Ecological Modelling, 43 (1988) 129–132
Elsevier Science Publishers B.V., Amsterdam – Printed in The Netherlands

Comments

NATURE OF ECOLOGICAL THEORIES

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During the discussion period of the ISEM/ESA symposium *An Evaluation of the Role of Theoretical Models in Ecology* at the AIBS meeting in August 1987 in Columbus, Ohio, several conclusions were reached. One of these was that "there are no proven ecological theories." I disagree with this statement, and I believe the misconception arises from a misunderstanding of the nature of ecological theories.

To avoid semantic argument I fist mention that in general, a theory can be defined as an hypothesis which has gained a certain level of acceptability by at least some of the individuals working in the field of interest. The distinction between an hypothesis and a theory is therefore largely subjective, and one which I do not think worth emphasizing.

I propose the following outline for the general development of theories as it normally occurs in ecology. First a relatively simplistic theory is proposed which takes the form of one or several mathematical or verbal statements. It may be recognised that the validity of the theory depends on certain assumptions and these will be incorporated in the statement of the theory. However, at this point a difficulty arises which is probably more common in theory-building in ecology than in other fields. Because of the complex and almost infinitely variable nature of ecological systems, many of the limiting assumptions which should be stated with the theory may be unknown at the point of its inception. These limiting assumptions are discovered gradually, as the theory is put to the test in the field, or as theoretical investigation continues. Under some circumstances the theory may be upheld, and under others it may be refuted. However, the point is that refutations of the theory do not necessarily disprove or invalidate it. Instead, they may suggest refinements of the limiting assumptions of the theory. If a number of cases can be found which irrefutably support it, the theory (along with its new, more extensive list of assumptions) should be considered to be proven. This conclusion is of course valid only if a theory is not considered to be brand new simply because its assumptions have been edited. If this semantic point is agreed upon, then there are clearly many proven ecological theories. I support this description of ecological theories with the following examples.

The first example is the theory of competitive exclusion of Gause (1934) and extended by S.A. Levin (1970), Strobeck (1973) and others. The theory states that if a number of species, n, are to coexist in a certain area, then there must be at least n limiting resources. Several field studies have apparently demonstrated violation of this theory (e.g., Ayala, 1969; Hutchinson, 1961: Woolhouse et al., 1985). Over the past 35 years a number of limiting assumptions have been added to the competitive exclusion theory. For example, under the following conditions the competitive exclusion theory may be violated: resource seasonality (Stewart and B. Levin, 1973), resource seasonality combined with immigration (Jaeger, 1974), environmental fluctuations (Hutchinson, 1961; Comins and Noble, 1985), predation (Caswell, 1978), density-dependent competitive abilities (Pimental et al., 1965: B. Levin, 1972), errors of exploitation (Istock, 1966), and habitat patchiness (Horn and MacArthur, 1972). The result of all of these exceptions is that the domain of applicability of the competitive exclusion theory has been significantly reduced, to the point where most workers agree that it is probably rare in nature. However, this does not invalidate the theory itself, since there are some cases in nature in which competitive exclusion is the most reasonable explanation for the observations (e.g., Koplin and Hoffman, 1968; Bovbjerg, 1970; Jaeger, 1980). The theory may therefore be considered to be proven, although its assumptions have been greatly extended and the recognised extent of its applicability has narrowed considerably.

Another example is the 'risk-spreading' theory (Den Boer, 1968) originally proposed by Andrewartha and Birch (1954). This theory states that dispersal between subpopulations causes damping of fluctuations in overall population size, thus increasing overall population stability. The theory has been demonstrated both mathematically (Hastings, 1982) and through computer simulations (Reddingius and Den Boer, 1970, Lefkovitch and Fahrig, 1985). However, some theoretical studies have suggested limitations on the theory. Gurney and Nisbet (1978) found that dispersal increases stability only if the number of occupied local habitat sites is above a certain threshold. Vance (1984) found that if population density strongly suppresses birth rate, then dispersal can actually decrease overall population stability. However, several field studies support the theory (e.g., Den Boer, 1981; Fahrig and Merriam, 1985; Root and Kareiva, 1984). Therefore, the risk spreading theory can be considered to be proven. However, some theoretical studies suggest that there may be some assumptions which limit the range of cases to which it is applicable. The full extent of these limitations must be determined through further study.

My final example is the 'resource concentration theory' proposed by Root (1973) to explain the density of insects on host plants. The theory states that insect herbivores are more likely to find and remain on host plants that are in large concentrated stands. Stanton (1983) conducted a survey of the literature and found the theory to be supported and refuted in approximately equal numbers of cases. Again, the fact that all species do not conform does not invalidate the theory, it merely restricts its applicability. In general the dispersal characteristics of a species will have an important effect on whether or not the resource concentration theory holds in nature. For example, if a species detects host plants at random and egg-laying rate does not depend on the size of the patch of host plants, then the reverse of the resource concentration theory occurs (Fahrig and Paloheimo, 1987).

It is clear then that theories in ecology range from those which apply to only one or a few ecological systems, to those which apply to a large number. When theories are initially proposed, it is hoped that they will have a wide range of applicability. Once the theory has been demonstrated to hold for at least some real ecological systems, it can be considered to be proven. However, the complete range of applicability is not known until many further theoretical and empirical investigations have been completed. Depending on the theory, discovery of this range of applicability may take a considerable length of time.

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