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Hypothetico-deductivism and the competition controversy in ecology

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Integrating interspecific competition with other factors that affect ecological communities can be regarded as the theoretical core of the competition controversy. Prevailing competition theories are built on the extrapolation of the analytic principle of competitive exclusion to the community level, but ecological realism is lost in the process. The basic methodological problem in the dispute is to unite analysis with synthesis, i.e. to achieve a synthetic view of communities. The hypothetico-deductive ideal of science, often considered in ecological contexts to be *the* method of doing science, has had a paradoxical role in the controversy, while both adherents and critics of the "theory of competition" have sought support from the ideal. A solution to the apparent contradiction recognizes that the domain of the hypothetico-deductive procedure comprises only specific tests under strictly defined conditions, but this alone is insufficient in determining the fate of ecological theories. With respect to interspecific competition, broad, synthetic hypotheses are needed that try to integrate competition with other ecological factors. Specific tests are a necessary link in the research strategy, but theories should be regarded also as synthetic hypotheses that are tested in the course of a long cognitive process.

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1. Introduction

The hypothetico-deductive ideal of science, based on Karl Popper's (1959, 1963, 1972) philosophy, has had a paradoxical role in discussion of the role of interspecific competition in modern ecology. Interest in competition as a structuring force of ecological communities has increased since the early 1960s, and some (Fretwell, 1975; see also Cody & Diamond 1975, McIntosh 1980) have associated this increase with the incorporation of hypothetico-deductivism into ecology. On the other hand, one feature of recent criticisms of competition models has been the accusation that competitionists have neglected basic requirements of the hypothetico-deductive ideal (e.g. Peters 1976, Simberloff 1980, Strong 1980, Wiens 1982).

Hutchinson (1975) summarized his view on studies of the competitive exclusion principle and the role of interspecific competition in communities by stating that "the relation of theory to observation and experiment has been very satisfactory and continues to develop fruitfully". On the other hand, criticism has been raised especially against the relationship between observations and theory in competition models (Wiens 1977, 1982, Strong et al. 1979, Connell 1980, Simberloff 1980). This contradiction of views brings forth the theoretical and methodological core of the competition controversy: how to integrate singular observations (statements) of interspecific competition into a wider theoretical frame in community ecology?

In this article I shall discuss the role of hypothetico-deductivism in ecology, taking the competition controversy as my focus. My intention is not to try to add another review of interspecific competition to the swelling literature (e.g. Pianka 1976, Wiens 1977, Diamond 1978, Connell 1975, 1980, Thomson 1980, Jackson 1981, Arthur 1982). Instead, I am interested in *why* such contradictory views on the state of the art should arise on the basis of basically similar methodological ideals?

2. The hypothetico-deductive procedure

In ecological contexts the hypothetico-deductive ideal, derived explicitly from Popper (1959, 1963, 1972), is usually presented as the procedure of scientific reasoning (Fretwell 1972, Stenseth 1977, Gilbert 1980, Jaksić 1981). According to this scheme, the correct procedure can be reduced to an algorithm comprising six steps (Fretwell 1972: xiv): (1) speculation, (2) formal hypothesis formation (model building), (3) deduction-prediction, (4) data gathering, (5) data-hypothesis evaluation, (6) =(1) explanation-speculation (if data refute prediction), and/or (6) = (3) new prediction (if data verify prediction). In the following I shall call this scheme *the hypothetico-deductive procedure.* In the competition controversy, reference to the hypothetico-deductive procedure has mostly been connected with the demand of considering alternative explanations (hypotheses) to interspecific competition (e.g. Wiens 1977, 1982, Connell 1975, 1980), or testing the conclusions against properly formulated null hypotheses (Simberloff 1978, Strong el al. 1979, Connor & Simberloff 1979).

An important concept in Popper's philosophy of science, lying at the basis of the hypothetico-deductive procedure, is falsifiability (Popper 1959). According to Popper, scientific theories are conjectures that can only be falsified, not verified. From the logical asymmetry between falsification and verification Popper defines his criterion of demarcation between science and metaphysics — scientific theories are falsifiable in principle by some specific observations contradicting predictions derived from the theories, whereas metaphysical theories cannot be tested against observations. Science proceeds through falsification of old hypotheses (theories) and a creative invention of new ones. Popper's own formula for the development of science is as follows (Popper 1972):

$$P_1 * TS * EE * P_2,$$

where P_1 = problem, TS = tentative solution (hypothesis), EE = error elimination (refutation), and P_2 = (new) problem. A cycle from problem to problem is formed, with hypotheses (TS) and refutations (EE) as intermediate steps between old and new problems.

The hypothetico-deductive procedure, as formulated in ecological discussions, conforms to the Popperian scheme in two important respects: First, the procedure is falsificationist, in that falsification, but not confirmation of hypotheses is possible. Second, the tentative or speculative character of hypotheses is often emphasized by maintaining that former experience or data have no role in the invention of explanatory hypotheses; matching up hypotheses and data can only be done afterwards, by testing specific predictions of the hypotheses (see Fretwell 1972).

Epistemologically an important problem lies hidden behind the Popperian scheme, namely: How can a tentative solution (hypothesis) be shown to be wrong? According to the scheme, the hypothesis is falsified whenever observations contradict predictions. In Popper's terminology, observations are described by "basic statements" (Popper 1959). But in order to contradict predictions of a hypothesis, some basic statements must be known to be true. How is this possible, if we cannot have any definite positive knowledge about reality?

Popper (1959: 105–106) answers: "The basic statements at which we stop, which we decide to accept as satisfactory, and as sufficiently tested, have admittedly the character of *dogmas*, but only in so far as we may desist from justifying them by further arguments (or further tests) . . . Basic statements are accepted as the result of a decision or agreement; and to that extent they are conventions" (emphasis in the original). In other words, the epistemological basis of Popperian error-elimination is conventionalism (see e.g. Ruml 1965, Bayertz 1977, Haila 1980). The conventionalism of basic statements is accentuated by the prevailing view of the theoryladenness of single observations, which means that the acceptance of basic statements depends on some pre-existing theoretical frame that gives significance to them. The thesis of theory-ladenness is stressed also by Popper (e.g. 1959).

This falsificationist conventionalist view of scientific theories leads to a relativistic attitude toward science in general, formulated by Fretwell (1972:ix) as follows: "The H-D scientist is never quite certain where he stands relative to the real world. He does not "believe" that a particular theory is or is not true, and does not talk much about facts, scientific or otherwise. Ideas play an important role in his investigations, and any sets of definitions or models that permit a clearer grasp of particular ideas are valuable research tools."

This relativism does not affect the logical validity of the procedure. Once the basic premises have been adopted, based on conventions or whatever, the algorithm can be used. In the same vein Van Valen (1982) emphasizes that the logical validity of deduction does not depend on the truth of the premises. The conventionalism and relativism inherent in the scheme, however, affect the role it can be given in the epistemological foundations of any branch of science, like ecology. I shall return to this problem after a more thorough look at the competition controversy.

3. The competition controversy

In many recent textbooks on ecology a specific "theory of competition" is presented as an ecological subtheory, often connected with "niche theory". I understand the competition controversy as a quest for the status of this subtheory in the corpus of modern ecology; is "interspecific competition" an essential part of ecological thinking?

The development of modern competition and niche theories is usually divided into three phases (Krebs 1978, Hutchinson 1978, Diamond 1978, McIntosh 1980, Simberloff 1980, Jackson 1981):

(1) The original phase was represented by the "new natural history" (see McIntosh 1980) that tried to document factors affecting natural populations along Darwinian lines, although mostly in a descriptive fashion. Not only abiotic factors but also biotic interactions were found important in many instances. Interspecific competition was emphasized especially among plant ecologists (see Zavadskij & Gall 1980, Jackson 1981); naturalists soon noticed that space is limited resource for which plant individuals of both the same and different species often compete. In particular, the phenomenon of succession led both plant and animal ecologists to assume that interspecific competition has significance in nature (see Elton 1927).

(2) The analytic Lotka-Volterra population models of the 1920s represented the next step. The models were developed as extensions of the logistic model of population growth. They tried to give an analytic expression to the effect that competing populations have on each other's growth, and to define the critical parameters needed to describe the process.

(3) Laboratory experiments, pioneered by Gause and continued later by workers such as Park and Birch (see Krebs 1978) constituted the third phase. Gause (1934: 61) explicitly expressed his indebtness to the Lotka-Volterra models. The aim of his laboratory experiments was to "verify" the equations by estimating values of the critical parameters and comparing them with expectations.

Widely differing opinions were held regarding the relevance of these results. Natural history early in the century was characterized by a theoretical dispute between organismic and individualistic views on communities, the former emphasizing biotic and the latter abiotic interactions (McIntosh 1980, Simberloff 1980). The analytic models were criticized for lack of realism, and their significance remained an open question for a long time (Park 1939, Kingsland 1982). The relevance of the laboratory experiments was also put into doubt by asking whether any inferences could be drawn from the results with respect to complicated natural situations (e.g. Smith 1952). The early steps (summarized by Gause 1934), however, showed that it was both theoretically feasible and observationally and experimentally evident that under strictly defined conditions interspecific competition affects the growth of populations.

Present theories of competition and niche have more or less grown from the soil of these early findings. According to Jackson (1981), the evolutionary synthesis influenced greatly the ideas of Lack and Hutchinson in the 1940s by underlining evolutionary consequences of population dynamics. The prevailing theories developed from inquiring how interspecific competition might affect communities. I divide the community level inferences schematically into three categories:

(1) The principle of competitive exclusion as an ecological "law" or rule. The principle states that species with identical niches cannot coexist. The principle is usually called "Gause's principle", although Gause never formally stated it (Krebs 1978); in fact, Gause (1934: 98) expressed rather strong reservations concerning the verification of competitive exclusion in natural conditions. I return later to the different interpretations that can be given to the principle.

(2) Ecological inferences accepting the principle of competitive exclusion as a substantial statement that predicts the structure of ecological communities, that is, the acceptance of interspecific competition as a primary agent structuring communities. In the ecological time scale, interspecific competition was assumed to result in resource partitioning between community members (Schoener 1974), species packing in a crystal-like fashion (McArthur 1972, Cody 1975), or realization of a limiting similarity between species of the same community (MacArthur & Levins 1967). This view of competition was firmly anchored in the Hutchinsonian conception of the niche (Hutchinson 1958) through the indentification of interspecific competition as the sole factor determining the difference between fundamental and realized niche (see Connell 1975). Observational evidence for the ecological effects of competition was mostly sought through examination of "natural experiments" (Diamond 1978), as in insular conditions where niche shifts (Diamond 1973) or density compensation (MacArthur et al. 1972, Yeaton & Cody 1974) could be interpreted as a result of differences in competitive pressure.

Competition, as *the* force structuring communities, was also assumed to lead to specific, repeatable patterns in community structure in different parts of the world (Cody 1974, 1975). The concept of "diffuse competition" was adopted (MacArthur 1972, Pianka 1974), so that the species involved in competitive interactions need not be identified, but it suffices to assume "a little bit of competitive inhibition by a lot of other species" (Pianka 1974) against any community member.

(3) Far reaching conclusions about the evolutionary consequences of interspecific competition or the coevolution of competitors. Evolutionary conclusions naturally follow from ecological premises, while ecological interactions of today can be assumed to lead to evolutionary consequences tomorrow. The integration of ecology and evolution also leads to difficult problems, however. If interspecific competition is not observed in a particular community, one may always claim that it is there in the evolutionary time scale and has already caused niche segregation; contradictory conclusions can be drawn from the same premises (see e.g. Wiens 1977, Connell 1980).

Analytic models have been derived for the coevolution of competitors that regard the coefficients of Lotka-Volterra equations as variables subjected to evolutionary change (see Roughgarden 1979). Substantiating evidence for the coevolution of competitors has been sought from the size-ratios of coexisting species utilizing similar resources (Hutchinson 1959, Schoener 1965) or from character displacement of competing species in regions of sympatry (Brown and Wilson 1965).

The criticisms against competition theories can also be divided into three categories, depending on which part of the theory has been questioned. The first class of criticism asks whether specific evidence for interspecific competition claimed by competitionists is valid. One of the first thorough studies in this vein was Grant's (1972, 1975) review of the evidence for character displacement. He found out that even in the classical case of character displacement, the difference in beak length between the nuthatches *Sitta neymayer* and *S. tephronota* (Grant 1975), the observed difference between sympatric and allopatric populations of the two species corresponded to geographic clines within the two species. Levinton (1982) studied another seemingly evident case of character displacement of two Atlantic mud-snails and found that it was extremely difficult to relate the size differences between individuals of allopatric and sympatric populations to differences in resource use. This finding emphasizes the point made by Connell (1980) that it is not enough to find a difference between species; the genetic basis of the difference as well as its relevance to resource use should also be shown. In his review of island land bird communities, Abbott (1980) emphasized that the habitat composition and resource level of islands compared with mainland conditions has only rarely been examined, despite the importance of such factors in affecting the habitat distribution and abundance of bird species (i.e. the components of niche shifts or density compensation). The significance of size patterns was questioned by Hespenheide (1973, 1975) and Wilson (1975), who showed that the size of a predator and the size of a prey do not parallel each other so deterministically as often assumed. Even the existence of regular size ratios in natural communities has been questioned by Wiens & Rotenberry (1981) and Simberloff & Boecklen (1981); for a review, see Wiens (this issue). Arthur (1982) summarizes his overview of the evidence for evolutionary consequences of interspecific competition by stating that in very few instances has the causal effect of interspecific competition on the variation of a character been conclusively demonstrated. A particularly bothersome concept is "diffuse competition" — if the participants in competitive interactions cannot be strictly defined, how can the reality of competitive interactions be demonstrated and measured?

A second class of criticism has pointed out that factors other than interspecific competition (e.g. environmental variability (Wiens 1977) or predation (Connell 1975, 1980)) may also play a role in community determination. Such alternative factors tend to be glossed over in standard competition explanations of community organization.

The most penetrating criticism, however, has questioned whether the underlying assumptions of competition theories are sound. The most important of the underlying assumptions is that natural communities are in general in equilibrium with environmental resources, or that they track resources very finely (Cody 1980, 1981). As it has been pointed out (Wiens 1977, 1980, Simberloff 1980), however, equilibrium is usually assumed as a fact without any search for tests. Heck (1976) showed that equilibrium assumptions are critical to the models of species packing and that the models become quite suspect if the underlying assumptions are not valid. Łomnicki (1980) asked whether the assumption of equality of population members underlying the logistic equation (and competition models derived from it) are realistic. If the equivalence of individuals within a population is not accepted, population growth patterns may deviate substantially from those predicted by the models.

Doubt has even been expressed as to whether natural communities in the sense assumed in competition theories are real (see Wiens 1980). Since the work of MacArthur (1972) it has been customary to define communities as collections of species living at the same place, where the scale is defined on the basis of convenience. The problem, however, is that different species living at one moment at one place may at other times be subject to very different conditions (Herrera 1980, Wiens 1981); what is, then, the "correct" scale in time and space? Variability in time and space may produce a fundamental change in the Darwinian landscape of selective pressures (Taylor & Taylor 1977).

To sum up, discussions of the competition controversy have shown that the "theory of competition" is not the unproblematic ecological subtheory that has been assumed in some textbooks of the 1970s. What kind of methodological generalizations can be made on the basis of the controversy?

4. Analysis and synthesis in theory construction

The problem of integrating *analysis* with *synthesis* is methodologically at the core of the competition controversy. Wiegert (1978) gives an intuitively appealing definition of the concepts by regarding analysis as the study of the component parts of a system and synthesis as the study of the whole.

I regard the principle of competitive exclusion, lying at the basis of the controversy, as an analytic "law" or rule. In the analysis of the principle I make use of the original work by Gause (1934), although the principle in the strict sense was formulated only later. Gause (1934) defined his task as the study of the "elementary phenomena" of struggle for existence in the "laboratory microcosm". Here the terms "elementary phenomena" and "laboratory microcosm" refer to the strictly controlled conditions of the laboratory.

Competitive exclusion is a "rule" if it is a result that necessarily follows from the basic assumptions. Empirical validation of this kind of rule can be achieved by showing that the basic assumptions are real at least in some conditions, i.e. that such a thing exists as competitive interactions between species. It follows that in *some idealized conditions* competitive exclusion will be the result. This was demonstrated by laboratory experiments, in a procedure called "steps of verification" by Gause (1934: 61). Note that nothing is implied about the generalizability of the underlying basic assumptions in this formulation of the rule.

The recognition of Gause's principle as an analytic rule means that it is futile to try to "refute" it. Rather, the real problem is *what does this rule mean for ecological theory in general?* There are two necessary, complementary research tasks in attacking this problem:

(1) Demonstrations and tests of how competition works (if it works) in specific natural situations. Controlled tests, preferably based on experiments (see Connell 1980) are needed, and this task can thus be characterized as the domain of the hypothetico-deductive prodedure. The tests are based on the *ceteris paribus* principle, i.e. initial conditions must be fixed. This requirement means, in turn, that naturalistic observations in the vein of the "new natural history" of the turn of the century, as praised by Diamond (1978), are not enough, as alternative explanations cannot be ruled out (cf. Connell 1980).

In some cases specific tests have yielded positive evidence for the reality of competitive interactions between some species pairs (see Connell 1980). The problem of specific tests is often that not only the alleged result of competition but also the *mechanism* of competition should be shown. For example, Högstedt (1980) determined the mechanism of resource competition during the breeding period between the Magpie (*Pica pica*) and the Jackdaw (*Corvus monedula*) that led to reduced reproductive output of magpies, and Svensson (1978) identified competitive interactions during the period of territory acquisition as the reason underlying the mutually exclusive pattern of habitat selection between two *Acrocephalus* warblers (*A. schoenobaenus* and *A. scirpaceus*). For additional examples, see Alatalo (this issue) and Vepsäläinen (this issue). Naturally, *negative* results of specific tests of interspecific competition in situations where established theory leads one to expect competition are equally important, although they have probably been published more rarely than positive results.

(2) The step of synthesis between competition and other ecological factors, that is, finding an answer to the questions: What is the role of interspecific competition in complex ecological situations *even if it is real* between some members of the community?

The methodological problem with a synthesis is that it cannot be achieved simply by an extrapolation of analytic rules. To be successful, a synthesis should reflect the way in which totality is formed of the component parts in reality. The problem is that a totality is not formed in a straightforward fashion from simple elements, but includes conflicting interactions between different components, especially because time, the real history of the system, is an essential dimension. Thus, even if competition has been confirmed as an analytic principle and observed as a fact in some specific situations, the problem of a synthetic integration of these principles with other possible ecological factors remains.

An approach typical of analytic scientific traditions that take analytic abstracta for reality (Ruben 1974), or "reify" them (Levins & Lewontin 1980), is simply to extrapolate and generalize accepted analytic principles. This is the methodological approach that led to the development of "niche theory" and the conception of "species packing", which are based on the extension of the analytic Lotka-Volterra equations to the community level. A serious problem arising in this procedure, however, is the loss of realism of basic assumptions. Jackson (1981) is thus right when he claims that the firm connection between the Hutchinsonian niche and theories of interspecific competition has produced a strong bias in the general comprehension of competition in modern ecology; the bias is expressed as the acceptance of the Lotka-Volterra niche conception and the equilibrium assumption. These premises are, however, premises of the analytic principle of competitive exclusion. It is quite another question whether they are useful when we try to synthesize interspecific competition into ecological theory.

An alternative to the extrapolation of analytic principles is a synthetic, dialectic (*sensu* Levins & Lewontin 1980) view of communities. This can be realized by considering simultaneously all the processes affecting populations in ecological communities and by trying to find theoretical concepts that can be used in describing and studying the total process. One candidate is the Darwinian concept of the "struggle for existence", used by Darwin as a synthetic principle uniting all the processes that present challenges to members of populations in the real world (be they caused by physical stress and disturbance, habitat structure, predation, competition, or whatever), and affecting the reproductive success of individuals (for Darwin's methodological approach, see Mayr 1982: 482-485). Gause utilized the Darwinian principle in his book bearing the same title (Gause 1934) by classifying the factors of struggle for existence into intra- and interspecific, and direct and indirect ones. ("Direct" factors refered to predation, and "indirect" to competitive interactions). The same tradition has been continued by, for example, S.A. Severtsov (1937), Gall (1976) and Zavadskij & Gall (1980). Shmalgauzen (1969, see also S.A. Severtsov 1981) analyzed the selective pressures on populations by using the concept of the struggle for existence as a synthetic expression for the overall total of all biotic and abiotic factors. In the same vein, Grime (1979) integrated different stress factors of plant populations under similar concepts.

Of course, the formulation of a concept is less important than its contents. The problem is to integrate the (analytic) principle of competitive exclusion with all of the other processes that may affect the ecological and evolutionary existence of populations. Much of the criticism against current competition theories is related to this statement; Wiens (1977, 1982) and Connell (1975, 1980), for example, have emphasized the need of integration of all relevant factors into the understanding of ecological communities.

Is there any use for analytic generalizations that are extrapolated from the basis of simple analytic models and principles? Several affirmative answers can be given. Firstly, analytic generalizations help to advance the theoretical development of science by making things clearer; analytic models must be studied strictly as models, to explore their hidden premises and limiting conditions (e.g. Levins 1968, Maynard Smith 1974). Analytic models also draw attention to important and substantive problems (Haila & Järvinen 1982). Secondly, analytic models may lead to complex mathematical derivations that seemingly stay very far from reality but that nonetheless bear on real situations by indicating possible outcomes of complex processes (see Lewontin 1980). Thirdly, it may be possible to find in nature situations simple enough for testing directly theoretical ideas derived from analytic models. Thus, Hanski (1980) derived from simple difference equations a model predicting the coexistence of species competing exploitatively with each other in a patchy habitat, and was able to test the model with experimental data.

5. On the role of hypotheses in ecology

It is generally accepted among philosophers of science that the Popperian hypothetico-deductive procedure does not exhaust the role of hypotheses in science. On the contrary, hypotheses have played an important role in scientific methodology for a long time, but in a wider meaning than in the hypothetico-deductive procedure as it is understood in ecological discussions (see von Wright 1972, Suppe 1977, Merkulov 1980, Laudan 1981). In a broader context, hypotheses can be characterized as preliminary, general assumptions about reality that bring together apparently separate facts or subtheories. Deduction of consequences and comparison of them with observations (i.e. hypothetico-deductivism) is a part of this wider understanding of hypotheses that might be called, following Hempel (1966) and Laudan (1981), *the method of hypothesis*. The essential difference from *the hypothetico-deductive procedure* (see Sect. 2) is that the logical form of the hypothesis is not restricted as it is in the Popperian scheme. Thus, for example, deductive hypotheses have a central role in evolutionary biology although they cannot be tested by the standard hypothetico-deductive procedure (Van Valen 1976, 1982).

In order to illustrate the need for different types of hypotheses I take three examples from recent ecological papers bearing on the competition controversy:

(1) Wiens (1977) suggested that populations may be subjected from time to time to "ecological crunches" in variable environmental conditions. These crunches may nullify the assumptions of competition theory and affect significantly the composition of natural communities.

(2) Wiens (1982) pursued further the problem of community equilibrium by suggesting that equilibrium and nonequilibrium could be regarded as a continuous spectrum, and a major objective of community ecology should be to place various communities at positions along this spectrum. The idea is similar to that of Grime (1979), who tried to classify plant communities according to dominating factors of struggle for existence. Both Grime (1979) and Wiens (1982) argue that interspecific competition should have variable role in communities situated in different places of their respective classifications.

(3) A specific problem of the niche theory has been that quantitative data have not been incorporated into the models (e.g. Levins 1968). Recently Hanski (1982a) presented an hypothesis that species inhabiting patchy environments can be divided into "core" species, which are regionally widely distributed and locally abundant, and "satellite" species, which are regionally patchily distributed and locally sparse. He suggested that competitive interactions should primarily affect the abundant core species, and he found preliminary support for this suggestion from North European bumblebee communities (Hanski 1982b and this issue).

All the three hypotheses presented above are synthetic in the sense that they try to integrate several factors affecting community composition. Obviously, they cannot be tested by the simplified hypothetico-deductive procedure, but other aspects, like mutual congruence of the underlying subhypotheses, must be studied as well.

The presentation of hypothetico-deductive procedure as *the* method of science is a child of the analytic thought patterns prevailing in the Western scientific community. This has also greatly affected the competition controversy, both through the formulation of competition theories as analytic generalizations and through the relatively slow development of more synthetic views on community processes. If the need for a broad, synthetic view on communities is accepted, concentration on specific tests is not likely to be a very impressive research strategy; specific tests are imprisoned in the conceptual structure of the hypotheses that are tested.

A common denominator of the three examples is, furthermore, that *ecological realism* of the models is emphasized. But the concept of ecological realism has interesting epistemological implications. If the relativism inherent in the hypothetico-deductive procedure (*sensu* Fretwell, see Sect. 2) is accepted, it does not make sense to speak of ecological (or any other type of) realism.

How can the ecological realism of our theories be improved? The strategy of model building of Levins (1966, 1968) presents an approach to this goal. According to Levins' scheme, model building starts with the identification of basic parameters ("a set of sufficient parameters"). By these parameters models are directly connected to the ontological commitments, that is, the entities and processes crucial to the models must be consciously determined. The final succes of a specific model also depends on the realism of the sufficient parameters. An example can be taken from the niche theory. Usually the niche of a population is defined on the basis of resource utilization, following Hutchinson (1958) (see e.g. Cody 1974, 1981, Diamond 1978), but an alternative would be to define niche, following Levins (1968: 40), as "a fitness measure on an environment space". The two definitions have quite different implications with respect to relevant research problems and design (see also Emlen 1973: 211–213).

Models can be regarded as tools invented or constructed in order to tackle aspects of reality in a scientific manner. Thus, Kingsland (1982) concludes that the value of the analytic population models of the 1920s was finally understood when the tool character of the models was accepted, and Jackson (1981) claims that the Lotka-Volterra competition models taught ecologists to think in terms of evolution. Synthetic theories can also be regarded as tools in the sense of heuristic research programs that help to identify important problems worth studying in detail and to integrate details together. Not single hypothetico-deductive tests, but a long process of cognitive work and factualization of the theories (Krajewski 1977, Haila & Järvinen 1982) determine their fate. Methodological pluralism (but *not* relativism) in needed, acknowledging that science, in facing the complexities of reality, requires different approaches in different situations.

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