, tertiary consumers ("top carnivores") can be important as regulators; that is, predation may have an important effect on energy flow at the herbivore level. . . .

The autotrophic-heterotrophic stratification, which we emphasized as a universal feature of community structure, results in two basic food chains. . . . The consumption of living plants by herbivores which live in the autotrophic stratum together with their predators may be considered as the *grazing food chain*. This is the classical food chain of ecology, as, for example, the phytoplankton-zooplankton-fish sequence or the grass-rabbit-fox sequence. However, a large proportion of the net production may not be consumed until dead, thus becoming the start of a rather different energy flow which we may conveniently designate as the *detritus food chain*. This energy flow takes place largely in the heterotrophic stratum. . . . the detritus energy flow takes place chiefly in the sediments of water systems, and in the litter and soil of land systems.

Ecologists have too often overlooked the fact that the detritus food chain is the more important energy pathway in many ecosystems. . . . a larger portion of net production is estimated to be consumed by grazers in the marine bay than in the forest; nine-tenths of the net production of the forest is estimated to be consumed as detritus (dead leaves, wood, etc.). It is not clear whether this difference is a direct or indirect result of the difference in community structure. One tentative generalization might be proposed as follows: communities of small, rapidly growing producers such as phytoplankton or grass can tolerate heavier grazing pressure than communities of large, slow-growing plants such as trees or large seaweeds. . . .

Despite the large difference in relative size of standing crops in the two extreme types of ecosystems, the actual energy flow may be of the same order of magnitude if light and available nutrients are similar. . . . Thus, 80 KCals of phytoplankton may have a net production almost as large as 5000 KCals of trees (or 500 KCals of green leaves). Therefore, productivity is not proportional to the size of the standing crop except in special cases involving annual plants (as in some agriculture). Unfortunately, many ecologists confuse productivity and standing crop. The relation between structure and function in this case depends on the size and rate of metabolism (and rate of turnover) of the organisms.

To summarize, we see that biological structure influences the pattern of energy flow, particularly the fate of net production and the relative importance of grazers and detritus consumers. However, total energy flow is less affected by structure, and is thus less variable than standing crop. A functional homeostasis has been evolved in nature despite the wide range in species structure and in biomass structure. . . .

. . . Now let us turn to structure and function at the population level and consider a second major aspect of function, namely, the cycling of nutrients. . . .

First, we shall take a look at the salt marsh ecosystem and the distribution of the species in the marsh. The mussels live partly buried in the sediments and attached to the stems and rhizomes of the marsh grass, *Spartina alterniflora*. Individuals are grouped into colonies (clumped distribution), but the colonies are widely scattered over the marsh. Numbers average $8/M^2$ for the entire marsh and $32/M^2$ in the most favorable parts of the marsh. Biomass in terms of ash-free dry weight averages 11.5 gms/M^2. When the tide covers the colonies the valves partly open and the animals begin to pump large quantities of water.

. . . Each day the population removes a large part of the phosphorus from the water, especially the particulate fraction. Most of this does not actually pass through the body but is sedimented in the form of pseudofeces which fall on the sediments. Thus, the mussels make large quantities of phosphorus available to microorganisms and to the autotrophs (benthic algae and marsh grass) . . . the energy flow was estimated to be about 0.15 $KCals/M^2/day$.

The most important finding of the study is . . . the ratio between flux and amount. Note that over one third of the 14 mgms of particulate phosphorus is removed from the water each day by the population, and thereby retained in the marsh. In contrast, less than one per

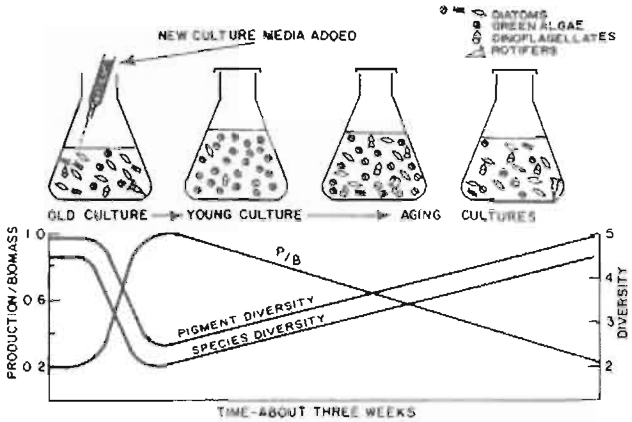

FIG. 3. *The Margelef model of ecological succession showing a simple type of succession which can be demanstrated in laboratory cultures. The flasks show changes in species composition occurring when succession is set in motion by the introduction of new nutrient media into an old "climax" culture. The graph shows resultant changes in two aspects of diversity and in the relation between production and biomass (P/B). See text for details of the experiment.*

cent of the 20 KCals of potential energy (net production estimate) available is actually utilized by the mussel population. In other words, the mussel population has a much more important effect on the community phosphorus cycle than it has on community energy flow . . . .

To summarize, the mussel study brings out two important points: (1) It is necessary to study both energy flow and biogeochemical cycles to determine the role of a particular species in its ecosystem, (2) animals may be important in the ecosystem not only in terms of food energy, but as agents which make basic nutrient more available to autotrophs. . . .

Now let us consider the third important aspect of ecological function, that is, community regulation. Ecological succession is one of the most important processes which result from the community modifying the environment. Fig. 3 illustrates a very simple type of ecological succession which can be demonstrated in a laboratory experiment. Yet the basic pattern shown here is the same as occurs in more complex succession of natural communities. The diagram (Fig. 3) was suggested to me by Dr. Ramon MARGELEF, hence we may call it the MARGELEF model of succession.

At the top of the diagram (Fig. 3) are a series of culture flasks containing plankton communities in different stages of succession. The graph shows changes in two aspects of structure and in one aspect of function. The first flask on the left contains an old and relatively stable community; this flask represents the climax. Diversity of species is high in the climax; species of diatoms, green flagellates, dinoflagellates and rotifers are shown in the diagram to illustrate the variety of plants and animals present. Biochemical diversity is also high as indieated by the ratio of yellow plant pigments (optical density at 430mμ) to chlorophyll-a (optical density at 665mμ). On the other hand the ratio of production to biomass (P/B in Fig. 3) is low in the old or climax culture, and gross production tends to equal community respiration. If we add fresh culture medium to the old culture, as shown in Fig. 3, ecological succession is set in motion. An early stage in succession is shown in the second flask. Species diversity is low, with one or two species of phytoplankton dominant. Chlorophylls predominate so that the yellow/green ratio (O.D.430/O.D.665) is low, indicating low biochemical diversity. On the other hand, production now exceeds respiration so that the ratio of production to biomass becomes higher. In other words, autotrophy greatly exceeds heterotrophy in the pioneer or early succession stage. The two flasks on the right side of the diagram (Fig. 3) show the gradual return to the climax or steady state where autotrophy tends to balance heterotrophy.

The changes which we have just described are apparently typical of all succession regardless of environment ortype of ecosystem. Although much more study is needed, it appears that differences in community structure mainly affect the time required, that is, whether the horizontal scale (X-axis in Fig. 3) is measured in weeks, months or years. . . .

To summarize, I am suggesting that the basic pattern of functional change in ecological succession is the same in all ecosystems, but that the species composition, rate of change and duration of succession is determined by the physical environment and the resultant community structure. . . .

ON CERTAIN UNIFYING PRINCIPLES IN ECOLOGY

Ramon Margalef—1963

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Admonishing ecologists for having been reluctant to orient their efforts in terms of a general theory, Margalef proposes some unifying principles with major emphasis on the maturity of the system as measured by diversity and in terms of energetics. Maturity is a quantitative measure of the pattern in which the components of the ecosystem are arranged and related. In spite of its theoretical orientation, the easy readability of the essay is credit to the author's clear perception and insight. The essay is largely a speculative interpretation encompassing both original and undeveloped ideas. Because of its speculative nature and theoretical ideas it should be read not as an instance of accomplished fact but as a possible indicator of future lines of inquiry.

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. . .

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 . . . .

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 and the productivity index under natural light conditions of Strickland. . . .

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. . . . 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. . . .

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. . . .

. . . 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. Homeostasis is higher. On the other hand, future states in less mature ecosystems are heavily influenced by external inputs, by changes in the physical environment. . . .

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 homeostasis 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. . . .

EXTENSIVE SYSTEMS WITH LOCAL DIFFERENCES IN THE VALUE OF MATURITY

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. . . .

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; others (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. . . .

. . . 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.