It must be remembered that we admit the essential uniformity of vegetation within a single community, and the frequent striking uniformity between adjacent communities. But the fact that these small cumulative differences do exist is basically important in the consideration of the general concept of the plant-association. They indicate that each community, and for that matter each fraction of one, is the product of its own independent causative factors, that each community in what we now choose to call an association-type is independent of every other one, except as a possible source of immigrating species. With no genetic connection, with no dynamic connection, with only superficial or accidental similarity, how can we logically class such a series of communities into a definite association-type? Truly the plant community is an individualistic phenomenon.

Every species of plant and animal migrates, whether as a mature individual, as many species of animals, or as a reproductive body, as the vast majority of plants. Among animals, migration is sometimes selective in its direction and goal, as illustrated by birds which follow definite routes to definite established breeding grounds. With other animals and with all plants, migration is purely fortuitous. It progresses by various means, it brings the organisms into various places and to varying distances, but only those organisms which have reached a favorable environment are able to continue their life. Into this favorable environment other species also immigrate, and from all of the arrivals the environment selects those species which may live and dooms the others.

In this migration each migrating body acts for itself and moves by itself, almost always completely independent of other species. The idea of an association migrating *en masse* and later reproducing itself faithfully is entirely without foundation. Those cases in which there is a semblance of such a condition are caused by the proximity of the original association and the advantage which its species therefore have in migration. Even then, certain species always precede and certain others lag behind.



CHAPTER 3

# The Use and Abuse of Vegetational Concepts and Terms

## Arthur G. Tansley

It is now generally admitted by plant ecologists, not only that vegetation is constantly undergoing various kinds of change, but that the increasing habit of concentrating attention on these changes instead of studying plant communities as if they were static entities is leading to a far deeper insight into the nature of vegetation and the parts it plays in the world. A great part of vegetational change is generally known as *succession,* which has become a recognized technical term in ecology, though there still seems to be some difference of opinion as to the proper limits of its connotation; and it is the study of succession in the widest sense which has contributed and is contributing more than any other single line of investigation to the deeper knowledge alluded to. . . .

In 1920 and in 1926 I wrote general articles [published in 1920 and 1929, respectively] on this and some related topics. My return to the subject today is immediately stimulated by the appearance of Professor John Phillips's three articles in the *Journal of Ecology* (1934, 1935a, 1935b) which seem to me to call rather urgently for comment and criticism. At the same time I shall take the opportunity of trying to clarify some of the logical foundations of modern vegetational theory.

If some of my comments are blunt and provocative I am sure my old friend Dr. Clements and my younger friend Professor Phillips will forgive me. Bluntness makes for conciseness and has other advantages, always provided that it is not malicious and does not overstep the line which separates it from rudeness. And at the outset let me express my conviction that Dr. Clements has given us a theory of vegetation which has formed an indispensable foundation for the most fruitful modern work. With some parts of that theory and of its expression, however, I have never agreed, and when it is pushed to its logical limit and perhaps beyond, as by Professor Phillips, the revolt becomes irrepressible. But I am sure nevertheless that Clements is by far the greatest indi-

From *Ecology* 16 (1935): 284–309. Notes omitted.

vidual creator of the modern science of vegetation and that history will say so. For Phillips's work too, and particularly for his intellectual energy and single-mindedness, I have a great admiration.

Phillips's articles remind one irresistibly of the exposition of a creed—of a closed system of religious or philosophical dogma. Clements appears as the major prophet and Phillips as the chief apostle, with the true apostolic fervor in abundant measure. Happily the *odium theologicum* is entirely absent: indeed the views of opponents are set out most fully and fairly, and the heresiarchs, and even the infidels, are treated with perfect courtesy. But while the survey is very complete and almost every conceivable shade of opinion which is or might be held is considered, there is a remarkable lack of any sustained criticism of opponents' arguments. Only here and there, as for instance in dealing with Gillman's and Michelmore's specific contentions, and in a few other places, does the author present scientific *arguments.* He is occupied for the most part in giving us the pure milk of the Clementsian word, in expounding and elaborating the organismal theory of vegetation. This exposition, with its very full citations and references, is a useful piece of work, but it invites attack at almost every point.

The three articles are respectively devoted to "Succession," "Development and the Climax," and "the Complex Organism." The greater part of the third article is mainly concerned with the relation of this last concept to the theory of "holism" as expounded by General Smuts [1926] and others, and is really a confession of the holistic faith. As to the repercussions of this faith on biology I shall have something to say in the sequel. But first let me deal with "Succession" and "Development and the Climax."

## Succession

My own views on succession are given fairly fully in my two papers already mentioned. In the first place I consider that the concept of succession can be given useful scientific significance only if we can trace in the sequences of vegetation "certain uniformities which we can make the subject of investigation, comparison, and the formulation of laws" (Tansley 1929). . . .

In 1926 (680) I proposed to distinguish between *autogenic succession,* in which the successive changes are brought about by the action of the plants themselves on the habitat, and *allogenic succession[,]* in which the changes are brought about by external factors. "It is true of course (I wrote) and must never be forgotten, that actual successions commonly show a mixture of these two classes of factors—the external and the internal" (678). I think now that I should have gone farther than this and applied my suggested new terms in the first place to the factors rather than to the successions. It is the fact, I think,



that autogenic and allogenic factors are present in all successions; but there is often a clear preponderance of one or the other, and where this is so we may fairly apply the terms, with any necessary qualifications, to the successions themselves. I went on to contend, as indeed I had already done in 1920 (136–39) though without using the terms, that only to autogenic succession can we apply the concept of development of what I called a "quasi-organism" (= climax vegetation), but that this developmental (or autogenic) succession is the normal typical process in the gradual production of climax vegetation.

Phillips, following Clements, contends, on the other hand, that "succession is due to biotic reactions only, and is always progressive . . . succession being developmental in nature, the process must and can be progressive only" (1934: 562); and again, "succession is the expression of development" (1935a: 214).

Now here we are concerned first of all with the use of words. If we choose to confine the use of the term *succession* to the series of phases of vegetation which lead up to a climatic climax, for example the various "priseres" from bare rock or water to forest, then it naturally follows that the process is "progressive only." If in addition we conceive of vegetation as an organism, of which the climax is the adult and the earlier phases of the prisere are successive larval forms, then also succession is clearly "developmental in nature," is "the expression of development." But if, on the other hand, we apply the term, as I do, and as I think most ecologists naturally do, to *any* series of vegetational phases following one another in one area, repeating themselves everywhere under similar conditions, and clearly due in each case to the same or a similar set of causes, then to say that "succession must and can be progressive only," or that it is always and everywhere developmental, is clearly contrary to the fact.

Most of the controversy about the possibility of "retrogressive succession" depends simply on this difference in the use of the word. It is true that Clements (1916: 146–63 [reproduced in this volume]) successfully showed that the phenomena represented by some of the looser uses of "retrogression" were more properly described as destruction of (for example) the climax phase, or of the dominants of the climax phase, a destruction which would normally initiate a subsere leading again to the climax if the vegetation were then let alone. But if on the other hand there is what Phillips would call a "continuative cause" at work which gradually leads to the degradation of vegetation to a lower type[,] it seems to me that the phenomenon is properly called retrogressive succession. Here I should include the continuous effect of grazing animals which may gradually reduce forest to grassland, the gradual leaching and concomitant raw humus formation which may ultimately reduce forest to heath, gradual increase of drainage leading to the replacement of a more luxuriant and mesophytic by a poorer and more xerophytic vegetation, or a gradual waterlogging which also leads to a change of type and usually the replacement of a "higher" by a "lower" one. All these are perfectly well-established vegetational processes. To me they are clear examples of allogenic retrogressive successions, and I cannot see how their title can be denied except by an arbitrary and unnatural limitation of the meaning of the word *succession.* All the processes mentioned certainly involve destruction, but they also involve the invasion, ecesis, and growth of new species. "Destruction" by itself is not a criterion: does not all *progressive* succession, as Cooper (1926: 402) has pointed out, involve constant destruction of the plants of the earlier phases? . . .

*Catastrophic* destruction, whether by "natural" agencies or by man, does, I think, remove the phenomena from the field of the proper connotation of succession, because catastrophes are unrelated to the causes of the vegetational changes involved in the actual process of succession. They are only initiating causes, as Clements rightly insists: they clear the field, so to speak, for a new succession. That is why I have insisted on gradualness as a character of succession. Gradualness in effect is the mark of the action of "continuative" causes.

## Development and the Quasi-Organism

The word *development* may be used in a very wide sense: thus we speak of the development of a theme or of the development of a situation, though always, I think, with the implication of becoming more complex or more explicit. Always, too, it is some kind of *entity* which develops, and in biology it is particularly to the growth and differentiation of that peculiarly well defined entity the individual organism that we apply the term. Hence we can perfectly well speak in a general way of the development of any piece of vegetation that has the character of an entity, such as marsh or forest, and in common language we actually do so; but we should use the term as part of the theory of vegetation, of a body of well-established and generally acceptable concepts and laws, only if we can recognize in vegetation a number of sufficiently well-defined entities whose development we can trace, and the laws of whose development we can formulate.

In 1920 I inquired whether we could recognize such entities in vegetation, and I analyzed the whole topic in considerable detail and with considerable care. To the best of my knowledge that analysis has not been seriously criticized or impugned, and I may be permitted to think it holds the field, though various divergent opinions unsupported by arguments have since been expressed. Briefly my conclusion was that mature well-integrated plant communities (which I identified with plant associations) had enough of the characters of organisms to be considered as *quasi-organisms,* in the same way that human societies are habitually so considered. Though plant communities are not and



cannot be so highly integrated as human societies and still less than certain animal communities such as those of termites, ants, and social bees, the comparison with an organism is not merely a loose analogy but is firmly based, at least in the case of the more complex and highly integrated communities, on the close interrelations of the parts of their structure, on their behavior as wholes, and on a whole series of other characters which Clements (1916 [reproduced in this volume]) was the first to point out. In 1926 (679) I called attention to another important similarity which, it seems to me, greatly strengthens the comparison between plant community and organism—the remarkable correspondence between the species of a plant community and the genes of an organism, both aggregates owing their "phenotypic" expression to development in the presence of all the other members of the aggregate and within a certain range of environmental conditions. But this position is far from satisfying Clements and Phillips. For them the plant community (or nowadays the "biotic community") *is* an organism, and he who does not believe it departs from the true faith. . . .

There is no need to weary the reader with a list of the points in which the biotic community does *not* resemble the single animal or plant. They are so obvious and so numerous that the dissent expressed and even the ridicule poured on the proposition that vegetation *is* an organism are easily understood. Of course Clements and Phillips reply that no one asserts that the plant community is an *individual* organism. In the more recent phrase it is a "complex organism"—a thoroughly bad term, as it seems to me, for it is firmly associated in the minds of biologists with the "higher" animals and plants—the mammals and spermaphytes [*sic*]. In any case it is, in my judgment, impossible to get the proposition generally accepted. Whether it is true or untrue depends entirely on the connotation of *organism,* and as to that the present generation of biologists have a firmly established use from which they will not depart—and I think they are right. We need a word for the peculiarly definite, sharply limited and unique type of organization embodied in the individual animal or plant, and *organism* is the accepted term. . . .

I can only conclude that the term *quasi-organism* is justified in its application to vegetation, but that the terms *organism* or *complex organism* are not.

## Climaxes

Professor Phillips's treatment of the concept of climax is open to nearly the same criticism as his treatment of succession. Just as he will only have one kind of succession, which is always progressive, and entirely caused by the "biotic reactions" of the community, so he will have only one kind of climax, the climatic climax, of which there is only one in each climatic region.

He rather ingenuously suggests that the adjective "climatic" had better be dropped: it is misleading to the uninitiated. Since there is only one kind of climax why qualify the word? The suggestion would be unanswerable if we all agreed with him! . . .

Clements realized from the first (1916 [reproduced in this volume]) that vegetation existed which was neither climatic climax nor part of a sere actually moving toward it, but might be in a permanent or quasi-permanent condition in some sense "short of" the climax, and all such vegetation he called *subclimax*. He used this term in two senses, for an actual seral stage which would normally lead to the climatic climax, and for a type of climax "subordinate to" the climatic climax. It was pointed out that this double use was undesirable, and that if we confined the term *subclimax* to the former case, terms were wanted for permanent or quasi-permanent vegetation which did not closely represent a particular phase of a sere leading to the climatic climax, but were dominated by species that did not enter into any of the "normal" seres. For such climaxes Clements has now (1934: 45) proposed the word *proclimax*, i.e., vegetation which appears *instead of* the climatic climax, or as he would say, instead of *the* climax. This I think is an unobjectionable term, but it does not specify the factors which have differentiated the different types of this sort of climax. . . .

As expounded by Phillips the "monoclimax theory" explains away the existence of what some of us are accustomed to call edaphic and physiographic climaxes within a climatic region in two ways. Either these supposed climaxes are not climaxes at all but stages in a sere leading to *the* climax, whose movement has been *retarded*, perhaps for a long time, by the edaphic or physiographic factors, or they are mere variations of "the formation" (the climatic climax). It is not to be supposed and is not in fact the case, it is argued, that either climate or soil will be absolutely uniform within a great climatic region, which often extends for many hundreds of miles. The climatic formation (*the* formation according to the "monoclimax theory") is often "a veritable mosaic" of vegetation (Clements). This of course is quite true: the only question is, *how great differences* are we to admit as mere variations within the formation? The difficulty disappears of course if we *define* a formation—a climatic climax—as *all* permanent vegetation within the climatic region and are therefore willing to swallow such differences, however great. But is this sound empirical method? [Is it] not rather a case of making the facts fit the theory? Is it not sounder scientific method *first* to recognize, describe, and study all the relationships of actually existing vegetation, and *then* to see how far they fit or do not fit any general hypothesis we may have provisionally adopted? . . .

I plead for empirical method and terminology in all work on vegetation, and avoidance of generalized interpretation based on a theory of what *must* happen because "vegetation is an organism."



## "The Complex Organism"

Professor Phillips's third article (1935b) is devoted to a discussion of the "complex organism," otherwise known as "the biotic community" (or "biome" of Clements) in the light of the doctrines of emergent evolution and of holism. On the biotic community he had already written (1931) and so also have Shelford (1931) and others.

I have already expressed a certain amount of skepticism of the soundness of the conception of the biotic community (1929: 680), without giving my reasons at all fully. It seems necessary now to state the grounds of my skepticism, and at the same time to make clear that I am not by any means wholly opposed to the ideas involved, though I think that these are more naturally expressed in another way.

On linguistic grounds I dislike the term biotic *community*. A "community," I think it will be generally agreed, implies *members*, and it seems to me that to lump animals and plants together as *members* of a community is to put on an equal footing things which in their whole nature and behavior are too different. Animals and plants are not common members of anything except the organic world (in the biological, not the "organicist" sense). One would not speak of the potato plants and ornamental trees and flowers in the gardens of a human community as *members* of that community, although they certainly enter into its constitution—it would be different without them. There must be some sort of *similarity*, though not of course *identity*, of nature and status between the members of a community if the term is not to be divorced too completely from its common meaning. . . .

Animal ecologists in their field work constantly find it necessary to speak of *different* animal communities living in or on a given plant community, and this is a much more natural conception, formed in the proper empirical manner as a direct description of experience, than the "biotic community." Some of the animals belonging to these various animal communities have very restricted habitats, others much wider ones, while others again such as the larger and more active predaceous birds and mammals range freely not only through an entire plant community but far outside its limits. For these reasons also, the practical necessity in field work of separating and independently studying the animal communities of a "biome," and for some purposes the necessity of regarding them as external factors acting on the plant community—I cannot accept the concept of the *biotic* community.

This refusal is[,] however[,] far from meaning that I do not realize that various "biomes," the whole webs of life adjusted to particular complexes of environmental factors, are real "wholes," often highly integrated wholes, which are the living nuclei of *systems* in the sense of the physicist. Only I do not think they are properly described as "organisms" (except in the "organicist" sense). I prefer to regard them, together with the whole of the effective physical factors involved, simply as "*systems.*"

I have already criticized the term *organism* as applied to communities of plants or animals, or to "communities" of plants *and* animals, on the ground that while these aggregations have *some* of the qualities of organisms (in the biological sense) they are too different from these to receive the same unqualified appellation. And I have criticized the term *complex organism* on the ground that it is already commonly applied to the species or individuals of the higher animals and plants. Professor Phillips's third article (1935b) is largely devoted to an exposition and defense of the concept of "the complex organism." According to the organicist philosophy, which he seems to espouse, though he does not specifically say so, he is perfectly justified in calling the whole formed by an integrated aggregate of animals and plants (the "biocenosis," to use the continental term) an "organism," provided that he includes the physical factors of the habitat in his conception. But then he must also call the universe an organism, and the solar system, and the sugar molecule, and the ion or free atom. They are all organized "wholes." The nature of what biologists call living organisms is wholly irrelevant to this concept. They are merely a special kind of "organism."

With the philosophical aspects of Phillips's discussion I cannot possibly deal adequately here. They involve, as indeed he recognizes, some of the most difficult and elusive problems of philosophy. The doctrine of "emergent evolution," stated in a particular way, I hold to be perfectly sound, and some, though not all, of the ideas contained in Smuts's [1926] holism I think are acceptable and useful. But on the scientific, as distinct from the philosophical plane, I do think a good deal of fuss is being made about very little. For example—"newness springing from the interaction, interrelation, integration and organisation of qualities . . . could not be predicted from the sum of the particular qualities or kinds of qualities concerned: integration of the qualities thus results in the development of a whole different from, unpredictable from, their mere summation." Can one in fact form any clear conception of what "mere summation" can mean, as contrasted with the actual relations and interactions observed between the components of an integrated system? Has "mere summation" any meaning at all in this connection? What we *observe* is juxtaposition and interaction, with the resulting emergence of what we call (and I agree *must* call) a "new" entity. And who will be so bold as to say that this new entity,



for example the molecule of water and its qualities, would be unpredictable, if we really understood *all* the properties of hydrogen and oxygen atoms and the forces brought into play by their union? Unpredictable by us with our present knowledge, yes; but *theoretically* unpredictable, surely not. When an inventor makes a new machine, he is just as certainly making a new entity, but he can predict with accuracy what it will be and what it will do, because within the limits of his purpose he *does* understand the whole of the relevant properties of his materials and knows what their interactions will be, given a particular set of spatial relations which he arranges.

In discussing General Smuts's doctrine of "holism" Phillips lays stress on the whole as a *cause,* "'holism' is called the fundamental factor operative towards the creation of wholes in the universe." It is an "operative cause" and an "inherent, dynamic characteristic" in communities. All but those who take "a static view of the structure, composition and life of communities—cannot fail to be impressed with the fundamental nature of the *factor of holism* innate in the very being of community, a factor of *cause*" (italics in the original). . . .

Is the community then the "cause" of its own activities? Here we touch the very difficult philosophical question of the meaning of causation, which I cannot possibly attempt to discuss here. In a certain sense however, the community as a whole may be said to be the "cause" of its own activities, because it represents the aggregation of components the sum (or more properly the synthesis) of whose actions we call the activities of the community—actions which would not be what they are unless the components were associated in the way in which they are associated. So far we may concede Phillips's contention. But it is important to remember that these activities of the community are *in analysis* nothing but the synthesized actions of the components in association. We have simply shifted our point of view and are contemplating a new entity, so that we now, quite properly, regard the totality of actions as the activity of a higher unit.

It is difficult to resist the impression that Professor Phillips's enthusiastic advocacy of holism is not wholly derived from an objective contemplation of the facts of nature, but is at least partly [motivated] by an imagined future "whole" to be realized in an ideal human society whose reflected glamour falls on less exalted wholes, illuminating with a false light the image of the "complex organism."

## The Ecosystem

I have already given my reasons for rejecting the terms *complex organism* and *biotic community.* Clements's earlier term *biome* for the whole complex of organisms inhabiting a given region is unobjectionable, and for some purposes convenient. But the more fundamental conception is, as it seems to me, the whole *system* (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense. Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system.

It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. Our natural human prejudices force us to consider the organisms (in the sense of the biologist) as the most important parts of these systems, but certainly the inorganic "factors" are also parts—there could be no systems without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and the inorganic. These *ecosystems*, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom. The whole method of science, as H. Levy (1932) has most convincingly pointed out, is to isolate systems mentally for the purposes of study, so that the series of *isolates* we make become the actual objects of our study, whether the isolate be a solar system, a planet, a climatic region, a plant or animal community, an individual organism, an organic molecule, or an atom. Actually the systems we isolate mentally are not only included as parts of larger ones, but they also overlap, interlock, and interact with one another. The isolation is partly artificial, but is the only possible way in which we can proceed.

Some of the systems are more isolated in nature, more autonomous, than others. They all show organization, which is the inevitable result of the interactions and consequent mutual adjustment of their components. If organization of the possible elements of a system does not result, no system forms or an incipient system breaks up. There is in fact a kind of natural selection of incipient systems, and those which can attain the most stable equilibrium survive the longest. It is in this way that the dynamic equilibrium, of which Professor Phillips writes, is attained. The universal tendency to the evolution of dynamic equilibria has long been recognized. A corresponding idea was fully worked out by Hume and even stated by Lucretius. The more relatively separate and autonomous the system, the more highly integrated it is, and the greater the stability of its dynamic equilibrium.

Some systems develop gradually, steadily becoming more highly integrated and more delicately adjusted in equilibrium. The ecosystems are of this kind, and the normal autogenic succession is a progress toward greater integration and stability. The "climax" represents the highest stage of integration and



the nearest approach to perfect dynamic equilibrium that can be attained in a system developed under the given conditions and with the available components.

The great regional climatic complexes of the world are important determinants of the primary terrestrial ecosystems, and they contribute *parts* (components) to the systems, just as do the soils and the organisms. In any fundamental consideration of the ecosystem it is arbitrary and misleading to abstract the climatic factors, though for purposes of separation and classification of systems it is a legitimate procedure. In fact the climatic complex has more effect on the organisms and on the soil of an ecosystem than these have on the climatic complex, but the reciprocal action is not wholly absent. Climate acts on the ecosystem rather like an acid or an alkaline "buffer" on a chemical soil complex.

Next comes the soil complex which is created and developed partly by the subjacent rock, partly by climate, and partly by the biome. Relative maturity of the soil complex, conditioned alike by climate, by subsoil, by physiography, and by the vegetation, may be reached at a different time from that at which the vegetation attains its climax. Owing to the much greater local variation of subsoil and physiography than of climate, and to the fact that some of the existing variants prevent the climatic factors from playing the full part of which they are capable, the developing soil complex, jointly with climate, may determine variants of the biome. Phillips's contention that soil never does this is too flatly contrary to the experience of too many ecologists to be admitted. Hence we must recognize ecosystems differentiated by soil complexes, subordinate to those primarily determined by climate, but none the less real.

Finally comes the organism-complex or biome, in which the vegetation is of primary importance, except in certain cases, for example many marine ecosystems. The primary importance of vegetation is what we should expect when we consider the complete dependence, direct or indirect, of animals upon plants. This fact cannot be altered or gainsaid, however loud the trumpets of the "biotic community" are blown. This is not to say that animals may not have important effects on the vegetation and thus on the whole organism-complex. They may even alter the primary structure of the climax vegetation, but usually they certainly do not. By all means let animal and plant ecologists study the composition, structure, and behavior of the biome together. Until they have done so we shall not be in possession of the facts which alone will enable us to get a true and complete picture of the life of the biome, for both animals and plants are components. But is it really necessary to formulate the unnatural conception of biotic *community* to get such cooperative work carried out? I think not. What we have to deal with is a *system*, of which plants and animals are components, though not the only components. The biome is determined by climate and soil and in its turn reacts, sometimes and to some extent on climate, always on soil.

Clements's "prisere" (1916 [reproduced in this volume]) is the gradual development of an ecosystem as we may see it taking place before us today. The gradual attainment of more complete dynamic equilibrium (which Phillips quite rightly stresses) is the fundamental characteristic of this development. It is a particular case of the universal process of the evolution of systems in dynamic equilibrium. The equilibrium attained is however never quite perfect: its degree of perfection is measured by its stability. The atoms of the chemical elements of low atomic number are examples of exceptionally stable systems—they have existed for many millions of millennia: those of the radioactive elements are decidedly less stable. But the order of stability of all the chemical elements is of course immensely higher than that of an ecosystem, which consists of components that are themselves more or less unstable—climate, soil, and organisms. Relatively to the more stable systems the ecosystems are extremely vulnerable, both on account of their own unstable components and because they are very liable to invasion by the components of other systems. Nevertheless some of the fully developed systems—the "climaxes"—have actually maintained themselves for thousands of years. In others there are elements whose slow change will ultimately bring about the disintegration of the system.

This relative instability of the ecosystem, due to the imperfections of its equilibrium, is of all degrees of magnitude, and our means of appreciating and measuring it are still very rudimentary. Many systems (represented by vegetation climaxes) which appear to be stable during the period for which they have been under accurate observation may in reality have been slowly changing all the time, because the changes effected have been too slight to be noted by observers. Many ecologists hold that *all* vegetation is *always* changing. It may be so: we do not know enough either to affirm or to deny so sweeping a statement. But there may clearly be minor changes within a system which do not bring about the destruction of the system as such.

Owing to the position of the climate-complexes as primary determinants of the major ecosystems, a marked change of climate must bring about destruction of the ecosystem of any given geographical region, and its replacement by another. This is the *clisere* of Clements (1916 [reproduced in this volume]). If a continental ice sheet slowly and continuously advances or recedes over a considerable period of time all the zoned climaxes which are subjected to the decreasing or increasing temperature will, according to Clements's conception, move across the continent "as if they were strung on a string," much as the plant communities zoned round a lake will move toward its center as the lake fills up. If on the other hand a whole continent desiccates or freezes[,] many of



the ecosystems which formerly occupied it will be destroyed altogether. Thus whereas the prisere is the development of a single ecosystem *in situ*, the clisere involves their destruction or bodily shifting.

When we consider long periods of geological time we must naturally also take into account the progressive evolution and rise to dominance of new types of organism and the decline and disappearance of older types. From the earlier Paleozoic, where we get the first glimpses of the constitution of the organic world, through the later Paleozoic where we can form some fairly comprehensive picture of what it was like, through the Mesozoic where we witness the decline and dying out of the dominant Paleozoic groups and the rise to prominence of others, the Tertiary with its overwhelming dominance of Angiosperms, and finally the Pleistocene ice age with its disastrous results for much of the life of the northern hemisphere, the shifting panorama of the organic world presents us with an infinitely complex history of the formation and destruction of ecosystems, conditioned not only by radical changes of land surface and climate but by the supply of constantly fresh organic components. We can never hope to achieve more than a fragmentary view of this history, though doubtless our knowledge will be very greatly extended in the future, as it has been already notably extended during the last thirty years. In detail the initiation and development of the ecosystems in past times must have been governed by the same principles that we can recognize today. But we gain nothing by trying to envisage in the same concepts such very different processes as are involved in the shifting or destruction of ecosystems on the one hand and the development of individual systems on the other. It is true, as Cooper insists (1926), that the changes of vegetation on the earth's surface form a continuous story: they form in fact only a part of the story of the changes of the surface of this planet. But to analyze them effectively we must split up the story and try to focus its phases according to the various kinds of process involved.

## Biotic Factors

Professor Phillips makes a point of separating the effect of grazing herbivorous animals *naturally* belonging to the "biotic community," e.g., the bison of the North American prairie or the antelopes, etc., of the South African veld, from the effect of grazing animals introduced by man. The former are said to have cooperated in the production of the short-grass vegetation of the Great Plains, which has even been called the *Bison-Bouteloa* climax, and to have kept back the forest from invading the edges of the grassland formation. The latter are supposed to be merely destructive in their effects, and to play no part in any successional or developmental process. This is perhaps legitimate as a description of the ecosystems of the world before the advent of man, or rather with the activities of man deliberately ignored. It is obvious that modern civilized man upsets the "natural" ecosystems or "biotic communities" on a very large scale. But it would be difficult, not to say impossible, to draw a natural line between the activities of the human tribes which presumably fitted into and formed parts of "biotic communities" and the destructive human activities of the modern world. Is man part of "nature" or not? Can his existence be harmonized with the conception of the "complex organism"? Regarded as an exceptionally powerful biotic factor which increasingly upsets the equilibrium of preexisting ecosystems and eventually destroys them, at the same time forming new ones of very different nature, human activity finds its proper place in ecology.

As an ecological factor acting on vegetation the effect of grazing heavy enough to prevent the development of woody plants is essentially the same effect wherever it occurs. If such grazing exists the grazing animals are an important factor in the biome . . . whether they came by themselves or were introduced by man. The dynamic equilibrium maintained is primarily an equilibrium between the grazing animals and the grasses and other hemicryptophytes which can exist and flourish although they are continually eaten back.

Forest may be converted into grassland by grazing animals. The substitution of the one type of vegetation for the other involves destruction of course, but not merely destruction: it also involves the appearance and gradual establishment of new vegetation. It is a successional process culminating in a climax under the influence of the actual combination of factors present and since this climax is a well-defined entity it is also the development of that entity. It is true of course that when man introduces sheep and cattle he protects them by destroying carnivores and thus artificially maintains the ecosystem whose essential feature is the equilibrium between the grassland and the grazing animals. He may also alter the position of equilibrium by feeding his animals not only on the pasture but also partly away from it, so that their dung represents food for the grassland brought from outside, and the floristic composition of the grassland is thereby altered. In such ways *anthropogenic ecosystems* differ from those developed independently of man. But the essential formative processes of the vegetation are the same, however the factors initiating them are [different].

We must have a system of ecological concepts which will allow of the inclusion of *all* forms of vegetational expression and activity. We cannot confine ourselves to the so-called "natural" entities and ignore the processes and expressions of vegetation now so abundantly provided us by the activities of man. Such a course is not scientifically sound, because scientific analysis must penetrate beneath the forms of the "natural" entities, and it is not practically useful because ecology must be applied to conditions brought about by human ac-



tivity. The "natural" entities and the anthropogenic derivates alike must be analyzed in terms of the most appropriate concepts we can find. Plant community, succession, development, climax, used in their wider and not in specialized senses, represent such concepts. They certainly involve an abstraction of the vegetation as such from the whole complex of components of the ecosystem, the remaining components being regarded as factors. This abstraction is a convenient isolate which has served and is continuing to serve us well. It has in fact many, though by no means all, of the qualities of an organism. The biome is a less convenient isolate for most purposes, though it has some uses, and it is not in the least improved by being called a "biotic community" or a "complex organism," terms which are illegitimately derived and which introduce misleading implications.

## Methodological Value of the Concepts Relating to Successional Change

There can be no doubt that the firm establishment of the concept of succession has led directly to the creation of what is now often called dynamic ecology and that this in its turn has greatly increased our insight into the nature and behavior of vegetation. The simplest possible scheme involves a succession of vegetational stages (the prisere of Clements) on an initially "bare" area, culminating in a stage (the climax) beyond which no further advance is possible under the given conditions of habitat (in the widest sense) and in the presence of the available colonizing species. If we recognize that the climax with its whole environment represents a system in relatively stable dynamic equilibrium while the preceding stages are not, we have already the *essential framework* into which we can fit our detailed investigations of particular successions. Unless we use this framework, unless we recognize the universal tendency of the system in which vegetation is the most conspicuous component to attain dynamic equilibrium by the most complete adjustment possible of all the complexes involved[,] we have no key to correct interpretation of the observed phenomena, which are open to every kind of misinterpretation. From the results of detailed investigations of successions, which incidentally throw a great deal of new light on existing vegetation whose nature and status were previously obscure, we may deduce certain general laws and formulate a number of useful subsidiary concepts. So far the concept of succession has proved itself of prime methodological value.

The same can scarcely be said of the concept of the climax as an organism and all that flows from its strict interpretation. On the contrary this leads to the dogmatic theses that development of the "complex organism" can *never* be retrogressive, because retrogression in development is supposed to be contrary to the nature of an organism, and that edaphic or biotic factors can *never* determine a climax, because this would cut across the conception of the climatic climax as *the* "complex organism."

Phillips says (1935a: 242) that "the utility of the climax in Clements' sense would be greatly impaired were we to attempt to isolate from it the concept of the community as a complex organism. Its natural dynamic utility for orientation of research in succession, development and classification would be distinctly diminished." And again (1935b: 503), "The biotic community is an organism, a highly complex one: this concept is fundamental to a natural setting and classification of the profoundly important processes of succession, development and attaining of dynamic equilibrium."

What is the justification for such statements? What researches have been stimulated or assisted by the concept of "the complex organism" *as such*? Professor Phillips seems to have in mind cooperative work in which plant and animal ecologists take part. But nobody denies the necessity for investigation of *all* the components of the ecosystem and of the ways in which they interact to bring about approximation to dynamic equilibrium. That is the prime task of the ecology of the future.

We cannot escape the conclusion that the supposed methodological value of the concept of the "complex organism," contrasted with the value of succession, development, climax, and ecosystem, is a false value, and can only mislead. And it is false because it is based either on illegitimate extension of the biological concept of organism (Clements) or on a confusion between the biological and "organicist" uses of the word (Phillips).



CHAPTER 4

# A Succession of Paradigms in Ecology: Essentialism to Materialism and Probabilism

Daniel Simberloff

## The Rise of Probabilism and Materialism in Ecology

Ecology has undergone, about half a century later than genetics and evolution, a transformation so strikingly similar in both outline and detail that one can scarcely doubt its debt to the same materialistic and probabilistic revolutions. Many major events in this transformation have been described by Ponyatovskaya (1961) and McIntosh (1975, 1976), but the relationship to developments both inside and outside biology seems not to have been noticed. An initial emphasis on similarity of isolated communities, replaced by concern about their differences; examination of groups of populations, largely superseded by study of individual populations; belief in deterministic succession shifting, with the widespread introduction of statistics into ecology, to realization that temporal community development is probabilistic; and a continuing struggle to focus on material, observable entities rather than ideal constructs; all parallel trends [in] genetics and evolution.

Ecology's first paradigm was the idea of the plant community as a superorganism, propounded by Clements in the first American ecology book (1905) and elaborated by him in numerous subsequent publications. The crux of this concept was that single-species populations in nature are integrated into well-defined, organic entities, and key subsidiary aspects were that temporal succession in a sere is utterly deterministic, analogous to development of an individual, and leads inevitably to one of a few climax communities. The relationship between the stylized, integrated superorganism and the deterministic successional development producing it is organic and fundamental, as pointed out by Tansley (1920): "When we have admitted the necessity of first determining empirically our natural units, we have to find ways of grouping them. This

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