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TAUTOLOGY IN EVOLUTION AND ECOLOGY

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Definition of the nature of scientific constructs can play as important a role in science as the original elaboration of an idea. Such clarification should eliminate confusion and lead to the construct's proper application. Although Darwinian evolution remains one of the greatest unifying concepts in biology, its utility has been questioned. Difficulties in defining "fittest" in the phrase "survival of the fittest" have led some authors to conclude that the Darwinian theory is a meaningless formulation because fitness is apparently equivalent to survival (Waddington 1957; Coffin, cited in Scriven 1959). The testing of evolutionary theory against observation is, at best, extremely difficult (Slobodkin 1968; Orians 1973), and Scriven (1959) suggests that it is not to be expected. Birch and Ehrlich (1967) maintain that our theory of evolution is "not necessarily false" but "outside of empirical science."

Although each of these authors has found fault with the theory of evolution, none has indicated precisely where Darwinian theory may be applied and what may be expected from such an application. In this essay, I argue that the "theory of evolution" does not make predictions, so far as ecology is concerned, but is instead a logical formula which can be used only to classify empiricisms and to show the relationships which such a classification implies. Similar criticisms are then made of several ecological concepts. The essence of the argument is that these "theories" are actually tautologies and, as such, cannot make empirically testable predictions. They are not scientific theories at all.

SCIENTIFIC THEORIES

My criteria for the acceptance of a scientific theory are derived from the logical positivists. Reichenbach (1951) gives a particularly intelligible account of this approach. Briefly, given a set of initial conditions or state variables which

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permit a series of possible empirical results, the scientific theory makes predictions or falsifiable inferences about which results will occur. The theory would be falsified if results other than those predicted occurred in greater than some stated or assumed proportion of all trials. My use of "predictions" includes certain inferences about the past which are sometimes called "postdictions."

The scientific theory is a formalized mode for treating and predicting facts from the empirical world. It contrasts with tautologies, which are part of the study of logical relations independent of empiricisms. Both have a place in science, but they must not be confused.

TAUTOLOGY

The tautology, or logical argument, consists of premises or axioms and the ramifications which follow by logical necessity. Because tautologies are self-contained or abstract deductive arguments, the premises need not have empirical correspondences, and the conclusions are implicit in the axioms. Thus tautologies are not subject to empirical falsification and are incapable of prediction.

Nevertheless, certain logical arguments are useful in science. If the premises suggest a classification of empiricisms, the abstract conclusions can be used to indicate what relations *must* exist among the classes. Of course, these relations exist by virtue of the classification and could be deduced each time the classification is made. However, the logical pattern provided by the abstract tautology allows us to state the conclusions without the labor of thinking through the logical implications of the classification each time it is used. Tautologies therefore lessen our logical work load; they do not substitute for theories. Assuming the logic is sound, disagreement between the logical conclusions and the empirical relations shows only that our classification is incorrect, not that the tautology is false.

Tautologies exist at many levels of complexity depending on the number of premises and the amount of analyses performed on these premises. At the simplest level, there is only one axiom and the emptiness of the argument is obvious. For example, if the theory of evolution were summarized as "evolution is the survival of the fittest" and "the fittest are those which survive," this two-axiom statement could be reduced to the single axiom "evolution is the survival of the survivors," a clearly empty phrase.

Far more interesting tautologies are created when the axioms are so complex that their deductive interrelations are not immediately apparent. All computer models are (or should be) of this type: the program represents the axioms and the computer makes their logical consequences explicit. The clearest and most familiar example of a complex tautology is Euclidian geometry, but the most powerful is mathematics. We are often tempted to create correspondences between these great logical systems and the real world, but we should not think that these correspondences prove the empirical value of the axioms in the way that an experiment may confirm a scientific hypothesis. For example, the fact that an apple and an apple presents us with two apples is not a proof that

$1 + 1 = 2$; this relation is derived in a system which can be formulated without reference to apples or other empiricisms.

The great danger of tautological systems is that they may become so accepted that our minds unconsciously classify empiricisms according to the tautology. This limits our capacity to see alternative logical systems and may lead us to substitute the tautology for predictive theory. Both Frank (1957) and Reichenbach (1951) point to the example of Euclidian geometry which was considered proven until the non-Euclidean geometers showed that the real world could correspond to other axiomatic formulations. Similarly, the "new mathematics" taught in our schools is an attempt to demonstrate the non-empirical, deductive nature of mathematics as opposed to its practical predecessor which became a natural law for generations of school children. For the blend of tautology and empiricism to which a high truth value is assigned, I will use the term "metaphysic."

Mathematics has shown that the tautology can be immensely useful. But if the tautology is internalized as a metaphysic, the beauty and clarity of the deductive system will be obscured with no compensatory gain as a predictive system.

THE THEORY OF EVOLUTION

It is extremely difficult to find a clear and precise statement of the theory of evolution. Consequently, I advance the following brief summary: Evolution is the process through which the variety of organisms inhabiting the earth emerged; it is achieved through the natural selection of organisms based on the differences among them. Undoubtedly, this short statement will be deemed insufficient; however, it is enough to support the following attack which, I believe, could be applied equally well to fuller formulations.

The evolutionary history of an organism, its phylogeny, is limited to speculation as opposed to experimentation by its setting in the past (Ehrlich and Holm 1962). Furthermore, the imperfections of the geological record make it relatively easy to explain away anomalies. The randomness of mutation coupled with the unpredictability of environmental changes makes prediction impracticable. Scriven (1959) maintains that the chief value of the theory of evolution is not in prediction but in explanation of the past, but Reichenbach (1951) argues that only predictive capability indicates knowledge. Thus a purely explanatory device is not knowledge and, I would suggest, cannot be called a scientific theory.

If phylogenetic history cannot be predicted from the theory of evolution, we must turn to those aspects of the theory which are current and so are subject to experimental analysis—the operation of natural selection on variations among organisms.

NATURAL SELECTION

Mason and Langenheim (1961) define natural selection as "the elemental operational relationships between an organism and its environmental conditions such that the organism satisfies all its physical needs for establishment

and survival." They then argue that this definition is sufficient because re-
jection, or "nonselection," is implied by selection, and "all else that has been
traditionally associated with this term (natural selection) results from classi-
fication and deduction." Mason and Langenheim further show that classifications
of the results of natural selection form a large part of the ecology of variations
in space and time (ecological patterning, ecotypes, community structure,
succession, etc.). These can be deduced by premising temporal or spatial changes
such that the environmental relations no longer permit the survival or establish-
ment of organism A but do permit the establishment of organism B. The point
is that the general statement of natural selection gives an exhaustive list of the
responses of an organism to the environment: selection or rejection. No result
could falsify the statement. However, the results of an empirical investigation
could be classified in terms of the general statement, and from this tautological
argument ("deduction") is possible.

Using a far more rigid analysis, Williams (1970) has reduced Darwinian
evolution to simple deductions based on a series of axioms without empirical
meaning. This shows that evolution can be reduced to a tautology. Williams
suggests that the axioms be "interpreted" at genetic, organismic, or population
levels to produce predictions. However, in doing so the researcher may do some
violence to her meaning. At this risk, I have interpreted her seven necessary
axioms for evolution at the organismic level. For all organisms: (1) no organism
is its own parent, and (2) no organism is the ancestor of its ancestors. For all
organisms which are undergoing evolution: (3) axioms 1 and 2 apply; (4) the
number of descendants is finite; (5) each organism has a certain quality called
fitness, and this differs among organisms; (6) an organism with a higher fitness
leaves more descendants; and (7) some of these fitness differences are hereditary.

The first three statements are tautological because of the definitions of
"parent" and "ancestor." The remaining axioms state the necessary and
sufficient properties of evolving organisms: hereditary survival differences
among a finite number of offspring. To apply these statements as predictions
we must show that the organisms are evolving; that is, it is necessary that the
organisms have these properties. Once this is done we can make no prediction
about evolution, since Williams maintains that these are sufficient for the
deduction of all other characteristics of Darwinian evolution. If we cannot
show that the organisms have these properties, they do not evolve, and no
prediction about their evolution is possible. Her axiomatization is extremely
valuable in showing the logical similarities of different classifications or "in-
terpretations" but not in making prediction.

If the generalities of natural selection and Darwinian evolution do not provide
unambiguous or falsifiable predictions, they cannot be called a scientific theory.
If, however, they provide a pattern of logic based on a few axioms, they do form
a tautology to which we may apply empirical correspondences. A tautology is
useful when, as in mathematics, the logical relations are too complex to be
recreated each time they are needed. I do not believe the logic of survival is so
complex; given an organism's limits of tolerance and the external conditions,
it is very easy to predict the outcome. In the last century, when naturalists'
minds were full of the creationist metaphysic, Darwin was useful in demonstrat-

ing an alternative set of possible relations. Now we are in danger from an evolutionary metaphysic in which the logical Darwinian devices have become great "empirical" truths.

ECOLOGICAL TAUTOLOGIES

With the example of evolutionary theory, the scientific aptitude for logical thought, and the length and difficulty of large-scale ecological experiment, it is not surprising that there should exist a body of ecological literature comprised of tautology. Nor is this bad in itself. However, ecologists must be careful to distinguish between tautologies and theories and to identify the logic of any tautology as sufficiently interesting to warrant its study. Only in this way can we preserve the scientific theories of ecology, make constructive use of the logical models, and prevent the introduction of new metaphysics. Ecologists have not always been so careful, and it is common to find a "theory" attacked as a tautology.

COMPETITION

A popular tautology is that presented by Volterra's model of competition (Volterra and d'Ancona 1935). It assumes that two populations grow in a limited system such that, eventually, increase in one population produces a decline of the other. These conditions are presented as constants in the Lotka-Volterra equations, from which a strictly mathematical logic shows that two results may be obtained: one population or the other disappears. Because the argument is logically derived from the assumptions, it is tautological. Nevertheless, the argument has received considerable attention, possibly because the conclusions, which are evident in a verbal statement, are more difficult for us to see in the mathematical form.

This tautology might form the deductive portion of a combined theory, but this would require that the axioms be phrased as testable theories. Andrewartha and Birch (1954) maintain that this is impossible: one can determine the necessary constants only by fitting the results of the competition experiment to the general form of the equations. Thus the results must be predicted from the results themselves. A more acceptable phrasing is that the results are classified in terms of the model. The verification offered by Gause (1935) represents a post facto correspondency with the model, not its proof.

Hardin (1960) points out that the third possible outcome, survival of both populations, could only indicate a misclassification; that is, that the original conditions were not met. He states that the principle is untestable and tautological, but suggests that it may be useful in ordering our thoughts. Cole (1960) was quick to point out that Hardin had thus raised the tautology to a dogma.

Despite these shortcomings, variations and extensions of Volterra's model have been widely used in ecology. Hutchinson (1959) presents this tautology in the broader form of the competitive exclusion principle. He begins with two statements: each species has its own niche which is defined as a hypervolume ordered by the organisms' environmental parameters, and when a system is in equilibrium no two species can occupy the same niche. He then uses set theory

to indicate the logically possible niche overlaps: exclusive, inclusive, partial, and coextensive. He then introduces a third statement, that no two species have identical physiologies, which removes the coextensive case. From these statements he deduces that two species cannot coexist in the remaining overlapping cases if the system is in equilibrium.

This formulation removes the necessity of measured constants and may at first seem predictive. But, if we examine his original statements, we find that they cannot be made predictive theories. We cannot completely identify the organism's niche because the number of environmental ordinates is practically infinite; although two species may appear to have the same niche after any given number of measurements, the possibility remains that one further measurement will separate them. It is equally difficult to decide if a system is "in equilibrium." Hutchinson does not indicate how we are to perform either operation. In practice he defines niche as habitat and equilibrium as the absence of coexistence. Thus he accepts MacArthur's (1958) elegant demonstration of habitat division by warblers as a suitable correspondency with the theory as habitat differences correlate with coexistence, but argues that Ross's (1957) demonstration of coexistence among leafhoppers indicates that this system was not in equilibrium, since no habitat differences could be found. Clearly this is not a theory but a tautology—a series of nonoperational axioms leading by logical deduction to conclusions which may be applied only post facto to empirical observations.

In their discussion of r and K selection, MacArthur and Wilson (1967) develop another form of Volterra's model and so provide another tautological set. They begin with a series of axioms, stating that any two populations of competitors in a limited system have a maximum sustainable population to which they tend, and that these maxima depend only on the numbers of each population. A mathematical logic, presented as a series of graphs, leads to a comprehensive list of possible outcomes. One population or the other disappears, or both survive in an equilibrium. Like Volterra's model, this formulation is a tautology because it may be applied only to systems which have previously been shown to behave according to the axioms. Results are not predicted, only interpreted.

However, MacArthur and Wilson develop this analysis further. They point out that among the possibilities is the case that the population with the higher specific rate of reproduction (r) at low densities may have a lower carrying capacity (K). At low densities this population is selected (this, of course, is circular, since r is a measure of survivorship and so of selection). This population will first reach K when $r = 0$, but the other population will continue to grow (i.e., its r exceeds 0). As this second population increases, the carrying capacity of the environment for the first population will decrease and the first population will drop to zero. Thus, given sufficient time, the population with the higher K will be selected; it will have the higher r. This argument is not predictive—it is not claimed that all populations follow this development, only that some may. Also, because this is only a special case of the more general axioms, the necessary conditions can only be identified by performing the competition experiment.

MacArthur and Wilson interpret Cody's (1966) work with bird clutch size in terms of their logic. Birds on more climatically stable oceanic islands lay

fewer eggs than birds in a more variable continental area. The inference is that in a more stable area, selection pressure switched from birds which have high r, as indicated by the higher specific natality b, to those which maintain themselves with a lower r. There is no indication that this was the historical sequence, however, and any other result could be shown to correspond to some part of their original logic.

Finally, they generalize their argument to state that stable environments select more efficient organisms and unstable environments select more productive organisms. This is not predictive. Not all populations need follow this course—only those which have been shown to change their relative survivorship with density. A change in survivorship is equivalent to a change in selection, and the argument is circular.

Ecological tautologies are not restricted to developments of Volterra's model, but the importance of competitive exclusion in many branches of theoretical ecology suggested that a more detailed examination of the tautologies of competition would not be out of place. This brief summary does not exhaust the topic either within competition theory or without.

Before leaving competition theory, it is interesting to note that these tautologies can be interpreted as special cases of Darwinian evolution. They are identical with Williams's (1970) theorems D_{10}–D_{12}.

THE MONOCLIMAX

Whittaker (1953) criticizes Clements's concept of a monoclimax as a tautology, although Whittaker does not use that particular word. He notes that the idea of a monoclimax has been so qualified that it is now impossible to test. Three basic arguments can fit any eventuality. The first premise, that vegetation in an area converges to identity, was testable and easily disproven. Two further qualifications vitiated this theory. First, that differences exist within identity, and second, that subclimaxes exist that only theoretically could be replaced by the climax. Thus the original theory has been modified to mean that vegetation in an area may or may not progress to different or similar endpoints. This is obviously circular. Yet, because the monoclimax became a metaphysic, a generation of phytosociologists remained unaware of the tautology, and bitter controversy ensued.

SUCCESSION

Odum (1969) introduced a number of tautologies in his discussion of succession. He first defined succession as follows:

1) It is an orderly process of community development that is reasonably directional and, therefore, predictable;
2) It results from the modification of the physical environment by the community . . . even though the physical environment determines the pattern of change and often sets limits as to how far development can go;
3) It culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit energy flow.

He then presented a table listing 24 differences to be "expected" between young and mature systems. If the definition of succession is considered a list of constraints and the expectations are taken to be predictions, this construct appears to be a theory. However, many of the expectations are merely tautological implications of the constraints.

At least one of these characteristics, the (1) increase of the ratio of biomass to energy flow (B/E), is simply a restatement of the definition and therefore is a tautology in its simplest form. An increase in (2) symbiosis and (3) information would be equally simple and tautological if these are to be expressed per unit energy flow. Odum seems to imply this with the phrase "within the limits set by available energy input which qualifies all of his successional trends."

Other characteristics are logically dependent upon his definition. For example, the extent that entropy is the opposite of information would imply that as information increased (4) entropy would decrease. Also, a stabilized ecosystem must have a (5) low net community production or yield. Low yield is otherwise expressed by (6) near unity of the ratio gross production: respiration (P/R). Since the P/R ratio in most young systems is greater than 1, (7) the amount of organic matter must increase. (This does not occur in the case of organic pollution, but Odum allows that not all systems will demonstrate all characteristics; by itself this statement renders the entire argument tautological.) Since total energy flow equals gross production, the constraint that B/E increase with maturity implies that (8) P/B decrease. For any given P/R greater than unity, small organisms will have a higher r than large organisms because they reach reproductive size sooner and must reproduce to maintain P; thus a new environment favors or selects (9) small organisms with (10) short life cycles. Larger organisms need not be eliminated, but will not spread so rapidly since they cannot reach large sizes or reproductive states until later in ecosystem development. Frank (1968) argued that the observed correlation between long life cycles and the stabilized community may be tautological. It also seems tautological that an increase in large organisms increases (11) spatial heterogencity.

Tautological problems can be expected in dealing with Odum's predictions of (12) shifts from r-selection to K selection and (13) from the production of quantity to production of quality as discussed above. Furthermore, the definition of (14) stability as resistance to external perturbation or stress involves circular reasoning, since a perturbation is defined in terms of its effects as discussed in the section on diversity below.

Certain other characteristics seem to be tautological pairs, in that the existence of one implies the existence of the other. Thus (15) the closure of mineral cycles would imply (16) greater conservation of nutrients. The change from (17) grazing food chains to detrital food chains would suggest that (18) the role of detritus in nutrient regeneration would be more important.

Other characteristics are only tautological if certain well-established biological properties are allowed as axioms in addition to the definition of succession. These are not tautological in Odum's frame of reference but, as his readers are likely to assume these properties, they are discussed as "quasi-tautological."

For example, since potential colonists require time to reach a new site, it is likely that (19, 20) new communities will be less diverse. Since it is probable that different species have different biochemistries, it is likely that (21) the biochemical diversity will also increase. Since the sum of the organisms in different series probably have similar ratios of biomass: mineral content, it is probable that as biomass increases (22) so will the amount of intrabiotic nutrient.

A number of traits that Odum lists remain unaffected by this analysis and could form true scientific theories. These would include the semitautologies of the preceding paragraph if the suggested biological generalities are not assumed. Others are the closure and (22) slowing of mineral cycles, (17) the ramification of food webs and their shift to a detrital base, and (24) the specialization of the niche. It should also be noted that, according to Frank (1968), more extensive data might show that an apparent tautology masks positive feedback. However, he does not indicate what data, either in general or in particular, would suffice.

DIVERSITY

Pianka (1966) has discussed six theories of diversity and tried to determine possible tests for each. He concludes that two of these, the evolutionary-time theory and the productivity theory, cannot be tested since the initial conditions cannot be met operationally. This easily leads to post facto rationalization of the observations to support the theory. The theory of climatic stability, the competition hypothesis, and the predation hypothesis are often difficult to distinguish in practice; the latter two can be tested only if competition can be measured on the same scale using different species in different environments, and the former two are often mixed in presentation. As Pianka (1966) writes, "the compounding of hypotheses is to be avoided" since "the more complex hypothesis tends to 'answer' all cases and becomes less testable and useful." That is, they become tautological.

Sanders (1968) provides a particular case of a complex hypothesis in advancing "the stability-time hypothesis" of species diversity. This states that ecosystems become more diverse in the course of evolutionary time, but that application of physiological stress will cause a reduction in this diversity. As these are verbally stated, the hypothesis can only be used to compare systems. Because evolutionary time and physiological stress are not commensurate qualities, no comparison can be made between systems unequal in both age and stress. The theory can be applied only to compare ecosystems of equal age under unequal stress, or of unequal age under the same stress. Pianka (1966) indicates that the effect of evolutionary time "is not ammenable to conclusive tests" because of difficulties in determining the age of an ecosystem and because experiments cannot be performed in evolutionary time. The test of Sanders's theory must therefore depend on an examination of physiological stress. By definition, stress is deleterious, and any environmental change which is not deleterious cannot be termed stress. Since stress must be defined in terms of its effects, there is a danger of circular reasoning. Indeed, Sanders finds that low temperature, which might be considered a stress a priori, is not because deep benthic fauna

in Lake Baikal and on the continental shelf are diverse. He defines high salinity and temperature as stresses to explain observations which suggest that certain tropical benthos is no more diverse than corresponding boreal fauna. These must be classed as correspondences rather than predictions, and "the stability-time hypothesis" cannot be accepted as a scientific theory as it now stands.

SPATIAL HETEROGENEITY

Smith (1972) states that a system is heterogeneous to a process if the rate of the process varies over space in relation to structural variations of the environment; he then discusses the effects of spatial heterogeneity on stability and diversity. It is clearly a logical argument; if diminished populations are less subject to predation than high populations in one system and equally pressured in another, the former population will persist longer. Stability in this sense is deducible from spatial heterogeneity. It is also clear that if classical competition theory is assumed, the presence of an unexploited prey population will permit the introduction of another predator which will increase diversity but decrease stability by increasing predation pressure on the prey. These outcomes are tautological implications of the definition of spatial heterogeneity. However, the main thrust of Smith's argument is directed to other models and is a suggestion for the improvement and extension of other logical constructs. So long as this logic is not confused with empiricisms it represents a valid use of the tautology. In his discussion, Smith weakens his position by using spatial heterogeneity to render certain experimental results "understandable." This identification of correspondences is unfortunate because it detracts from the previously wholly logical argument and may suggest to Smith's readers that his tautology may be used as a true theory.

CONCLUSION

In preparing this paper, I was led to wonder if competitive exclusion, succession, and diversity are tractable scientific problems—that is, if they can be resolved or if by their nature they are beyond resolution. I cannot prove my suspicions, but we must be aware of the possibility of intractable problems and not be surprised if another mode of thought produces more fruitful science than these. Perhaps the existence of so much logic and so little theory indicates that this is infertile ground on which to raise predictive hypotheses. If this is the case, then the dedication of so much of ecology to these topics is wasted energy.

Papers were chosen for this discussion for more reasons than availability and personal preference. They are meant to indicate the range of tautological thought in ecology and to indicate that even our greatest thinkers may occasionally introduce circular reasoning into their arguments. I have no doubt that a selection from other areas in ecology would reveal similar tautologies.

Because the utility of a logical aid depends on the deductive capacity of the individual scientist, I cannot judge if the above tautologies are useful to scientists dealing with empirical problems. Nonoperational assumptions are of

little use and no purely logical system can lead to predictions, but the pattern provided by some tautologies may lead to an ordering of the facts which the researcher might not otherwise see. However, in examining this small portion of the literature, I came to feel that the effort required to follow the abstractions of other authors was far greater than that required to deal with suitable empiricisms. I am convinced that the utility of ecological tautologies would be better appreciated if we recognize their logical nature more explicitly.

SUMMARY

Analysis of a number of popular ecological tenets, including natural selection, competitive exclusion, and parts of succession, species diversity, and spatial heterogeneity, reveals that they lack the predictive and operational qualities which define scientific theories. Instead they consist of the logical elaboration of certain axioms. Consequently, they must be termed tautologies. Tautologies may be useful logical aids, but they cannot replace true theories. Unless ecologists are careful to distinguish the two, their confusion may produce a body of thought resting on metaphysical rationale rather than empirical, predictive science.

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LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago. 782 pp.

Birch, L. C., and P. R. Ehrlich. 1967. Evolutionary history and population biology. Nature 214:349–352.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20:174–184.

Cole, L. C. 1960. Competitive exclusion. Science 132:348–349.

Ehrlich, P. R., and R. W. Holm. 1962. Patterns and populations. Science 137:652–657.

Frank, P. 1957. Philosophy of science. Prentice-Hall, Englewood Cliffs, N.J. 394 pp.

Frank, P. W. 1968. Life histories and community stability. Ecology 49:355–357.

Gause, G. F. 1935. Vérifications expérimentales de la théorie mathématique de la lutte pour la vie. Actualités Sci. 277:1–61.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Hutchinson, G. E. 1959. Il concetto moderno di nicchia ecologica. Mem. Istituto Ital. Idrobiologia 11:9–22.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J. 203 pp.

Mason, H. L., and J. H. Langenheim. 1961. Natural selection as an ecological concept. Ecology 42:158–165.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Orians, G. H. 1973. Review of growth by intussusception. Limnol. Oceanogr. 18:347–348.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Amer. Natur. 100:33–46.

Reichenbach, H. 1951. The rise of scientific philosophy. University of California Press, Berkeley. 333 pp.

Ross, H. 1957. Principles of natural coexistence indicated by leafhopper populations. Evolution 11:113–129.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. Amer. Natur. 102:243–282.

Scriven, M. 1959. Explanation and prediction in evolutionary theory. Science 130:477–482.

Slobodkin, L. B. 1968. Towards a predictive theory of evolution. Pages 317–340 *in* R. Lewontin, ed. Population biology and evolution. Syracuse University Press, Syracuse, N.Y.

Smith, F. E. 1972. Spatial heterogeneity, stability and diversity in ecosystems. Growth by intussusception: ecological essays in honor of G. Evelyn Hutchinson. Trans. Connecticut Acad. Sci. 44:309–335.

Volterra, V., and U. d'Ancona. 1935. Les associations biologiques au point de vue mathématique. Actualités Sci. 243:1–96.

Waddington, C. H. 1957. The strategy of the genes. Allen & Unwin, London. 154 pp.

Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and a pattern. Ecol. Monogr. 23:41–78.

Williams, M. B. 1970. Deducing the consequences of evolution: a mathematical model. J. Theoretical Biol. 29:343–385.