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AN OUTLINE OF THE RELATIONS OF ANIMALS TO THEIR INLAND ENVIRONMENTS

BY

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ERRATA AND ADDENDA.

Page 50, second column, line 13 from bottom, for *Danais archippus* read *Anosia plexippus;* line 8 from bottom, for *mellifica* read *mellifera.*

Page 51, line 11 from bottom, for *Danais* read *Anosia.*

Page 159, at right of diagram, for *Bracon agrilli* read *Bracon agrili.*

Page 289, second column, last line but one, for *Scalops* real *Scalopus.*

Page 294, line 3, for *catcsbeana* read *catesbiana.*

Pages 327 and 330, line 12, for *orcus* read *oreas.*

Page 347, line 4, for Cecidomyidæ read Cecidomyiidæ.

Page 356, line 7, for Anthomyidæ read Anthomyiidæ.

Page 368, line 18, dele second word.

Page 373, after line 10 insert as follows: 53a, *subpruinosa* Casey, 1884, p. 38.

Page 375, after *submucida* Le Conte, 48, insert *subpruinosa* Casey, 53a.

Page 377, after line 7, insert as follows:—

1884. Casey, Thomas L.

Contributions to the Descriptive and Systematic Coleopterology of North America. Part I.

Page 379, line 11 from bottom, for *sensu lata* read *sensu lato.*

Page 382, line 12, for VII read VIII.

Page 408, line 2, for *the next article in* read *Article VIII of.*

Page 410, line 6 from bottom, for *= 4* read *'11.*

Page 412, line 7, for 31 read 30.

Page 421, line 17 from bottom, insert *it* before *grows.*

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Article I.—*An Outline of the Relations of Animals to their Inland Environments.* By Charles C. Adams, Ph.D.

The Dynamic Relations of Animals

1. introductory note

As creatures of habit, the attitude of mind with which we approach a scientific problem has much influence upon what we see in it or get from it. Although the essence of life is activity—the response of the changing organism to its changing environment—yet this dynamic conception of animal relations, *and all that it implies*, has not become as prevalent a mental habit among biologists as one might expect. While some naturalists view the animal from a more or less dynamic standpoint, they do not include a similar conception of the relation of an animal to its environment. Still others view the environment more or less dynamically but do not extend this conception to the animal, and thus both of these conceptions lack completeness and are not thoroughgoing and consistent. The study of activities, or in other words the study of processes, has made great progress in the allied sciences, much to their advantage, and undoubtedly the prevalence of similar conceptions will lead to similar advances in biology.

In the present brief paper I have attempted to discuss only certain phases of the problem with the idea of emphasizing the general principles involved, and in the hope that it may aid in making these conceptions of more practical value in investigation, and also facilitate an understanding of the discussion contained in a report on the invertebrates of the Charleston (Illinois) region, to appear in a subsequent paper of this volume of the Laboratory Bulletin.

2. the relations of animals to their environment

The study of animal ecology may be taken up from many sides and in many ways. One of the most interesting and fundamental of these is that which considers the *dependence* of the animal upon its environment, and at the same time orients it in the gamut of energies and substances. Many phases of this discussion, though elementary and for this reason easily overlooked, are yet of fundamental importance. Every boy who has kept pets in confinement, and who has had the responsibility of caring for them, and every one who has cared for domestic animals, knows what constant attention must be given to keep them supplied with food, water, shelter, and other "necessities of life." And who can overlook the fact that it requires attention to maintain his own physical health? In the laboratory this dependence upon the environment is readily tested experimentally by any method of isolation which will prevent an animal from securing any "vital necessity": as air—when sealed in a vessel; or food—when locked up without it; or a favorable temperature. No animal can survive such isolation from its normal environment. Every student of animals in nature must also realize that similar supplies and conditions determine and control the existence and welfare of all *wild* animals. The animal is not self-sustaining, but requires a constant intake of energy and substance from its environment. Chemical methods will readily show the source from which the materials composing the animal body have been derived. The ash came from the soil or rock, and shows the animal's dependence upon the solid earth; the liquids came from the water of the earth and constitute from fifty to ninety-five per cent. of the bulk of the animal's body, showing that a relatively large quantity of this substance is essential to all living animals; the abundant gaseous element was derived from the atmosphere, to which it will again return. The substance composing the animal body is thus derived mainly from the water and the air rather than from the relatively inert and stable earth. It will be profitable for us to imagine these proportions so changed that the solids instead of the relatively mobile liquids and gases form the principal mass of the body, keeping in mind meanwhile the slow rate of chemical change in solids compared with the change in substances in a finely divided condition, such as liquids and gases. If the solids predominated, the rate of the chemical change, upon which the active life of animals depends, would be greatly retarded, and animals, including man, would be stolid beyond comprehension. Furthermore, we must not overlook the fact that animals are not maintained solely by substance, because substances are also carriers of energy, substance and energy never being separated. The living animal is not a *producer:* it can make neither substance nor energy, nor is it a kind of energy; it is solely a *transformer*, a chemical engine which changes the form of substance and chemical energy and produces new combinations from the old. The living plant transforms energy and inorganic substance, from the air, water, and earth, into complex chemical compounds, and thus concentrates powerful chemical energy in such a form that the animal, by a further change, is able to set it free and to utilize it. Sugar, starch, and gluten are familiar examples of this "tablet" or "cartridge" form of chemical energy which animals explode or set free and then use in maintenance. During this transformation, in which chemical energy is set free, waste products—inert chemical substances—are formed which if not eliminated from the animal system will prevent its operation, just as ashes if not removed will check a furnace. Respiration aids in the removal of carbonic acid gas— a waste product—from the body, but we often forget that the chemical energy derived from the oxygen is an important feature in respiration. By another process the liquid and the solid waste is removed. Thus gases, liquids, and solids are taken into the body and later returned to the environment in a different chemical condition, thus completing a cycle of transformation. That the animal body is so largely made up of solutions and gaseous substances is an important factor in its relatively unstable chemical condition, a condition of *unstable equilibrium*, which determines the active and dynamic character of the animal. Since, then, chemical activity is one of the essential characteristics of a living organism, its influence forms one of the main problems of the zoologist when studying the changes in animal activities; their orderly sequence and the laws which govern them.

On account of the fact that the animal is a chemical engine, it is able to use chemical energy to the fullest extent. If we assume a hierarchy in the forms of energy, chemical energy seems to belong to the upper class; for though some forms of energy are not readily transformed into chemical energy, chemical energy can be transformed into *all others*. As a result the animal, being a chemical engine, has, as it were, an "inside track" to the main sources of energy, and thus by transformation is able to utilize chemical energy to form light, as in the firefly, or electricity, as in the electric eel; and other forms of energy useful to the animal are similarly derived. This study of the activities of living animals, as contrasted with the study of dead ones, is a phase of the general science of energetics, a science which furnishes the basis for the correlation of many diverse branches of knowledge.

The activities and transformations within the animal body show us very clearly how an animal is dependent upon environmental conditions. The animal transforms air, water, and rock, and all animal habitats and environments must contain these elements. In nature these are combined in a multitude of ways. The interrelations of these fundamental environmental units have been strikingly expressed by Powell ('95: *22–23*) as follows:

"The envelopes of air, water, and rock are so distinct that they can be clearly distinguished; and yet, when they are carefully studied, it is discovered that every one encroaches upon the territory of the others, not only by interaction, but also by interpenetration. It has already been shown that the water penetrates deep into the rock. Every spring that falls from the hillside gives proof that the rocks above its level hold water, which they yield slowly as a perennial supply; and the innumerable hills of the continents and islands have their innumerable springs. Every well proves that there is water below; every artesian fountain shows the existence of underground waters; and every boring in the crust of the earth, and every excavation in underground mining, discovers the presence of water.

"Wherever water flows, air flows with it, and all natural waters are permeated with air.

"The aqueous envelope is everywhere permeated with rock, which it holds in solution or suspension, and there is no natural water absolutely pure. The sea is full of salt. Salt lakes are more than full of salt, and so they must throw it upon the bottom; and the waters hold lime and many other substances. Not a drop of pure water can be found in the sea; not a drop can be found in a lake; not a drop of pure water can be found in any river, creek, brook, or spring; and not a drop of pure water can be found underground: it is all mixed to some degree with rock.

"All natural waters are aerated. No drop of water unmixed with rock and air can be found, except by the process of artificial purification.

"But surely there is pure air? Nay, not so. There is no natural air unmixed with rock and water. All the air that circulates above the land and sea, within the ken of man, and all the air which circulates underground, is mixed with rock and water.

"Pure air is invisible: it will not reflect light; it is transparent, but will not convey light. Light is conveyed through the atmosphere by ether, and is reflected and refracted by rock and water; and it seems to be largely affected in this manner by rock. If the ambient air of the earth were pure, there would be no color in the sky, no rainbow in the heavens, no gray, no purple, no crimson, no gold, in the clouds. All these are due largely to the dust in the air. The purple cloud is painted with dust, and the sapphire sky is adamant on wings.

"Land plants live on underground waters: were there no subterranean circulation of water, there would be no land plants. Fishes live on under-water air: were there no circulation of subaqueous air, there would be no fishes in the sea. The clouds are formed by particles of dust in the air, which gather the vapor: were there no dust in the air, there would be no clouds; were there no clouds, there would be no rain."

Up to this point we have considered mainly the processes of maintenance of the animal body, but there are other processes as well which must be called to mind, such as growth, development, multiplication, and behavior. Physiologically considered, none of these activities are essentially different from the fundamental phases of metabolism and all are dependent upon it; they are special forms of the transformation of substances and energy within the animal. As the individual animal grows and develops in its life cycle, its metabolism, form, and behavior change in an orderly manner, and this transformation is in the main a continuous process like the other transformations of matter and energy. The changes which take place during entogeny are often greater than the differences which exist between very distantly related adults, and these differences result in very different rôles which the animal often plays in the economy of nature.

Comparable to the responses of the animal to its environment, and indeed essentially of the same kind, are the responses of any part of an animal to all its other parts, the entire organism, in this case, being considered as a unit. The environment of an internal parasite is formed by the body of its host, and in a similar sense the different parts of the body are parts of the environment of the other parts. The different parts of the animal body are what they are on account of three conditions. The first is determined by its relative position and responses as a member of a series of successive generations. In this way the hereditary potentialities are determined. Ecologically considered heredity may be regarded both as the response of individuals (unicellular) and germs to the conditions of life, and as the mutual responses of different germs to one another. The crossing and intermingling of germinal elements is as truly a response as are other forms of activity. Secondly, there is considerable evidence which indicates that *at some stage* in the development of an animal any part is potentially capable of developing into any other part. The character of development, then, is conditioned by the character of the cell-environment—its relative position, and all that implies with regard to environment. A fragment of a regenerating animal develops differently according to its position, and this is a response to its relative position in the cell community. Thirdly, the development of an animal is conditioned by its external environment. The external conditions influence animals by changing their internal activities. The internal changes modify the cell community and change development. In this manner every part of the animal is influenced by the conditions of its existence.

The processes of metabolism are continuous as long as life lasts. Thus, as an animal respires there is a gaseous exchange, from the earliest stages of its existence until its maturity and death. Eggs respire as surely as larvæ and adults, and the chemical, physical, and physiological changes within them vary with their growth and development. Some of these changes are primarily dependent on the orderly course of development during the life cycle, and are therefore irreversible processes, because no higher animal which is mature may reverse its development and become young again. At different stages of development different enzymes and harmones appear which modify the physiological conditions of growth, development, and behavior. Environmental changes, persistent and uniform, or periodic in character, tend to modify and alter these internal processes, and are an additional source of change, which is particularly shown in behavior.

It is interesting to observe in this connection that certain factors are important as they *hasten* or *retard* other processes. Thus enzymes hasten chemical changes which without them would take place at a very slow rate, and they set free much energy in a relatively short time. Temperature is another hastener of chemical reaction. Not only is it a condition which sets limitations on the chemical reaction in animals, but it also influences their optimum, and with increasing temperature chemical changes take place within the animal irrespective of the control of the animal, except in the warm-blooded animals, where a mechanism exists which regulates, within certain limits, temperature conditions.

3. OPTIMA AND LIMITING FACTORS

We have seen that the animal is dependent upon its environment for both substance and energy. If, therefore, the environment does not contain, in available form, both substance and energy, animals will not be able to live in it permanently, although with energy stored in their bodies they may be able to make more or less prolonged and successful invasions into such an environment. The optimum is the most favorable condition for any function. We may consider optima corresponding to units of different rank: a single cell or tissue in action, an organ or system of organs, the animal as a whole, a taxonomic unit—and so on, to an animal community or association. There are, then, many kinds of optima, and the study of the conditions which produce them is a complex subject. The optima for different functions may differ much; for example, that for growth is often different from that for reproduction, and the optima may also change greatly with the development of the animal. Optima, therefore, are not fixed conditions, even though they do represent a condition of physiological *relative equilibrium.* The amount or intensity of substance and energy which produces an optimum is limited above by the maximum and below by the minimum. Thus departures from the optimum, toward an increase or a decrease, are departures *from* the most favorable conditions toward less favorable conditions, and hence toward limiting conditions. This form of expression is mainly that of the laboratory; it is desirable therefore, in addition, to express it in terms of the normal habitat. In nature we look upon the optimum as that complex of habitat factors which is the most favorable, and departure in any direction from this optimum intensity is in the direction of a less favorable degree of intensity or into unfavorable conditions. From this standpoint *any unfavorable condition is a limiting factor* and may retard, hasten, or prevent vital and ecological activities. Optima are thus almost ideal conditions, and are probably realized in nature only to a limited degree; in other words only approximately. Here also, as in the laboratory, they represent a condition of *relative equilibrium*. The laws of the transformation and development of optima are of great ecological importance, as I pointed out several years ago ('04). In field study probably the most valuable criterion to be used in the recognition of ecological optima is the normal relative abundance and influence of animals in their breeding environment.

In the preceding discussion no special emphasis has been placed upon the time element, or the rate at which changes may take place. Natural environments are complexes, in the composition of which several factors are involved. This being true, it is desirable to recall the fact that the *rate of change* is determined by the pace of the slowest factor, or, as Blackman ('05: 289) has expressed it: "When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor." This is a general law and applies to all changes, internal as well as environmental.

In closing this section, I wish to call attention to another conclusion of the English plant physiologists Blackman and Smith. They state ('11) that from experimental study of the assimilation of water plants, the conception of the optima is untenable, and that the phenomena are better explained as the result of "interacting limiting factors than by the conception of optima" (p. 412). This principle is formulated as follows (p. 397): "When several factors are possibly controlling a function, a small increase or decrease of the factor that is limiting, and of that factor only, will bring about an alternation of the magnitude of the functional activity." It will be of much importance to test the application of this idea to animal responses.

4. DETERMINATION OF DYNAMIC STATUS

In any study of the energetics of organisms it is desirable to have clearly in mind one of the fundamental conceptions of this science—

the dynamic status. The law of conservation of energy teaches us that energy can not be destroyed; that it is transformed only, and thus undergoes a cycle of changes. The animal or an animal community, as a unit and as an agent or transformer, is constantly transforming energy, setting it free. In this sense it originates, but not at a uniform rate. At one time much energy may be transformed, and at another very little. When a great amount of energy is being set free, when the animal or community is exerting much influence, we may look upon it as producing pressure or strain. A condition of stress is not a permanent one, because the pressure tends to cause such changes as will equalize or relieve this condition. This is considered as the process of adjustment to strain, and is called Bancroft's law ('11). An animal in an unfavorable condition is stimulated, its normal activities are interfered with, and a physiological condition of stress is produced which lasts until by repeated responses or "trials" the animal escapes stimulation or succumbs and a relative equilibrium is established. An area may become overpopulated and consequently there may be established a condition of stress, which results in an adjustment by a reduction (through many causes) in the excess of population and a restoration of the normal, or a condition of relative equilibrium. From these examples it may be seen that the *dynamic status* means the condition of a *unit* or system with regard to its *degree of relative equilibrium.* The cycle of change may be considered to begin at any point. I have taken as the initial stage of the cycle the condition of *stress* or *pressure*, and have indicated how this condition tends to change in response to pressure, bringing about the *process* of adjustment to strain, and leading to the *condition* of adjustment to strain, or that of relative equilibrium. The activity of the agent produces the condition of stress, the process of adjustment to the strain follows, and this leads to the product—the establishment of the condition of adjustment or of relative equilibrium.

These conceptions are very suggestive when applied to various phases of organic activity, and aid greatly in utilizing the dynamic conceptions which are in constant use in many of the physical sciences. But we can not assume that these ideas will take definite form unless the student makes some special effort to master the principles involved.

5. ANIMAL RESPONSES

The general character of the changes within the animal, which result in the transformations of energy and substance, or the process of metabolism in its broadest sense, is the basis of all animal responses. It is well known that growth, development, and behavior are conditioned by certain metabolic processes, the rate of which are further conditioned by the presence of certain substances, as enzymes (from liver, etc.), and internal secretions (from thyroid, testes, adrenals, etc.). The influence of certain physiological conditions or processes is thus well known to affect the behavior of animals. The changes of instinct through the removal of the testes or ovaries, may be cited as examples of this influence. An animal whose metabolic processes have reached a certain stage is said to be satiated; later it is in the condition of incipient hunger; and still later, in the physiological condition of intense hunger. These internal changes cause the animal to react very differently to any food which is in its immediate vicinity. These changes in physiological conditions are strictly comparable to the change which an animal passes through in its ontogeny; to the life cycle of an insect, for example, in which the physiological conditions and behavior of a caterpillar are very different from those of the pupa and of the adult or moth. One of the higher animals, a dog, for instance, will undergo internal changes which will completely alter its responses at the sight of an old rival or enemy. Such considerations as those just cited show clearly that extensive internal physiological changes take place in animals, and that while some of them are very gradual others are exceedingly rapid. These internal conditions or changes have been well characterized by Jennings ('06: 289) as follows: "The 'physiological state' is evidently to be looked upon as a dynamic condition, not as a static one. It is a certain way in which bodily processes are taking place, and tends directly to the production of some change. In this respect the 'law of dynamogenesis,' propounded for ideas of movement in man, applies to it directly (Baldwin, '97: 167); ideas must indeed be considered so far as their objective accompaniments are concerned, as certain physiological states in higher organisms. The changes toward which the physiological state tends are of two kinds. First, the physiological state (like the idea) tends to produce movement. This movement often results in such a change of conditions as destroys the physiological state under consideration. But in case it does not, then the second tendency of the physiological state shows itself. It tends to resolve itself into another and different state."

I may thus summarize the relation of metabolic processes to physiological conditions and processes of behavior by the following table.

TABLE 1.—THE DYNAMIC RELATIONS OF ANIMAL ACTIVITIES

The Animal as an Agent (Activity of an Agent)	*Processes of Activity*	*Products of Activity*
The animal as an agent transforms energy and substance by its metabolic processes. These are accompanied by physiological conditions or states; they constitute a condition of unstable equilibrium. The transformations take place as— (1) Continuous and irreversible processes, as development, differentiation, etc.; or are— (2) Periodic or rhythmic processes, as digestion sexual activity, etc. ——— Changes in the internal conditions are produced also by external stimuli.	This unstable internal condition tends towards change, resulting in— (1) New conditions; (2) Movement; (3) The processes of behavior: trial, experiment, investigation, etc.	New states. Movement. Response. Regulation. Adjustment. Relative equilibrium. Learning. Orientation. Data. Concepts. Explanation. Theory. Hypotheses. Ideals.

The responses of animals to the conditions in which they live are of a composite character. Certain responses, such as the chirping response of a coot within the egg, are inherited and are relatively automatic in character; others are greatly modified by experience, as when an animal "learns," or forms a habit by repeated responses.

The responses of animals to the conditions of existence are the basis for any study of their relations, not only to other members of their own species, but to all elements, living or otherwise, of their complete environment. It is from this standpoint that animals must be considered in estimating their place in the economy of nature; that is, in estimating how they influence one another in an association of animals living together in the same habitat, and in judging of their relation to the succession of animal communities, and even to man himself.

6. THE INTERRELATIONS OF ANIMALS

"A group or association of animals or plants is like a single organism in the fact that it brings to bear upon the outer world only the surplus of forces remaining after all conflicts interior to itself have been adjusted. Whatever expenditure of energy is necessary to maintain the existing internal balance amounts to so much power locked up, and rendered unavailable for external use."—S. A. FORBES.

We have now seen the dependence of the animal upon its environment, as this forms the basis for an understanding of conditions involved in the problem of *maintenance* or the upkeep of the animal. The optimum conditions for prolonged maintenance produce the vital and ecological optima. These conditions imply more than mere maintenance; they mean as well, a degree of favorable conditions which permits the animal to exert an influence or stress upon its environment. As Forbes has said, if all the energy available to the animal is utilized internally there will be nothing left to influence the environment. Metabolic changes show that large amounts of energy and substance are used in maintenance. Under optimum conditions even greater amounts must exist. An animal must not only be able to maintain itself against other kinds of animals but even against its own kind, for the overproduction of its own race will be practically self-destructive. A good example of this kind of influence is seen in the hordes of lemmings which migrate, even into the sea, when overproduction becomes extreme.

The vital and ecological optima are thus to be looked upon as internally balanced, but externally, not as a state of balance or poise, but as a condition in which the animal is exerting stress, pressure, or influence upon its environment, instead of being passive or inert. A group of animals living together in any given condition such as an association, is an assemblage of interacting organisms. The active, free-moving animals collide with each other, with other kinds of animals, especially the relatively sedentary kinds, and with their environment of plants and the inorganic factors. The relatively sedentary animals are correspondingly bombarded by all elements of their environment. The association, as a whole, is thus in a continuous process of bombardment and response from every possible angle, and just as the individual animal is stimulated and responds, so all the members of any association are stimulated and respond in a similar manner. It is by this form of activity that animals not only maintain themselves but exert a radiating influence.

It will assist in realizing the constant pressure exerted by animals if we compare their activity to the flow of a stream. The pressure exerted by the stream may be realized if by a dam or similar means the current is resisted. Think for a moment of the amount of energy which would be transformed in an effort to prevent animals (or plants) from taking possession of a *favorable* habitat. Imagine an area 10 feet square and think of the effort it would require to prevent animals permanently from invading and establishing themselves in this habitat if no barriers were interposed, and if the means of destruction of the invaders were not so drastic that they materially changed the character of the habitat. Increase the size of the area and the difficulties will increase in geometrical ratio, and the utter futility of such an undertaking will soon be realized. The spreading processes of the gypsy moth in Massachusetts, and of the San Jose scale and the cotton boll weevil, show us in terms of human experience something of the energy expended by these radiating animal activities even when there are strong human economic inducements against such invasions.

When a balanced condition, or relative equilibrium, in nature is referred to, we must not assume that all balances are alike, for some are disturbed with little effort and others are exceedingly difficult to change. This distinction is an important one. Once the balance is disturbed, the process of readjustment begins. This is a phase of the balancing of a complex of forces. Just what stages this process will pass through will depend, to an important degree, upon the extent of the disturbance. Slight disturbances are taking place all the time and grade imperceptibly into the normal process of maintenance, as when a tree dies in the forest and its neighbors or suppressed trees expand and take possession of the vacancy thus formed. Disturbances of a greater degree, on the other hand, may only be adjusted by a long cumulative process. This change can progress no faster than the rate at which its slowest member can advance. Thus a forest association of animals may be destroyed by a fire so severe that all the litter and humus of the forest floor is burned. The animals which live in the moist humic layer as a habitat, such as many land snails, diplopods, and certain insects, can not maintain themselves upon a mineral soil, rock, or clay. As such a forest area becomes reforested, these animals can only find the optimum conditions when the slow process of humus formation reaches a *certain degree of cumulative development.* Under such circumstances this later stage must be preceded by *antecedent processes,* and restoration of the balance is long delayed. Some adjustments take place so quickly that little can be learned of the stages through which they pass. There are, however, many slow processes which afford an abundance of time for study; in fact some are too slow to study during a lifetime. The processes which are moderately slow are often particularly illuminating because all stages are frequently so well preserved that comparison is a very useful method of study; the slowness of a process has a certain resolving power, as it were, recalling the influence of a prism upon a beam of white light, which reveals many characteristics obscure to direct vision. A study of the processes of adjustment among animals is a study of an important phase of the problem of maintenance. The continued process of response will, if circumstances permit, lead to a condition of relative adjustment, or to a balancing among all the factors in operation.

7. ECOLOGICAL UNITS FOR STUDY

In the study of animal responses many different units are available, and a brief consideration of these will aid in an understanding of the methods which are useful. Because the animal body has been found to be composed of a single cell or a multitude of cells, a common belief has grown up that the cell is the natural unit for study. This opinion seems to be due to overlooking the fact that there is just as much reason for considering the *whole animal* as the unit. The unicellular animals are *whole animals* as truly as they are cells, and in multicellular animals the activity of single cells means little independently of the animal as a whole. It thus seems that ecologically at least the smallest valuable unit for study is the *individual animal*. The responses of the individual, as a kind of animal, to its condition of existence form the basis for what may be called *individual ecology*. Animals which are related by descent from common ancestors, as a community of social animals (e. g., an ant colony), or taxonomic units, such as genera, families, orders, etc. (e. g., fish, birds, catfishes, and salamanders), are also units which may be studied ecologically. Some of these hereditary units are, ecologically, fairly homogeneous, as, for instance, when a taxonomic unit is equally distinct ecologically: e. g., the woodpeckers with their arboreal habits. In other cases the taxonomic unit contains animals of great ecological diversity, as in the case of beetles, which possess almost unlimited ecological diversity, including littoral, aquatic, subterranean, and arboreal habitats, and parasitic, herbivorous, and predaceous habits. The study of ecology, upon the basis of such a unit, may be called *aggregate ecology*. Still another unit is available, based upon the animals which live together in a given combination of environmental conditions, as in a pond, on the shore of the sea, in a cave, within the bodies of animals, on the floor of the forest, or in the tree tops, etc. The animals found living together in such conditions form an *animal association* or a social community, and the study of the responses of such a community is the province of *associational ecology*.

8. THE ANIMAL ASSOCIATION

In the study of the animal association as a unit, we consider it as an agent, whose modes of activity, or responses, are of primary interest. We desire to know the kinds of animals which compose the community, the optimum and limiting influences which control its activity, the character of its responses, and the orderly sequence of changes in the environment to which it is responding.

The maintenance of an association depends upon the maintenance of the individual members which compose it, just as the maintenance of the entire animal depends upon the activities of the cells. There is the same basis for speaking of the responses of the association as there is for speaking of the responses of the individual. The association can continue to exist indefinitely only in such environments as possess, in available form, substance and energy for its individual members. The activities of the individuals transform energy and substance, producing growth, development, multiplication, and behavior. The persistence of an association in a given habitat brings about the formation of certain waste products, which if not changed or transformed at a certain rate, or transported from the environment in some way, tend to limit the optimum activity of the individuals and of the association. In the association, as in the individual, there must be an internal relative balance before there can be such a surplus of energy that the association can radiate or exert outward stress or pressure. An association which is only maintaining itself is not at an optimum, for in this latter condition there is a surplus of energy, and the activity, rate of multiplication, and favorable development under normal conditions are favorable to the extension of the association. The pressure which such an association exerts is shown by the progressive extension of its range of influence. By the active movements of the animals, by the activity of the environment, or by both together, they tend to invade other habitats and areas, and in such of these as afford favorable conditions they tend to survive and extend the area of the association. From the standpoint of the association the behavior of these active pioneering animals corresponds to the trial activities in the behavior of the individual animal. These activities are not different in kind from those which are involved in normal maintenance. They are those which form the initial stages in the establishment and extension of the association in a new locality or the re-establishment in an old one, and thus lead to a sequence or succession of associations. Ecological succession thus consists in an orderly sequence or series of associations which occur successively and form a genetic series.

9. ASSOCIATIONAL SUCCESSION

A succession of associations takes place either through the transformation of older ones, or through the origin of a new one on a surface which has been newly formed and has had no population. A favorable habitat without a population of animals is comparable in some respects to a vacuum; it exists as a condition of unstable equilibrium which tends to change toward a more stable state. The active life of animals tends to lead them into all possible habitats, and where they find the conditions favorable for existence they tend to survive and thus bring about the establishment of an association. Each association, like the individual animal, has a certain amount of unity and tends to maintain or perpetuate itself. But the stability of associations is only relative, and some are much more stable than others. Naturally the unstable ones are those which show succession most readily. Thus if we destroy a few trees in a hardwood forest and produce a glade, a large number of the characteristic animals of the dense forest will disappear and be replaced by animals which normally frequent open places; then in a few years sprout-growth and young and suppressed trees will change the conditions so much that the kind of forest animals which were eliminated for a time will begin to return; and when the new growth is replaced by the mature forest the animals of the mature forest will return and a new equilibrium will be formed. In such a forested region the glade is to be looked upon as an unstable condition, which through a succession of associations will later arrive at a relatively stable condition, which is able to perpetuate itself indefinitely under existing conditions. Such an association is considered a *climax*, or the culmination of a series of successions under existing conditions. The succession of associations leading to a climax represents the process of adjustment to the conditions of stress, and the climax represents a condition of relative equilibrium. Climax associations are large units, and are the resultants of certain climatic, geological, physiographic, and biological conditions.

The Dynamic Relations of the Environment

I. Introductory

In the preceding section we have seen that to understand animals we must consider them as active living agents which are constantly changing and responding to their environment. That the environment of animals should also be studied as an *actively changing medium* has not been as clearly recognized by students of plants and animals as one might anticipate from its importance. Some students feel that the study and understanding of the environment is not a part of zoology, or at least not an essential part. Furthermore, to some of these students at least, the environment seems largely chaotic, a confused unwieldy mass with no evident favorable point of attack. This view is quite natural to those who have had no training and practical experience in recognizing the "orderly sequence" or laws of environmental changes, and particularly to those who do not feel that environmental relations are an essential part of their subject. By many such students the environment is viewed in a manner comparable to the prevailing chaotic views on weather before meteorology became a science, or on taxonomy before Linnaeus, or on geology before Lyell. If one has serious doubts on this point, he need only turn to the standard treatises on zoology and search for a comprehensive and adequate recognition and utilization of the orderly and regulatory character of the environment as an essential part of the subject.

The fallacy of this position has been well expressed as follows by Brooks ('99): "I shall try to show that life is response to the order of nature. . . . But if it be admitted, it follows that biology is the study of response, and that the study of that order of nature to which response is made is as well within its province as the study of the living organism which responds, for all the knowledge we can get of both these aspects of nature is needed as a preparation for the study of that relation between them which constitute life." Later he says: "But if we stop there, neglecting the relation of the living being to its environment, our study is not biology or the science of life." No one seems to have attempted to refute this; naturally an easier path is followed—to ignore it. Perhaps up to the time of the present generation there has been some excuse for this confusion; but now the responsibility does not rest upon students of the physical and vegetational environment but upon students of animals, because the former students have arranged their scientific data in a manner which clearly shows the orderly lawful sequence of changes in environmental activities. This should form the basis for a study of the corresponding series of changes which take place within the animal, and also be the basis for a study of the reciprocal responses taking place between the animal and the environment.

In this section an outline will be given of some of the most important phases of environmental changes in inland areas viewed as lawful and orderly, particularly those changes which influence animal habitats.

2. THE DYNAMIC AND GENETIC STANDPOINT

Since Lyell taught the scientific world that a study of processes now in operation is the key to an understanding of the present as well as of the past, the *process* method has been slowly but inevitably penetrating to the utmost subdivisions of inquiry. With the progressive appreciation and use of this method its efficiency has been increased. Its progress has been the most rapid where the principles of its application have been most clearly understood. As models become known in each field of work others will find the method much easier to apply, and for this reason it is desirable that such examples become fairly numerous and wide-spread.

In the application of the process method to an imperfectly understood subject, and particularly to a complex one, it is desirable to consider the subject as a *unit* or entity. This unit may then be regarded as an agent whose process of activity is to be studied, for the activity of an agent gives us a process. Thus an organism, a plant society, or an animal community is a very complex unit or agent, which largely through chemical energy, under conditions of a normal environment, responds in an orderly sequence or changes. The environment changes, the internal conditions of the animal change, and so do the corresponding responses on the part of the animal. When all of these changes are studied as *orderly processes* we are able to see the advantage of this method of study. It is desirable to investigate all phases of animal responses in this manner, such as growth, development, heredity, etc., in order to determine the causes and conditions of this orderly sequence. As a rule our recognition of the *orderly sequence* or laws of action or succession precedes our knowledge of the causes and conditions of the sequence. This order of sequence is thus of fundamental importance and must be recognized before it can be investigated or explained. This method of studying the activity of agents, the character of their processes, constitutes the dynamic standpoint.

When the dynamic relations of an agent have been investigated, the orderly sequence of its responses established, and the causes and conditions of its activity determined, it is then possible to explain fully the origin or genesis of its activities. The *genetic method* is the study of origins in *terms of the processes involved,* and therefore the classification of facts genetically implies a knowledge of the processes involved in their origin. There are thus many degrees or stages in the development of a genetic classification, the first step of which is to determine the orderly sequence of changes. In a certain sense, in its broadest application, the process method is universal and includes the genetic, but until their mutual relations become clearly recognized and are generally understood both should be emphasized.

Particular attention should be called to the fact that the activity of an agent results in a process, and processes give us the *laws of change.* Many processes are reversible; that is a process may go forward in one direction and then become reversed and proceed in the opposite direction. Other processes are non-reversible, and operate in only one direction, being in a sense orthogenetic, as in the later stages of the ontogenetic process.

Let us summarize the main characteristics and principles involved in the dynamic and genetic method. They have been well expressed by Keyes ('98), and for my purpose are arranged as follows:

"A truly genetic scheme for the classification of natural phenomena thus always has prominently presented its underlying principle of cause and effect. . . . To begin with, an adequate scheme should be based directly upon . . . agencies. . . . All products must find accurate expression in terms of *the agencies.* . . . The primary groupings of the . . . processes must be based, therefore, upon the manner in which these agencies affect the . . . materials. . . . Constructive and destructive agencies can be recognized only when the phenomena are made the basis for the scheme. Processes are merely operative. If coupled with products at all, in classification, all must be regarded as formative or constructive. The product's destruction, its loss of identity, is wholly immaterial. The action of agencies is merely to produce constant change."

Van Hise ('04) has formulated other principles of the process method as follows:

"The agent is the substance containing energy which it expends in doing work upon other substances. The substance upon which work is done may thereby receive energy, and thus become an agent which does work upon other substances; and so on indefinitely. Indeed, the rule is that one process follows another in the sequence of events, until the energy concerned becomes so dispersed as to be no longer traceable. Theoretically this goes on indefinitely. . . . We have seen that the action of one or more agents through the exertion of force and the expenditure of energy upon one or more substances is a geological process. It is rare indeed, if it ever happens, that a single agent works through a single force upon a single substance. . . . If geology is to be simplified, the processes must be analyzed and classified in terms of energies, agents, and results. Each of the classes of energy and agent should be taken up, and the different kinds of work done by it discussed. . . . The general work of each of the agents and the results accomplished should be similarly considered. Not only so, but the work of the different forms that each of the agents takes should be separately treated. Thus, besides considering the work of water generally, the work which it does both running and standing must be treated. The first involves the work of streams; the second, the work of lakes and oceans. This involves the treatment of streams as entities. . . . The treatment of the agents will be more satisfactory in proportion as the work done by each of the forms of each of the agents is explained under physical and chemical principles in the terms of energy."

Viewed from this standpoint it is remarkable how many of our current zoological conceptions are essentially static, and how confused are our conceptions of the process method. Physiology is supposed to be devoted solely to processes, yet physiologists use the terms anabolism and katabolism, constructive and destructive influences, and, likewise, zoologists frequently use the expressions "the friends" or "the enemies" of animals—a dual terminology which has a certain utility but which exists mainly on account of the static conceptions of organic relations.

The dynamic or process concept is a difficult one to attain, and to apply in all cases, as any one will soon learn if he strives to do this consistently; and yet as a scientific ideal there can be no doubt that it has the same superiority over the older static methods and point of view that an explanation has over an empirical description.

3. DYNAMIC AND GENETIC CLASSIFICATION OF ENVIRONMENTS

In the natural history sciences we have two main sorts of classifications of phenomena, those which we call "natural" and those which we call "artificial." Natural classifications are those in which the basal criteria are of *origin,* the method of processes or genesis. A classification of lakes upon the basis of the *processes which operated in their origin*—crustal movements of the earth, the meanders of streams, the work of an ice-sheet, volcanic activity, etc.—would at the same time furnish an *explanation of them in terms of their origin.* Artificial classifications are those in which the criteria are arbitrarily chosen. Any character may be made the basis for an artificial classification. Thus lakes may be classified upon the basis of their size, depth, color of the water, distance from cities, number of boats upon them, etc., but such classification would not furnish the basis for a *scientific explanation of lakes.* The artificial is often useful or convenient for a special purpose; the genetic is illuminating from the standpoint of *scientific interpretation.* This method may be applied to any kind of environment, physical, physical and biological combined, or solely biological. To the degree that the environment is dominated by the physical conditions the laws of physical change and physical genesis will preponderate in the origin of such environments, and corresponding relations apply to biological environments.

The dependence of the genetic method upon causes and conditions makes it impossible to divorce it from the local conditions. This is at once the strength and weakness of this method, for it is particular, and generalized averages mean little because origins are different under different conditions; this is the key to *individuality.* Thus streams viewed as stages in the progressive transformation of a liquid medium for life, may be formed in many diverse ways, and for this reason the general principles of the method of genesis may be expressed most simply in an *ideal case.* Genetic series are *unending,* they extend into the past and will continue in the future. The point of departure for study must therefore be arbitrarily chosen, and the more nearly a nat ural basis can be approximated the simpler its application becomes

For this reason a cycle will be followed here which begins with a condition of *stress,* advances through the *process of adjustment to strain,* and reaches a *condition of relative equilibrium.* The starting point in such a cycle we will consider as the *original conditions,* and the later activities as the derived ones. The original conditions we will assume to be an uplifted undulating plain, composed of relatively homogeneous materials, in a humid climate, and covered by a varied vegetation including trees. The elevated condition of the land produces a condition of *unstable equilibrium* or *stress* for the rain falling upon its surface; and, furthermore, the vegetation will tend to spread over the entire surface, and thus exert a certain pressure also These original conditions are, therefore, unstable and destined to change, and mutually to influence and regulate one another.

If we now imagine the rain "turned on" under such conditions, what are the main processes which will operate? The rain falling in a depression will be supplemented by that which drains from the elevations; thus, through the *agency* of running water, a standing water habitat will have its origin. With this concentration of water will come also a burden of debris from the upland; and in this way the "constructive" and "destructive" processes will begin at the same time. Plants will invade such a depression and add their remains. Some of the depressions will overflow and the outflowing streams will cut down the outlet to progressively lower levels, and ultimately drain the basin. On the other hand, inwash and organic debris may together accumulate at such a rate as to raise the level of the basin above ground water and thus transform the conditions to that of land. The progressive stages of the *process of degradation* thus favor the transformation of the depression and a progressive formation of lakes, which are converted into ponds and swamps and ultimately, with drainage, to dry land. For depressions we thus get a genetic series which we may call the lake, pond, and swamp series. This does not classify the depression series according to size, depth, character of water, etc., as in an artificial classification, but in the *order of their development or genesis* through the *agency* of running water. Accompanying this *sequence* there are of course changes in size, depth, etc., but these are subordinated in the classification to the *developmental sequence centering about the process of the degradation of the land by the agency of running water.* This is therefore a classification of environments, not on the basis of the product, as it might appear from calling it a depression or standing-water series, but upon the *basis of the activity or processes of the dominant agent.*

We will assume that all the lakes, ponds, and swamps, due to the original relief of the land, become drained and constructively converted into streams or dry land. Let us consider the streams, particularly those which did not develop from the lake, pond, and swamp series, in order to consider them in their simpler conditions of development.

The first shower on the new land surface, or the beginning of a cycle, forms an extensive ramification of small streamlets, their dendritic branches flowing down all slopes. With the confluence of the smaller branches the progressively larger trunks are formed, and with their increase in volume, cutting progresses; but all traces of this stream itself tend to vanish soon after the shower is over, although some water may linger in pools in the deeper depressions. These conditions form an *initial stage* in the development of the activity of running water as an animal habitat. These temporary streams are rain waters intermingled with dust from the air and soil from the ground. Since, viewed chemically, such waters have not existed as a liquid long enough to dissolve much gaseous and solid material, they represent a relatively original condition, or an initial stage in the chemical development of the stream as a medium for living animals. Again and again these showers are repeated, and where there is a slight variation in the hardness of the substratum small pools are formed on the softer materials, where erosion is more rapid. In these pools it is possible for some aquatic or amphibious animals, of marked powers of dispersal, to become lodged, or even entrapped, as in the case of animals which migrate up the stream during its temporary flow; such pools, in fact, may be reached even by individuals from the ground water.

Finally these temporary streams cut down to ground-water level and become permanent. Such a stream then, in addition to the fresh rain-water which it receives with each shower, has a permanent supply of ground water. This water, having filtered through the soil, contains both gas, particularly CO_2, and minerals, and thus as a solution differs much from rain water. The composition of ground water varies much with the chemical differences of the substratum. Such water generally contains enough substance in solution to be a favorable medium for plant growth, such as algæ—aquatic pioneers which are comparable to the lichens in their invasion upon bare rock. But the temporary flow of water is still dominant, and will remain so until the supply of permanent ground water is of such a volume that, having a good current, it rushes over the obstacles in its path; then a permanent brook has been evolved, and a permanent rapid-water habitat has originated.

As the erosion of the stream advances, organic debris not only multiplies indigenously in the water, but it is also washed and blown in, and through its decay the composition of the water is changed.

particularly in the amount of CO_2 present. This gas causes the water to take into solution a greater amount of lime; and at the same time the agitation to which it is subjected while dashing over obstacles or flowing over falls increases the amount of oxygen present, a process further aided by the oxygen set free in it by water plants. Carbonic acid, moreover, is set free by the rapids and falls. It is thus very evident that the chemical processes are undergoing an important development as the stream progresses, since there are going on both the process of gaseous equilibrium with the air, and an increase of the solids in solution. The stream is progressively becoming a more favorable or enriched culture medium for organisms. The rapidly flowing water which characterizes the brook is the predominant physical feature of this environment, the stretches of relatively quiet water which form the pools, between the more rapidly flowing parts, anticipating the kind of conditions which are destined to increase with the transformation of the brook conditions into those of a creek. With the progress of development in drainage a brook is progressively transformed by the processes of erosion into a creek. Here the rapid-water conditions are more nearly equaled by a corresponding enlargement of the pool or the quieter stretches of water, where the finer sediments are deposited and the animals dwelling on the surface film or in the mud and sand, find suitable conditions. The falls and rapids which characterize the brook are exceptional in the creek, but may linger where the rate of change has been very slow on account of the resistance of the substratum. The alternation of rapid and slower water, which characterizes the creek stage, with the preponderance of the relatively rapidly flowing water, is gradually transformed into that of a river, where the water flows at a slower rate and rapids and falls have as a rule become extinct, and where a condition of relative chemical equilibrium has also been reached. Here the burden of coarse debris is at a minimum, and the surface, sides, and bottom of the stream, have become differentiated as relatively distinct habitats. With progressive approach toward baselevel all conditions of the environment tend to become more stable and equalized until the stream erodes to tide level, becomes brackish and finally as salt as the sea itself, and reaches an equilibrium determined by the dominant animal environment upon the earth—that of the sea.

We have now outlined the developmental sequence of wet depressions, the lake-pond-swamp series, and the running water, the brook-creek-river series, these two series including the main inland animal environments in a liquid medium in a humid climate. We have yet to consider the animal environments of land animals proper, those which live in the gaseous medium of air. The complexity of conditions upon land is much greater than that in water, either fresh or salt. In other words the land habitats are the most complex on earth. For simplicity in handling this involved problem, an ideal series will also be followed, and instead of attempting to discuss all the principles involved, only such will be mentioned as may be illustrated by a single example. This will serve to show the application of the method. We shall consider the process of degradation of the land, such as might be developed during a topographic cycle of erosion, and as applied to a snow-capped conical mountain in a temperate humid region.

Let us consider the series of processes which operate upon such a mountain. The snow and rain which fall upon it are in unstable equilibrium, the snow creeps or plunges down the slopes, and the water flows down. In the zone of ice and snow physical and mechanical changes preponderate; but at lower altitudes, with the melting of the snow and ice, on account of the higher temperature, chemical changes become more prominent and supplement the mechanical work of running water. Here, also, plants and animals become an important factor in modifying the processes of change by hastening or retarding the processes of degradation. We thus see that on different parts of a mountain there are important modifications in the processes of degradation. The same general processes which operate to form lakes, ponds, swamps, brooks, creeks, and rivers, are also at the same time producing changes in the land habitats. The entire surface of such a mountain is undergoing change, but because of the concentration of degradative progress near its base, particularly on account of the concentration of the drainage there, ravines and valleys develop here more rapidly and converge toward the main divide, the mountain top. As these ravines and valleys enlarge, the mountain is lowered; and ultimately all is reduced to a plain, and to baselevel. The condition of stress which existed upon the slopes of such a mountain as degradation progressed, became relatively adjusted *at that place*, but where the degraded materials were deposited a stress was *becoming cumulative*, and it is this ever changing adjustment of stresses which makes natural processes unending.

With the degradation of the mountain, progressively higher zones are lowered; the snow cap disappears; the region above the tree limit, and later the lower parts, are spread over a large area, and the mountainous character is largely gone. In this manner and at the same time as the land is degraded to a lowland by running water, in the water itself a series of habitats is developing, and thus *all the environment is being transformed, along relatively distinct but mutually interdependent lines, toward the same general direction or condition*—a relative equilibrium resulting from the balancing of all stresses near sea level.

In the preceding discussion no emphasis has been placed on the fact that degradation of the land is only a part of a large cycle of activity, and that the deposition of the degraded materials may be a cause of so much stress as to initiate an elevation of the land. If the heavy soluble materials from the land are washed into the sea and only lighter materials remain behind, the increased stress resulting between the sea and the land will tend to elevate the lighter areas until an equilibrium is established between the heavy sea and the lighter land; therefore, some crustal movements, at least, may be complementary phases of the degradation of the land. The elevations and depressions of the surface of the land with regard to the sea level may thus initiate new cycles of transformation in all environments. These processes do not need amplification here, although they should be noted; but this lack of amplification does not imply a minor influence of this factor. Still another cycle may be initiated by the processes of vulcanism, a factor the influence of which is easily overlooked in large parts of the world but in others is very prominent. Only one more comprehensive physical factor will be mentioned; that due to alterations in the atmosphere—climatic changes. Although the temperate humid climate has been made the basis for the preceding discussion, it must be remembered not only that there are other kinds of climates, but that these undergo transformation or changes from such extremes as the cold arctic deserts on the one hand, to the dry hot deserts on the other. Within this great amplitude of climatic possibility is found one of the greatest causes both of complexity in land environment and of many local differences in the transformation of habitats.

To simplify this sketch of the operation of the physical features of the environment the organic factors have been neglected, and these should now be considered. On account of the ultimate dependence of animals for food upon vegetation, many intimate relations exist between plants and animals; furthermore, in addition to the food relations there are many other important ones, such as the physical and chemical influence of the vegetation upon the soil, its influence upon the temperature and humidity of the air and on light; and, finally, there is qualification of these influences by the different kinds of vegetation. A vegetational cover of grass has a very different effect from one of shrubs or a forest cover; conifers and hard-wood forests differ in effect also; and the succession of plant societies varies, not only with different kinds of vegetation but also in different climates, and with different physiographic conditions. As Cowles ('11) has shown, there are several cycles or series of successions of vegetation. Many of these changes are dependent upon physical conditions which are equally potent in their influence upon animals. Thus physical and vegetational changes in combination influence animals directly and indirectly, and in the conditions due to this fact we find the basis for the important control which vegetation exerts upon animals.

Animals themselves form an important part of their own environment, not only in their relation to their own kind, as mates or as progeny, but also as members of an animal community whose members must adjust their activities to one another through symbiotic, competitive, or predatory relations. If any animal becomes abnormally abundant, that is, more numerous than the conditions can support, this number in itself becomes a weakness, through the positive attraction of the organisms (plant and animal) which are able to prey upon it, and soon the normal abundance is restored. For example, in a coniferous forest, bark-beetles (*Scolytoidea*) may increase to such an extent that the forest is largely destroyed, and a succession is produced in the vegetation as the conifers are replaced by a growth of aspen and birch. As a result of this destruction of the kind of food and habitat essential for the next generation of beetles, a proper habitat is lacking, and the restoration of the normal number of beetles is hastened. This same example also shows how one kind of animal may influence the character of a whole community by its control over the vegetation.

The influence of man must be looked on from the same standpoint as one views the activity of any other animal; as that of a member of an animal community. He hastens and retards the changes in his environment as do other animals. In general his early methods are predatory; he reaps where he does not sow; but later the milder competitive and symbiotic relations and the constructive or productive aspect become more prominent. Civilization is an attempt to make the environment "to order," but as yet man has not learned how to produce a permanent "optimum" along the lines of an ecological community. As has already been said, to understand man we should view him as an integral part of an ecological community, as one member of a biotic community of plants and animals, or at least of an animal community which includes all animals that are influenced by man—and not consider him, as some students do, as a distinct entity with little regard to his animal and plant associates.

The main features of the preceding discussion may be summarized as in the following table.

TABLE 2.—THE GENESIS AND FORMATION OF INLAND HABITATS IN A HUMID CLIMATE AND THE DYNAMIC STATUS OF THE PROCESSES

Dynamic status.	Phases in the formation of inland environments.				
I. Unstable equilibrium—condition of stress or pressure	*Original conditions;* elevated land area, or new land surface, or beginning of new cycle.				
II. Process of adjustment to stress or strain.	Process of *formation* of habitats; all habits are *constructive.*				
(The following are examples of the major processes): 1. The processes of degradation of the land. 2. The processes of adjustment to climate. 3. The process of the establishment of biotic (plant or animal) dominance.	Sequence of stream habitats, depression series; partly reversible.	Temporary stream	Brook	Creek	River
	Sequence of land habitats, elevation series; reversible process.	Upland	Lowland		Baseleveled plain
	Sequence of standing water series (depression series); reversible series.	Lake	Pond	Swamp	Drained land
	Biotic sequence in all habitats and all series, as a *part* of the animal environment.	Initial phase	Intermediate phase		Dominant phase
III. Relative equilibrium.	*Derived conditions;* lowland area, old land surface (baseleveled to the marine environment), end of a cycle, or dominance; under relatively stable conditions.				

The preceding discussion is based upon the conditions of a humid climate, but the semi-arid and the arid climates should also be touched on. In time, as ecological studies are extended to all kinds of land areas, it will be possible to formulate all of the general principles ot the origin or process of development of land habitats; but at present vast areas of the land have never been observed by a zoologist from a modern ecological standpoint. Most of the ecological studies of animals have been carried on in a humid climate, only slight attention having been given to the ecological relations existing in an arid climate, and still less to those in alpine and polar regions. After the humid regions have been better studied, the arid regions will probably be the next to be carefully investigated. The plant ecologists, by their studies in these regions, have already furnished important facts preparing the way for the animal ecologist, because they investigate both the physical and vegetational conditions upon the prairies and plains of the West. If the regions of progressively increasing aridity are examined, there will be found to be a corresponding series of changes in the animal habitats. The standing-water series of habitats found in such a series, in contrast with those of humid regions with fresh-water lakes, ponds, and swamps in addition to the temporary fresh waters, are alkaline and salt waters, and we find an extensive series ranging from Great Salt Lake, Salton Sea, and Devil's Lake, to strong briny pools and alkaline mud flats. These are, of course, as capable of a genetic treatment as are the corresponding fresh-water bodies of humid areas. The stream series is also present in the arid region, but it exists under conditions quite different from those in humid areas. The through-flowing streams are *relatively* independent of local conditions because their main supply of water is from the mountain; but they are nevertheless much modified by the character and amount of the burden which they carry during the time of high water, and they tend to become clogged at low water stages. The chemical composition of such waters is quite different from that of regions continually leached by rains. The small streams flowing from the mountains, whose diminishing volume does not allow them to traverse the arid regions, succumb, and disappear in the dry earth—examples of a second degree of dominance of the desert or plains. But the truly characteristic streams of the arid regions are those primarily dependent upon the desert conditions. Such streams are well within the arid regions and are dominated wholly by them. They are solely of a temporary character, and correspond to the initial stage of stream development, the temporary stream, in a humid climate. In an arid climate, however, development does not proceed beyond this early stage, and the degradation and baseleveling of the land is due to the combined influence of water and the wind.

On land, the movements of the soil by the wind, as in the sand-dune regions of true deserts, show us a characteristic condition; in a more humid climate, however, the dunes would tend to become anchored by vegetation. Other soils than sand are also blown about. The extreme of dry desert conditions must be looked upon as the ultimate or climax condition, a condition of relative equilibrium, under present climatic conditions, for certain regions. A slight departure from these extreme conditions is seen in such localities as receive most abundant showers during the growing season for vegetation. These are able to influence the development of the drainage only in a minor way, but they moisten a shallow surface layer of soil and permit the growth of short grasses, such as the buffalo-grass (Schantz, '11 : 40). Very recently another important source of water in the arid regions has come to be recognized. This, McGee has shown to be the subsurface or artesian waters which come up from below; and this is an important supplementary source of moisture in extensive areas in the arid West (McGee, '13), where the evaporation is large. It is not unlikely that even in humid regions where the soils are very sandy, as upon the Coastal Plain, and where the strata dip in such a manner as to favor an underflow of water, this supply may be of considerable importance to the biota. With a greater rainfall during the growing season, permitting a relative humidity greater than on the short-grass area of the plains, a deeper-rooted vegetational cover gives us the long prairie grasses of the eastern prairie.

As soon as the physical conditions permit a growth of vegetation this material becomes an environmental factor which reflexly modifies the physical conditions of the air, the soil, and the animal habitat. This is shown to a marked degree in the humid area of the southeastern United States, where the rainfall, greater than that on the arid plains and prairies, favors the development of a forest cover. Such a forest not only tends to retard evaporation but also acts as a sponge and by its vegetable debris and loose soil retards the run-off. In this manner not only are land habitats influenced, but this conservation of moisture tends to prolong the duration of temporary streams, and to stabilize the flow of permanent ones; and, further, through the same influence, the ground-water level declines slowly, and bodies of standing water are also influenced. Thus all the more important habitats are to some degree regulated and made more stable by a forest cover.

The foregoing discussion and examples, selected from the activities of animals and changes in their environments, are varied enough to show how diverse are the applications of the process method to investigation. The general idea is easily grasped, but to make the dynamic method a regular habitual procedure in investigation is truly difficult, so difficult, indeed, that there is reasonable ground for doubting if this method can be mastered without a practical application of it to a concrete problem, at the same time giving special attention to the method of procedure.

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