The Use and Abuse of Vegetational Concepts and Terms

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THE USE AND ABUSE OF VEGETATIONAL CONCEPTS AND TERMS

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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 recognised 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.

It is to Henry Chandler Cowles that we owe, not indeed the first recognition or even the first study of succession, but certainly the first thorough working out of a strikingly complete and beautiful successional series (1899), which together with later more comprehensive studies ('01, '11) brought before the minds of ecologists the reality and the universality of the process in so vivid a manner as to stimulate everywhere—at least in the English-speaking world—that interest and enthusiasm for the subject which has led and is leading to such great results. During the first decade of this century indeed Cowles did far more than any one else to create and to increase our knowledge of succession and to deduce its general laws. By acute and thorough observation and by lucid exposition he became the great pioneer in the subject. It is therefore natural and fitting that my contribution to a volume

intended to express the honour and affection in which Cowles is held by his fellow botanists should deal with this subject.

In 1920 and in 1926 I wrote general articles ('20, '29)[1] on this and some related topics. My return to the subject to-day is immediately stimulated by the appearance of Professor John Phillips' three articles in the *Journal of Ecology* ('34, '35) 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 individual creator of the modern science of vegetation and that history will say so. For Phillips' work too, and particularly for his intellectual energy and single-mindedness, I have a great admiration.

Phillips' 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 fervour 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.

[1] The latter was not published till 1929 owing to the long delay in the appearance of the Proceedings of the International Congress of Plant Sciences at Ithaca, N. Y. It was unfortunate too that certain misprints appeared in the paper because the proof corrections were not incorporated in the published text. Since some of these misprints destroy the sense intended it may be useful to call attention to them here.

P. 677, third line from bottom: Insert "these" after "All".
P. 684, line 2: delete second comma.
P. 685, line 2: for "criticism" read "criterion".
line 13: for "cause" read "causes".
line 14, third word from end; for "of" read "on".

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 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 signifiance 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" ('29). In a paper also read at the Ithaca Congress, Cooper ('26) takes the view that since succession is the universal process of vegetational change "all vegetational changes must of necessity be successional." But I think the concept of succession involves not *merely* change, but the recognition of a *sequence of phases* (admittedly continuous from one phase to another) subject to ascertainable laws: otherwise why do we employ the term succession instead of change? And also I cannot admit that catastrophic changes due to external factors form parts of succession. Suppose an area of forest (A) to be suddenly invaded and devastated but not completely destroyed by a herd of elephants which then departs to other feeding grounds. Suppose that after partial regrowth (B) the vegetation of the same area is completely destroyed by a volcanic eruption and that on the volcanic ash which has buried B a new vegetation (C) appears. Can A, B and C be usefully regarded as parts of *any* succession? Cooper calls the catastrophes "landmarks." I should say they were clearly *interruptions,* each initiating a new succession (sere). I think Cooper is somewhat obsessed by his image of universal vegetational change as a "braided stream," just as Clements and Phillips are obsessed by their "complex organism." A stream is continuous, *therefore* all vegetational change must also be continuous. Succession (according to my definition) *is* continuous, but it may be interrupted by catastrophes unrelated to successional processes, which last are subject to ascertainable laws. The stream analogy has its points, particularly the separation and re-uniting of currents, but it breaks down as applied to the entire history of vegetation on the earth, just because of the catastrophes; nor do I find it constructively very helpful in considering the processes of succession itself.

In 1926 (p. 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" (p. 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 (pp. 136–9) 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" ('34, p. 562); and again, "succession is the expression of development" ('35, II, p. 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 ('16, pp. 146–63) 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 ('26, p. 402) has pointed out, involve constant destruction of the plants of the earlier phases?

In the discussion referred to Clements ('16, pp. 155–9) questions the reality of the retrogressive changes posited by European ecologists in the conversion of forest into heath, in the absence of violent destruction or of change of climate. Along with his insistence on the prime importance of the water-relations in succession goes a refusal to accept the possibility of a gradual change in the soil factors as a result of progressive leaching without change of climate. We may agree with Clements that strict proof of the reality of a retrogression caused in this way must be lacking unless and until we have the results of long-continued observation and properly controlled experiment with the appropriate quantitative data; and we may also agree that " biotic factors " have not always been satisfactorily excluded from the demonstration of examples supposed to be primarily due to leaching. But we can say from numerous observations in the oceanic and sub-oceanic regions of Europe that retrogression due to leaching and concomitant soil and vegetational changes is extremely probable—at least as probable as many successions which have been inferred rather than demonstrated. And to these examples I should add the retrogression of life form involved in the gradual conversion of forest to heath or grassland and of heath to grassland due to persistent grazing.

I agree with Clements that the invasion and destruction of forest (or heath) by Sphagnum bog is not properly considered as retrogression. I should call it the conquest and suppression of a " higher " type of community by a " lower " one, owing to the peculiar nature of the latter. That the power to effect this invasion and conquest is largely due to the power of Sphagnum to hold water and to carry water with it as it invades, is certainly true, and also that Sphagnum thereby establishes a new hydrophytic habitat, which may become the starting point of a new hydrarch " prisere." But such events cannot quite be *equated,* as Clements would equate them, with

the formation of new "bare" (water) areas. Sphagnum is after all a plant, and the dominant of very extensive and important communities. Under certain conditions, which are due partly to climate and partly to topography, it may retain its dominance indefinitely. I myself should not hesitate to describe it as the primary dominant of a distinct plant formation, but then I am a heretic (or should I say a schismatic?) ('20, pp. 139–145). The weakness of this discussion of Clements, which is both able and ingenious, seems to me to reside partly in his too exclusive insistence on the water factor (which we all admit to be of prime importance), partly on his rather undiscriminating use of "destruction," but very largely on the assumption which governs the whole argument, and, as it seems to me, is quite illegitimate, that vegetation *is* an organism and therefore *must* obey the laws of development of what we commonly know as organisms.

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 recognise 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 enquired whether we could recognise such entities in vegetation, and I analysed the whole topic in considerable detail and with considerable care. To the best of my knowledge that analysis has not been seriously criticised 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 inter-relations of the parts of their structure, on their behaviour as wholes, and on a whole series of other characters which Clements ('16) was the first to point out. In 1926 (p. 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.

Here we are back again at the question of the meanings of words. Professor Phillips writes as if he believed words to have perfectly precise and invariable meanings, and that a given verbal proposition *must* either be true or not true, whereas in fact a proposition obviously has different meanings according to the exact connotation of the words employed. The word organism can be applied very widely indeed. Thus we have Professor Whitehead's "Philosophy of Organism" and a whole school of "organicist" philosophers: many have not hesitated to call the universe an organism. Indeed it would seem from the quotations given in the Oxford "New English Dictionary" that the application of the term primarily to individual animals and plants did not begin till less than a century ago. Professor Phillips undoubtedly has some such wide conception in the back of his mind, and indeed his confession in Part III ('35) of the holistic faith and his citations of organicist philosophers make it certain that he has. But he should remember that he is writing primarily for ecologists, who are biologists, and that the modern biologist *means* by an organism an individual animal or plant, and would usually refuse to apply the term to anything else. At the most we may be able to get the average biologist to admit that plant (or biotic) communities have *some* of the characters of organisms, and that it may be permissible to apply to them some such term as quasi-organism. That I think would be a useful gain because I believe (with Clements and Phillips) the idea to be of great service.

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. 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 organisation embodied in the individual animal or plant, and " organism " is the accepted term.

It may be said, as I imagine Cooper would say, that even such a term as " quasi-organism " is quite unnecessary if we keep the concept of " climax," which is very widely accepted. I do not agree, because climax does not suggest *organisation,* and the organisation of a mature complex plant association is a very real thing. The relatively stable climax community is a complex whole with more or less definite structure, *i.e.,* inter-relation of parts adjusted to exist in the given habitat and to co-exist with one another. It has come into being through a series of stages which have approximated more and more to dynamic equilibrium in these relations. This surely *is* " organisation," and organisation of the same type as, though by no means identical with, that of the single animal or plant. The organising factors are on the one hand the total net action of the effective environmental factors, on the other the combined actions of the individual organisms themselves. Phillips aptly quotes Karzinkin (1927) working on the " biocenoses " of animals living on water plants. Karzinkin found that changes in the external biota or in the constituents of the biocenosis disturb its equilibrium; but while the disturbance may be long-continued and complicated, equilibrium is ultimately again attained. It is possible therefore to speak of a " biocenosis " only when it reacts as a whole on the changes of the external and also of the internal factors. Cooper, who says ('26, p. 402) that progress in vegetational change is developmental " not because the vegetation unit is an organism but because it is made up of organisms undergoing development," adds that the progress of the whole is " subject to modifications due to mass action." It is precisely this " mass action," together with the actions due to the close and often delicate interlocking of the functions of the constituent organisms, which gives coherence to the aggregation, forces us to call it a " unit," justifies us in considering it as an organic entity, and makes it reasonable to speak of the development *of* that entity.

That this " development " is something very different from the ontogeny of a plant or animal (though even here there are also striking similarities) goes without saying. The adult quasi-organism can develop from beginnings which are totally opposed—a phenomenon completely alien from the ontogeny of a plant or animal—it can be hydrarch or xerarch; and the constituents of the " developmental stages " are quite different from the constituents of the

"adult." Starting from the type of the individual organism we have here something so different that it is no wonder there is refusal to call it by the same name, but at the same time something like enough to justify a related name.

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' 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!

First there are some ecologists who believe there may be more than one climax in a climatic region, each with distinct dominants. This is the so-called "polyclimax theory," opposed to the "monoclimax" doctrine of Clements and Phillips, which supposes that there is only one "true" climax in each "climatic region," and that this should therefore be called *the* climax.

Now the so-called "polyclimax theory" takes what appear to be permanent types of vegetation under given conditions and calls them climaxes, because they are culminations of successions. The usual view is that under the "typical" climatic conditions of the region and on the most favourable soils the climatic climax is reached by the succession; but that on less favourable soils of special character different kinds of stable vegetation are developed and remain in possession of the ground, to all appearance as permanently as the climatic climax. These are called *edaphic climaxes,* because the differentiating factor is a special soil type. Similarly special local climates determined by topography (*i.e.,* land relief) determine *physiographic climaxes.* But we may go farther than this and say that the incidence and maintenance of a decisive "biotic factor" such as the continuous grazing of animals may determine a *biotic climax.* And again we may speak of a *fire climax* when a region swept by constantly recurrent fires shows a vegetation consisting only of species able to survive under these trying conditions of life; or of a *mowing climax* established as a result of the regular periodic cutting of grasses or sedges. In each case the vegetation appears to be in equilibrium with *all* the effective factors present, including of course the climatic factors, and the climax is named from the special factor differentiating the vegetation from the climatic climax. The edaphic climaxes correspond in general with Schimper's edaphic formations.

I should not myself call the usage embodied in this terminology a "theory" of any kind. It is simply an empirical terminology applied to what seem rather obvious facts of vegetational distribution. The word climax is used in its simple and natural signification of a culmination of development—a permanent or apparently permanent condition reached when the vegetation is in equilibrium with all the incident factors.

Clements realised from the first ('16) that vegetation existed which was neither climatic climax nor part of a sere actually moving towards it, but might be in a permanent or quasi-permanent condition in some sense "short of" the climax, and all such vegetation he called *sub-climax*. 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 ('34, p. 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.

Godwin ('29) has insisted that the factors which prevent a sere from reaching the climatic climax not only *arrest* the sere, but also *deflect* it from its normal course, which may be re-entered when these factors are removed. He is sceptical of the existence of subclimaxes in the strict sense, and prefers to speak of "deflected succession." We might call such successions, which undoubtedly exist, *plagioseres, i.e.,* "bent" or "twisted" seres, and if the vegetation really does come into equilibrium with the deflecting factor, of a *plagioclimax,* if such terms are considered useful.

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? It is not rather a case of making the facts fit the theory? Is it not sounder scientific method *first* to recognise, 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?

Most of the kinds of vegetation which some of Phillips' colleagues in Africa consider as separate formations Phillips declares to be seral stages—examples of retarded succession, and if they are not that then they are variations of the climax. It is impossible for one who has not studied this vegetation at first hand to decide which is right—Phillips or his critics. My general impression after reading the discussion, so far as it has gone, is that not enough is known of the behaviour of the vegetation in question to enable one to be at all sure which view interprets the facts more naturally. It is possible that Phillips is right in his particular interpretations, for some of which he seems to make a good case. His general view seems to be that the so-called "edaphic climaxes" or "edaphic formations" are *never* permanent, but *always* seral stages, in which the succession may be delayed for a longer or shorter time, but which will always ultimately progress to the climatic climax. If this were true they would be excluded from Clements' category of "proclimaxes," which is intended to be applied ('34, p. 45) to climaxes produced by such allogenic factors as fire or grazing. If on the other hand edaphic factors are really capable of holding vegetation in a permanent or quasi-permanent equilibrium—and I am far from being convinced that they are not—then, as it seems to me, such vegetation is quite reasonably included in the general concept of the "proclimax," though it is clear that specific edaphic factors stand in a relationship to vegetation different from that of fire or grazing, both because they form part of the "original" environment and because they themselves usually undergo continuous change.

Here we encounter a complication which has not hitherto, so far as I know, received any adequate consideration in the literature—I mean the influence of the modern theory of soil development on the theory and classification of vegetation. It is a simple and attractive idea that development of the soil profile runs *pari passu* with development of the vegetation it bears, and that consequently the mature climatic soil type corresponds and co-exists with the climatic climax community. It is however quite premature and probably untrue to make any such general assertion. It may very well be that in particular cases such a correspondence actually exists. But on the other hand, even when profile development under the influence of climate is perfectly normal and regular, the climatic climax community may establish itself long before the soil is mature, and may not be substantially altered by the later stages of profile maturation. Again a climatic climax may establish itself on a soil which is *kept immature* by geological and physiographic causes, as on a steep slope. And finally it is now generally agreed by pedologists

that some rocks, owing to the simplicity of their composition, produce soils which can *never* form the normal climatic mature profile, and these may or may not bear the typical climatic climax vegetation. Whether any deviating communities which they may bear should be included as *parts* of the climatic climax should depend, as it seems to me, on the *extent* of that deviation. If it is wide, involving for example the dominance of different life forms, to assert that such vegetation *must* be part of the climatic climax *because* it appears in the same climatic region is surely to force the facts into a bed of Procrustes, to classify vegetation arbitrarily and unnaturally in the interests of a pre-conceived theory. Exactly the same is true of vegetation determined by any other edaphic factor, *e.g.,* permanent waterlogging for part at least of the year, or high soil acidity due to the poverty of the subsoil in basic ions or to the high rate of leaching in a highly permeable soil—which checks the maturation of the soil or diverts its course and thus prevents the appearance of climatic climax communities. There is no evidence that such kinds of vegetation represent stages of seres which will lead to climatic climax, nor can they be naturally regarded as parts of that climax.

On the other hand Bourne ('34) would have us regard every distinct variation of the climatic formation as a separate climax, *e.g.,* the spruce forests of the Vosges and of the Jura. No doubt they differ, as he says, quite markedly in certain respects which may be very important to a forester and for detailed ecological studies; and they may perhaps be suitably distinguished as separate *climax sociations.* But his general view reminds one of the taxonomists who will attend to nothing but " microspecies," losing sight of the higher grades of the taxonomic hierarchy.

I have even heard the argument that immature topography, for example, the slope of a hill, bears immature vegetation, and that since the slope will eventually disappear because it will ultimately be worn down to the base level of erosion, its vegetation must be regarded as seral. But this is surely to assert that tectonic and vegetational development must always run *pari passu,* whereas their time factors are usually widely different. They are very far from always keeping step, and immature topography is actually often clothed with climax vegetation, though Cowles ('01) has cited some striking cases of correlated development between physiography and vegetation.

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

" The Complex Organism "

Professor Phillips' third article ('35, III) 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 ('31) and so also have Shelford ('31) and others.

I have already expressed a certain amount of scepticism of the soundness of the conception of the biotic community ('29, p. 680), without giving my reasons at all fully. It seems necessary now to state the grounds of my scepticism, 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 behaviour 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. It may of course be argued by advocates of the term that the disparity of nature and behaviour between autotrophic plants and parasites—fungal or phanerogamic—is nearly as great as between animals and plants. But it may be rejoined that "human parasites" are well known in the societies of men, and that though it may well be held that a human society would get on better without them, yet they are in some sense members of the community. Though fungi are so different from autotrophic plants that they have even been regarded as forming a third "kingdom," distinct from both animals and plants, they are at least a good deal closer to green plants than they are to animals; and parasitic phanerogams undoubtedly form a link in nature and behaviour between parasitic fungi and autophytes, while saprophytic fungi are brought within the conceptual framework as "members" of a complex community such as a forest without any violence at all. Between all these organisms and the members of the animal kingdom there is however a very big gap in every respect.

Animal ecologists in their field work constantly find it neceessary 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 animals 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 realise 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 criticised 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 criticised 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' third article ('35, III) is largely devoted to an exposition and defence 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 organised "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' discussion I cannot possibly deal adequately here. They involve, as indeed he recognises, 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' 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 connexion? 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' 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).

How is this view justified? "At different levels the whole reacts upon habitat, changing (ameliorating) this for higher level wholes: the reaction of a whole, taken into account with its particular habitat and with the interrelations existing among its constituent organisms, shows as emergent changes in the habitat that are different from the sum of the changes that the constituent organisms would undergo were these not in communal association" [2] ('35, III, p. 498).

In this statement, we may note, it is not the mysterious "factor" called "holism" but the *particular* "whole" which is supposed to act as cause. Perhaps the "factor of holism" is intended as an abstraction from the effects of all the particular observed wholes. There is here again the artificial antithesis of an abstraction, "the sum of the changes that the constituent organisms would undergo" if they were not "in communal association," with what actually takes place in the community. Such a "sum" is quite unreal, there can be no meaning in considering the total activities *under unspecified conditions* of a particular lot of organisms taken together unless they *are* "in communal association." And if they are, they act upon one another, modify one another's actions, and produce new actions which are jointly dependent on two or more components. And it is precisely the sum of these modified and new actions which constitutes what we call, and rightly call, the activity of the community as a whole, because they depend upon the existence of that particular association of organisms with that particular habitat.

Is the community then the "cause" of its own activities? Here we touch

[2] Phillips however seems to think his statement is open to logical objection, but adds that "the accumulation of ecological evidence is becoming so impressive that I am not seriously perturbed by the strictures of pure logic." Surely it is his business either to show that the logic referred to is bad logic, or else to *be* "seriously perturbed" by it.

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' contention. But it is important to remember that these activities of the community are *in analysis* nothing but the synthesised 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.[3]

It is difficult to resist the impression that Professor Phillips' enthusiastic advocacy of holism is not wholly derived from an objective contemplation of the facts of nature, but is at least partly motived by an imagined future "whole" to be realised 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' 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 ('32) has most convincingly pointed

[3] If this statement is applied to the individual organism, it of course involves the repudiation of belief in any form of vitalism. But I do not understand Professor Phillips to endow the "complex organism" with a "vital principle."

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.[4]

Some of the systems are more isolated in nature, more autonomous, than others. They all show organisation, which is the inevitable result of the interactions and consequent mutual adjustment of their components. If organisation 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 recognised. 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 towards 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

[4] The mental isolates we make are by no means all coincident with physical systems, though many of them are, and the ecosystems among them.

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' contention that soil never does this is too flatly contrary to the experience of too many ecologists to be admitted. Hence we must recognise 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 behaviour 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 co-operative 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' " prisere " ('16) is the gradual development of an ecosystem as we may see it taking place before us to-day. 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 radio-active 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 ('16). 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' conception, move across the continent " as if they were strung on a string," much as the plant communities zoned round a lake will move towards its centre 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 Palaeozoic, where we get the first glimpses of the constitution of the organic world, through the later Palaeozoic 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 Palaeozoic 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 30 years. In detail the initiation and development of the ecosystems in past times must have been governed by the same principles that we can recognise to-day. 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 ('26), 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 analyse 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 co-operated 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 civilised 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 harmonised 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 actually present 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 directed.

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 activity. The " natural " entities and the anthropogenic derivates alike must be analysed in terms of the most appropriate concepts we can find. Plant community, succession, development, climax, used in their wider and not in specialised 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 behaviour 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 colonising species. If we recognise 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 recognise 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 ('35, II, p. 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 ('35, III, p. 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 co-operative 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 [5] (Clements) or on a confusion between the biological and "organicist" uses of the word (Phillips).

[5] Clements is quoted as saying that biologists present at the evolution of multicellular from unicellular organisms would have denied that they *were* organisms, because they were *different*. Perhaps; but from our superior vantage point we can assert with perfect confidence that the so-called "complex organism" is vastly *more* different from either multicellular or unicellular organisms than they are from one another.

Conclusions

Succession is a continuous process of change in vegetation which can be separated into a series of phases. When the dominating factors of change depend directly on the activities of the plants themselves (autogenic factors) the succession is *autogenic:* when the dominating factors are external to the plants (allogenic factors) it is *allogenic.* The successions (priseres) which lead from bare substrata to the highest types of vegetation actually present in a climatic region (progressive) are primarily autogenic. Those which lead away from these higher forms of vegetation (retrogressive) are largely allogenic, though both types of factor enter into all successions.

A *climax* is a relatively stable phase reached by successional change. Change may still be proceeding within a climax, but if it is too slow to appreciate or too small to affect the general nature of the vegetation, the apparently stable phase must still be called a climax. The highest types of vegetation characteristic of a climatic region and limited only by climate form the *climatic climax.* Other climaxes may be determined by other factors such as certain soil types, grazing animals, fire and the like.

The term *development* may be applied, as in ordinary speech, to the appearance of any well-defined vegetational entity; but the term is more strictly applied to the autogenic successions leading to climaxes, which have several features in common with the development of organisms. Such climaxes may be considered as *quasi-organisms.*

The concept of the "biotic community" is unnatural because animals and plants are too different in nature to be considered as members of the same community. The whole complex of organisms present in an ecological unit may be called the *biome.*

The concept of the "complex organism" as applied to the biome is objectionable both because the term is already in common use for an individual higher animal or plant, and because the biome is not an organism except in the sense in which inorganic systems are organisms.

The fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment is the *ecosystem,* which is a particular category among the physical systems that make up the universe. In an ecosystem the organisms and the inorganic factors alike are *components* which are in relatively stable dynamic equilibrium. Succession and development are instances of the universal processes tending towards the creation of such equilibrated systems.

From the standpoint of vegetation biotic factors, in the sense of decisive influences of animal action, are a legitimate and useful conception. Of these biotic factors heavy and continuous grazing which changes and stabilises the vegetation is an outstanding example.

The supposed methodological value of the ideas of the biotic community and the complex organism is illusory, unlike the values of plant community,

succession, development, climax and ecosystem, the concepts of which form the essential framework into which detailed studies of successional processes must be fitted.

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