Science has made the world one through the facilities of communications and transport now available; and it recognizes no political or racial boundaries in its fields of knowledge. Among modern social and intellectual forces, science alone speaks in a tongue which meets with universal understanding. The conception of science as a social factor intimately linked up with human history and human destiny gives a new meaning not only to scientific research but also to the position of citizens who are engaged in it.

Both rightly and wrongly, science has been blamed for much of the wastage of life which has been brought about by the rapid applications of scientific knowledge to purposes of peace and of war. Men of science are, however, citizens as well as scientific workers; and they are beginning to realize their special responsibilities for making sure that the fruits of scientific knowledge are used for human welfare. They can no longer remain indifferent to the social consequences of discovery and invention, or be silent while they are blamed for increasing powers of production of food supplies, providing means of superseding manual labor by machines and discovering substances which can be used for destructive purposes. It would be a betrayal of the scientific movement if scientific workers failed to play an active part in solving the social problems which their contributions to natural knowledge have created.

The view that the sole function of science is the discovery and study of natural facts and principles without regard to the social implications of the knowledge gained can no longer be maintained. It is being widely realized that science can not be divorced from ethics or rightly absolve itself from human responsibilities in the application of its discoveries to destructive purposes in war or economic disturbances in times of peace. Men of science can no longer stand aside from the social and political questions involved in the structure which has been built up from the materials provided by them, and which their discoveries may be used to destroy. It is their duty to assist in the establishment of a rational and harmonious social order out of the welter of human conflict into which the world has been thrown through the release of uncontrolled sources of industrial production and of lethal weapons.

Science can only continue to render its fullest service to the community as the relations between the general scientific worker and the general citizen are harmonized and the purposes and methods of science are widely understood. In the establishment of such a sympathy, a nobler type of citizenship becomes possible, adequate to defend us against the dangers to which civilization is exposed and to build a social order worthy of the limitless powers which the advance of science has placed in the hands of man. It is in the light of service to these high ideals that science, without which we can not live, and religion, without which most people see no meaning in life, can find a field in which both can work together for the highest human destiny.

CONCERNING ECOLOGICAL PRINCIPLES[1]

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THE statement is frequently made that ecology deals mainly with facts which are organized around relatively few principles. Usually this is given as a reproach by non-ecologists, sometimes if not with pride, at least with resignation, by ecologists. If such a condition exists, it seems to us to be a cause for regret. For a number of years we have been interested in thinking over this problem and in collecting distinctly ecological principles from the literature as well as in amassing evidence dealing with more specific problems. The present paper is presented as a report of progress in the hope of provoking discussion which may make future ecological work more effective.

In making this study we are not conscious of having contributed anything new, even though we find the results at least mildly stimulating. It is not our concern at present to deal with the history, with the personalities associated with the different principles or with the date of their discovery. This means that we are not particularly interested in the percentage of these principles which have grown out of modern, self-conscious ecology. Our only care has been to select and make some preliminary attempts at classification of those principles that deal in the main with interrelations between an organism, or one or more groups of organisms, and its or their environment.

It would be relatively easy to become entangled in a discussion of terminology in connection with the consideration of ecological principles. We wish to avoid this as far as possible and shall at times use only one of a number of common terms associated with a given idea. Our selection in such cases will be based on our personal usage rather than on a fully reasoned consideration of the merits of possible alternative terms. Our whole emphasis for the moment is on ecological ideas which we think have merit, rather than on ter-

1 We are indebted to Alfred E. Emerson and to Karl P. Schmidt for reading a preliminary draft of this manuscript and for making pertinent suggestions.

minology or even on the evidence that supports these generalizations.

With this general introduction, it is desirable to give a few orienting definitions and ideas. A principle is a fundamental truth or a proposition which can form the basis of reasoning. It represents a synthesis of data and concepts which have been gained by analysis. A living organism, as well as we can define it, is a physico-chemical mechanism in dynamic equilibrium which displays the self-regulating, self-perpetuating qualities which in the aggregate we call life; or it is such a mechanism plus some powers and forces unknown to modern physics and chemistry, which may or may not be within the range of human knowledge. The environment of any organism consists of everything in the universe external to the cells and intimately utilized cell products of that particular organism. No part of this environment is without potential effect on any organism, although some phases have such a direct importance that they are regarded as comprising the effective environment. The distinction between the effective and the non-effective environment is one of degree of influence rather than of kind. The relation between any living organism and its environment is, in the language of Professor Pearl,[2] (1) particular, (2) continuous, (3) reciprocal and (4) indissoluble. Since we are considering the organism as a unit, we do not need to discuss matters concerned with the intra-organismal environment.

It is not advisable in the present state of our knowledge to dwell upon a general scheme of classification of ecological generalizations. We feel, however, that such a scheme can be worked out and that by making certain assumptions, ecological concepts and principles may be grouped at least as logically as the phenomena on which they are based.

Some of the possible subdivisions are (a) into these generalizations which are primarily quantitative as contrasted with those which, as far as we now can see, are qualitative only. The former may be illustrated by what we know concerning the growth of experimental populations. On the other hand, our information about protective coloration, for example, is as yet primarily qualitative. From a different point of view (b) principles can also be divided into the relatively few in which causal relations are known, as contrasted with the many for which the underlying causes are still obscure. The rough classification we shall follow is mainly one of convenience and is based on fairly obvious primary relationships.

There is a whole series of principles concerned more primarily with the environment than with the organism and another series in which the point of view is reversed. To the working ecologist the environment is holocoenotic, that is, it is a unit composed of many parts, as a rope is made of many strands. Even though holocoenotic, the different parts may at times assume control as the concentration of one of them approaches the minimum or maximum which the animal can tolerate and hence acts as a limiting factor. Here we have the well-known "law" of the minimum and the less emphasized "law" of the maximum. Here also arises the concept of an ecological optimum and with its opposite, an ecological pessimum. The degree of fitness which organisms and environment exhibit may be thought of as ecological valence or öky. From this we move on the one hand to the general idea of euröky and stenöky, which may be broken down into wide or narrow toleration for the different elements in the environment. On the other hand, there is the concept of vagility which is concerned with the powers of dispersal of a given species, or by extension, of a given community. This capacity for active dispersal or passive transport is an important factor in determining geographic range.

There are many rules that have been worked out concerning the effect of environmental factors on organisms; for example, the Arrhenius, Van't Hoff and Krogh temperature equations, the matter of temperature summation and its corollary, the life zone concept, which is closely related to the so-called bioclimatic law. In this general category belong also the different principles concerning the effect of light on organisms, such as the Bunsen-Roscoe "law" which states that the effect of light is, within limits, a function of intensity multiplied by duration of its action; the rule that only absorbed light is effective and that the percentage of incident light which is absorbed is independent of the amount present; and many more. There are also the various applicable laws concerning vapor pressure of water, of hydrostatics and of similarly fundamental principles of meteorology, geology, physics and chemistry which concern the fitness of the environment to support life. In many of these physical relations we must recognize short, intermediate and long-time periodicities as well as important elements of stability in the environmental complex. Phenomena associated with migration and emigration are related to certain of these environmental periodicities.

In shifting our attention so as to consider organisms more directly, we come immediately upon adaptation, which is, of course, correlated with ecological valence. The latter is a term sometimes used by ecologists to express the mutual requirements of environment and organism. Various attempts to organize ecology about types of specific adaptation have failed, but the fact remains that an organism must have a somewhat larger number of positive than of negative adaptations to its environment if it is to persist. This, we submit, is a

[2] Unpublished lecture.

fundamental principle for biology in general as well as for ecology; it must hold for the biotic community as a unit as well as for the individual or the species.

Certain environmental adjustments are apparently adaptive, for example, Bergmann's rule that related warm-blooded animals tend to be smaller as one approaches the tropics and the related rule of Allen that the appendages of such animals tend to be smaller the colder the climate. The rule of Gloger, that animals in warm humid regions tend to be more melanic than those in arid or in cool climates, is not so obviously adaptive. In this respect there is resemblance to Jordan's rule of the relation between numbers of vertebrae of fishes and temperature. The general principle of environmental induction that finds a striking demonstration in the determination of the fundamental organization by environmental action on the eggs of *Fucus* is more plainly adaptive, as is the widespread principle of convergence and of generalized mimicry which, in fact, may be merely a special instance of convergence.

The community concept is frequently thought of as being the only major ecological principle, an idea with which we do not agree. The self-evident individuality of animals makes equally self-evident the fact that individual animals have environmental relations with their physical environment as well as being immersed in a biotic community; hence the community, while important, is not all-important in ecology. All animals live in communities which include plants as well as other animals. These biotic communities range from those primarily integrated by environmental action, the so-called ecofaunae of Uvarov and ecoflorae, through the less closely knit biocoenoses to the truly social groups. Within all sorts of communities, animal aggregations may exist as more or less dense, more or less temporary collections of the same or of different species.

From the fact that animals live in communities it follows, even without the recent laboratory analyses of increased survival values that are frequently shown by aggregated animals, that there must be certain cooperative relations between organisms. This does not refute the obvious point that organisms also interact with each other to their disadvantage as well as to their advantage. The word cooperation has picked up certain engrafted meanings; basically it signifies working together and in this sense, as unconscious cooperation or automatic mutualism, it is one of the important integrating forces in community life. Much of the significance of this fact has long been recognized in the literature concerned with symbiosis in its various degrees from commensalism through mutualism and the truly social phenomena.

The gregarious habit also gives rise to generalizations which may be basically biotic or may grow out of relations with the physical environment. Thus there is a tendency for the animals at the base of food-pyramids to be gregarious and for the predators at their apices to be solitary. Also the larger animals in monotonous physical habitats tend to be more gregarious than are similar forms in strongly dissected habitats.

Communities have internal, spacial and temporal organization. Within the community there are various degrees of influence, which range from marked dominance to incidental or accidental forms. The organization in time introduces ecological succession or community evolution, which proceeds as a result of both biotic and of physical causes and which is essentially predictable. There is also the process of maturation of the community without evolution during which the pioneer forms develop to a mature stage of the community in question without ecological succession taking place. Community evolution tends towards a climax. This may be local, or as a biotic formation may be geographic in extent and composed of similar but slightly different associations or other less important units which are determined primarily by the dominant organisms but which may be recognized at times by differences in other influential constituents.

Communities are organized about the web-of-life relationships which include such factors as the utilization of environmental niches. In this connection, particularly with the vertebrates, there is a whole set of principles connected with territory, migration and with breeding, shelter and feeding ranges. These include such ideas as those connected with habitat "selection," as for example Hopkins' host selection principle and the concept of a "forced selection of habitat." The web-of-life is also concerned with food chain, food web and food pyramid relationships.

A quantitative approach to communities introduces the problems and theories concerned with longer cycles and with biotic balance or unbalance. To our way of thinking it is solely a matter of point of view whether we regard the community as being in the state of balance implied by the concept of dynamic equilibrium or think of it as being in perpetual unbalance. Both express the same general idea. It is significant that the periodic fluctuations in numbers may be conditioned by biotic interrelations as emphasized by the equations of Lotka and Volterra and/or by long-range environmental disturbances which may be either mundane or extra-mundane in origin. To sum up these relationships succinctly, they may be the result of the interplay of biotic potential, meaning the rate of increase, checked by environmental resistance which may be primarily an effect of the physical or of the biotic elements in the environment or of both acting together. We put the same idea into entirely biotic terms when we speak of the ratio between birth rate and death rate. Under many conditions these quantitative aspects of population growth are well summarized by the logistic curve of Verhulst and Pearl.

The increased crowding of animals often results in harm to the animals involved. This may produce a lowered survival and even extinction. This is one phase of the modern concept of the struggle for existence which is essentially a statistical principle and deals with changes in the birth-death ratio.

By the interaction of automatic cooperation and competition, that is through the activities involved in the struggle for existence, we come upon a whole set of ecological principles that center about organic evolution. This is a field which many modern ecologists appear to have avoided. All the factors of natural selection, *e.g.*, variation, overproduction, struggle for existence and the survival of the fittest are definitely ecological except for the important matter of the origin of those crucial variations which are not environmentally induced. At this one strategic point genetics has its only distinctive claim in the whole of the evolutionary field; otherwise, evolutionary dynamics belong in the realm of ecology.

Almost all other evolutionary principles are also ecological in nature: Lamarckian use and disuse, if these ideas have any place in modern thinking, Buffonian induction, orthogenesis in part and orthoselection wholly, and of course all isolation whether geographic, ecologic or physiologic in character. Subsidiary evolutionary theories such as sexual selection, mimicry and adaptive radiation are also wholly or mainly ecological.

Ecology deals not only with individuals and with communities of these individuals; it is concerned also with species and with their relations. This widespread, useful concept is in part an ecological tool and in part an expression of ecological forces. Among the ecological principles related to species there is another important rule of Jordan's that the nearest ally of a given species tends to occupy an adjacent area. This may be expanded to state that related and neighboring species tend to occupy separate niches and hence are in less direct competition than they would be otherwise. Stated with slightly different emphasis this takes consideration of the fact that the closest competitors of a given individual are the members of its own species; this forms the basis of territorial relationships such as have recently been much discussed, particularly among birds. The next closest competition for the individual comes from members of closely related species with similar ecological requirements. Hence related species find greater stability in their community relations if they occupy separate niches.

There is another set of principles that concern us which center about geographical distribution. Among these there is the generalization that vigorous species tend to occupy more space the greater their age; this is generally known as the age and area hypothesis and has limited application. Related to this is the extension that old races on the road towards extinction tend to be locally distributed over wide areas. Another related principle is the depth-age formulation of A. Agassiz, which states for oceanic life that forms with the greatest range in depth are those that show the greatest span in time. Among other principles of geographic ecology there is the tendency of the animals in the Arctic to resemble those in the Antarctic. This is usually called the principle of biopolarity. There is also the tendency for tropical oceanic communities to have fewer individuals per species as contrasted with the large numbers of individuals of the same species in colder waters. The fundamental principle of the relative stability of the present ocean basins, which limits our ideas concerning the extent and importance of land bridges, although still a matter of discussion, seems to be reasonably well established.

Then there are the principles related to emigration or dispersal, among which may be mentioned the suggestion of Matthew and Griffith Taylor that primitive animals tend to be located in remote corners of the world far from their centers of origin. Under other conditions, the primitive forms are located in the center of distribution which may or may not also be a center of origin and a center of survival.

In conclusion we recognize the inadequacy of the present presentation. We have not listed all those principles known to us as definitely ecological, and the selection has been uneven in quality. Possibly more relatively unimportant principles have been included than important ones omitted. Even this brief summary indicates that, plentiful as are the facts, there is no dearth of major and minor ecological principles about which to orient them. We trust that the analysis here presented and which may be elaborated in the future may contribute toward a more adequate synthesis of ecological knowledge. We believe that focusing attention on a theoretical framework will lead to more important work in ecology.

OBITUARY

STUART T. DANFORTH
1900–1938

ORNITHOLOGISTS, entomologists and naturalists who have visited Puerto Rico in the past dozen years will mourn the death of Dr. Stuart T. Danforth, which occurred at West Boylston, Mass., on November 25. Going to Puerto Rico soon after his graduation from Rutgers in 1921 to visit his father, Ralph E.