

THE STRATEGY OF MODEL BUILDING IN ECOLOGY, REVISITED

Peter J. Taylor  
Energy and Resources Group  
University of California  
Berkeley, CA 94720, U.S.A.

Running head: Modeling strategies in ecology

October 27, 1987

## ABSTRACT

The Strategy of Model Building in Ecology, Revisited.

Peter J. Taylor, Energy and Resources Group, University of California, Berkeley, CA 94720.

This paper analyzes strategies of model building in ecology twenty years after Levins advocated the use of simple models to generate supposedly qualitative and general biological insights. Modeling has five aspects: elevation of biological processes, construction and analysis of the model, and of observations, analysis of correspondence between the model and observations, and model-based action. I distinguish four different roles we can assign to models: schemata, exploratory tools, redescriptions, and representations of generative biological relations. In the analysis of correspondence fidelity of fit and accuracy of predictions are insufficient evidence that a model represents the biological processes that generated the observations. In order to confirm the model a variety of "accessory conditions" need to be established; these are often overlooked and difficult to establish, especially in the case of simple models of naturally variable situations. I reinterpret the strategy of using simple models in community ecology as exploratory. The simplicity may ensure mathematical generality but not ecological generality; the models are only suggestive of -- not support for -- ecological hypotheses. Generality in ecological theory will require much more particularity.

## KEYWORDS

Modeling strategies, ecology, analysis of correspondence, confirmation, accessory conditions, simplicity, generality, particularity, Levins, MacArthur.

Particularism often has a special appeal to Americans, raised in our empiricist intellectual tradition. Its special danger lies in the propensity to accumulate facts like so many grains of sand to produce merely bigger and bigger sand piles. Generality without particularism, on the other hand, tends to abstract from questions on mechanism, and thus fall into the opposite danger of imputing an autonomous cumulative motion to phenomena... Both extremes are the products of impatience, of the wish to obtain "hard" results, coupled with an intolerance for inconsistencies and uncertainties, which are not merely unavoidable in the study of a complex subject matter but which constitute its inherent appeal.

Wolf (1974:30)

In a frequently cited American Scientist article of 1966 Richard Levins sketches a "strategy of model building in population biology." He favors the sacrifice of "precision to realism and generality." For Levins a simple model is necessarily "false, incomplete [and] inadequate"; nevertheless we can use it to generate qualitative and general insights. We can interpret discrepancies between the model and reality to imply the need for some additional biological postulate(s). Qualitative insights and discrepancies together enable us to generate interesting questions to investigate until the model becomes "outgrown when the live issues are not any longer those for which it was designed" (Levins 1966).

I will focus on this paper on modeling in ecology and re-examine Levins' strategy of model-building. In ecology the strategy was equally well that applied by Levins' colleague, MacArthur (1972), perhaps its most influential proponent, and advocated by MacArthur's former teacher, Hutchinson (1978). So let me call this strategy the "MLH" (MacArthur-Levins-Hutchinson) strategy. Models have proliferated since 1966 in both ecosystem ecology and community ecology. And, although contemporary models demand of ecologists a high level of mathematical sophistication (e.g. Schaffer 1985), the MLH strategy has endured, remaining popular and influential (Kingsland 1985).

In recent years, however, there has been a strong reaction against ecological theory drawn from simple, general models (Simberloff 1980, 1982; Strong et al. 1984). The thrust of this reaction is that modeling should be replaced by "investigation" (Simberloff 1982). The argument goes as follows: There are many factors operating in nature and in any particular case at least some of these will be significant. A model cannot capture these and still have general application. Instead, we should investigate

particular situations and experimentally test specific hypotheses about these situations, guided by and adding to knowledge about similar cases.

This "particularist" reaction has been criticized and the MLH strategy defended from various standpoints, from that of dialectics (Levins and Lewontin 1980), of commonsense (Roughgarden 1983), and of pluralism (May 1984, see also Hall and DeAngelis 1985). There is, however, a significant point of unity between the opposing intellectual armies. They share in common the belief that models are intended to be representations of reality, necessarily "caricatures" of reality simplified according to the modeler's stated or implicit purpose, but nonetheless statements about the real world and subject to refutation. For MLH modelers, conclusions that are drawn from models having a minimum of assumptions about particular biological detail are considered applicable to broad classes of ecological situations (Post et al. 1978). In the particularist response, in complementary opposition, such conclusions about biology are rejected if there is an alternative "null" hypothesis or random model that fits the observed data equally well. In both approaches reality and model are related in a simple, direct way (Fig. 1).

In this paper I present a different view of the modeling process. (Although I concentrate on modeling in community ecology the framework could also be employed for ecosystem ecology and simulation modeling, for population genetics, and other fields.) I distinguish four different roles or interpretations which we can give to models: schemata, exploratory tools, redescriptions, and representations of generative biological relations. (These roles are equivalently four broad classes of intent with which we engage in modeling.) I analyze the modeling process in some detail and make, or emphasize, certain distinctions where other authors have not. In particular, when the correspondence between a model and observations is analyzed, fidelity of fit and accuracy of predictions are insufficient evidence that a model represents the biological processes that generated the observations. There are, in addition, a variety of "accessory conditions" that we need to establish in order to confirm the model. These accessory conditions are often overlooked and difficult to establish. With this requirement in mind I reinterpret the MLH strategy and the use of simple models in community ecology as exploratory modeling. The simplicity may ensure mathematical generality, but not ecological

generality; the models are only suggestive of, not support for, ecological hypotheses. Generality will require much more particularity.

In calling for greater discrimination in thinking about the relationships of models to reality, I am not advocating concentrating on the "truth" status of models. On the contrary, my paper is intended to stimulate modelers and philosophers to turn their attention to what modelers actually do when they model. To the extent that modelers are prepared to act as if their models represent nature and to generalize from models which are only locally true or perhaps even false (Wimsatt 1986), students of models need to examine the actions of modelers, not simple the degree of confirmation of their models (Haila 1986). The framework of this paper then facilitates subsequent work which would examine the different factors influencing the decisions that modelers make during the modeling process -- decisions about the questions to put to nature, the observations to make, the analyses to perform, the degree of confirmation to accept, the vigor of attempts to disturb acceptance of explanations and, most importantly, the subsequent actions (including research) to take based on the outcomes of any particular modeling exercise. As an observation of the history and sociology of biology it seems that the practical importance of a model corresponds not just to its confirmation as a representation of biological reality. In addition, a model is important to the extent to which modelers can employ the model to mobilize the activities of a discipline around it, and to the extent that the model resonates with the commitments of that discipline (Shanin 1972, Yoxen 1980, Haraway 1981). Having signaled this larger scope for a studies of modeling I will, however, focus here on the smaller, simpler topic: the work of modelers as it relates to explanation of ecological processes.

## I. PRELIMINARIES

Before I present my analysis of modeling I will make some preliminary statements about explanation and about confirmation of models. These statements will be brief -- a conceptual "Materials and Methods" section -- but their significance will become clear in the subsequent discussion.

### A. Explanation

All explanations have a causal structure: a phenomenon is claimed to be an outcome of a previous sequence of phenomena; the past provides a sufficient set of conditions for the present to have occurred. A causal structure of explanation is not synonymous with having a basis for positive predictions of future phenomena. In most explanations there are too many contingent conditions for any component of the sequence to be deduced via a general law from the preceding components. We associate these explanations with history and narrative. We recognize readily that they are provisional, being subject both to competition from other "plausible stories," each providing a sufficient set of conditions to account for the phenomenon, and to analysis in greater detail, "lightening the weight of causality" (Foucault 1981) borne by the original and less specific set of conditions.

A special form of explanation is favored in the sciences that make extensive use of controlled experiments. Historically and locally contingent conditions are minimized so that we can specify the necessary and sufficient set of conditions to explain a phenomenon. We attempt, moreover, to subsume the phenomenon as a particular case of a general phenomenon and thereby generate positive predictions for situations not yet observed. I will call such explanations "generative," in contrast with "historical" explanations. (See Goudge (1961) and Taylor (1987a) for an examination of historical and generative (=systematic (Goudge) or selectionist (Taylor)) explanations in the context of evolutionary theory.)

Although models can form part of either historical or generative explanations, I will argue that because of the high status given to generative explanations and predictions, mathematical modelers often elevate their models prematurely to the status of generative explanations. To support such an argument it is helpful to draw attention to the conditional form of the model-based explanations. When models are used in explanation they are used metaphorically: If we think that there are categories and processes in nature corresponding to the ones in the model, then, when the model has an outcome that matches some natural outcome, the model is a satisfactory explanation for the natural outcome. Many of the distinctions I make between different roles given to models will be based on the type of support (or lack thereof) for the condition of correspondence between nature and the model. In particular, when we use a

model in a generative explanation it should be confirmed, the subject of the next section.

## B. Confirmation

Every model has two faces. On the one side there is some distinguishing feature(s) by which the model is known. For example, the logistic equation is synonymous with the principle that the per capita growth rate of the modeled population declines linearly with increasing population size. On the other side there are the accessory conditions. These are inevitable if we intend the abstractions of the model to be relevant to the original phenomena of interest. For example, the logistic equation is self-contained as a mathematical system, yet as a model of biology it involves, in addition, conditions such as: the "environment, with respect to all properties that perceptibly affect the organisms, is constant in space -- and time" (Williams 1972).

A model is confirmed, that is, we are justified in acting as if the model represented generative biological relations, if two criteria are fulfilled (Lloyd 1984). The first is that the model fits the observations better than the corresponding model without the distinguishing feature. The second is that accessory conditions have been established, and established independently of the fit used to fulfill the first criterion. Of course, there are degrees of confirmation, according to the degree of fit, the strictness with which the accessory conditions have been established, and the variety of circumstances in which the two criteria are fulfilled.

Not only is confirmation relative, but it is provisional, contingent both on the stated level of resolution and the range of circumstances in which confirmation was achieved. At some level of resolution any accessory condition will become false. For example, although organisms are abstracted as identical units in order that we can subsume them in the logistic equation into a single variable, the population measure, they are usually genetically heterogeneous (Lomnicki 1980). Similarly, in extreme circumstances the fit between a model and observations may break down, e.g. high bacterial inoculations in a one-stage chemostat generate growth that overshoots then returns to an equilibrium, in contrast with the usual

logistic-like growth (Taylor 1985).

Confirmation is not the only admissible justification for acting as if a model represented generative relations. We can compensate for false accessory conditions by stating those false accessory conditions explicitly but then arguing that their falsity is unimportant. Alternatively, we can construct a range of un- or dis-confirmed models and choose the best of these on the basis of degree of confirmation. In both cases, however, the challenge remains: to replace the unconfirmed(-able) account by an underlying, confirmable model which indicates either why the falsity of accessory conditions was unimportant or the extent of circumstances in which the earlier, unconfirmed model will fit. (Wimsatt (1986) provides a detailed study of the way in which false models can be a "means to truer theories.")

In any case, since confirmation is both relative and provisional, we should not treat confirmation as the sole purpose of modeling. Instead confirmation is an ideal; in practice, we should scrutinize and make explicit the support established for the generative status of a model, including the level of resolution and range of circumstances from which that support was derived. If this requirement is met other modelers can assess the generality of the model, whether it constitutes a satisfactory explanation within their domain of interest, and how to learn from its limitations.

## II. THE PROCESS OF MODELING AND A TAXONOMY OF MODELS

The modeling process consists of five aspects (see overview in Fig. 2):

- A. Elevation of biological processes into the biologists view;
- B. Construction and analysis of the model;
- C. Construction and analysis of observations;
- D. Analysis of correspondence between the model and observations; and
- E. Action.

In this section I elaborate on these aspects. At appropriate points in the



analysis I introduce each of the four different roles or interpretations which we can give to models: 1) schemata, 2) exploratory tools, 3) redescriptions, and 4) representations of generative biological relations. (My initial presentation of these roles will be indented to separate it from the surrounding text.) The roles are distinguished on the degree of confirmation (or lack thereof) and on the biological insight that can, correspondingly, be derived from the model. In making these distinctions I am arguing against the conflation of roles and the equivocation about purpose that occurs when a modelers defend their models as simply caricatures of reality. In the last part of this section, I examine the different courses of action appropriate to the use of models in each of the four roles.

#### A. Elevation of biological processes into the biologist's view (Fig. 3)

As biologists we determine what, at first, is to be seen of biological processes and what questions will be put to nature. What we subsequently model, therefore, is some particular elevated view of biological processes. This elevation is reflected in the extent and the degree of resolution of observations. It is also reflected in the technology of making those observations. We may use microscopes or record species cover in a quadrat. Our observations may be every hour or once a year. We may restrict them to a particular north facing slope or we may sample all dry sclerophyll forests in Southeastern Australia, and so on. Our choice of elevation is also reflected in the terms we adopt, e.g. molecular biologists using gene expression as a synonym for development, or some ecologists defining ecology as the study of interacting individuals or populations, and other ecologists, as the study of communities or ecosystems.

#### B. Construction and analysis of the model (Fig. 4)

The first step in constructing a model is to abstract from the view of biological processes and, in conjunction, to simplify the questions being asked. Abstraction consists of four parts; we:

a) aggregate, or adopt nominal kinds in order to delimit the potential

- elements of the model;
- b) select from those elements a subset that we consider relevant;
  - c) postulate relationships among these elements; and
  - d) restrict the domain of applicability of the model.

For example, in the initial work on island biogeography (IB) (MacArthur and Wilson 1967) a group of individuals of a species was taken to be the same kind of thing as a group from another species -- an element in the theory. The domain of applicability was restricted to reptiles because it was plausible that reptilian species might be affected similarly by the processes being modeled. The internal heterogeneity of each group was considered to be irrelevant to these processes. In the early work only true islands, i.e. those separated by water, were actually analyzed. The biological processes affecting the ecology of the islands were simplified to unitary processes -- immigration and extinction. In turn, these simplified processes were thought of as functions of proximity to the mainland and size of the island, respectively. The simplified question was how immigration and extinction, in opposition to each other, determine the number of species on an island.

Contemplation and subsequent adjustment of the model or question may follow the initial formulation. In IB the model became focused on the equilibrium number of species, occurring at the point of balance of immigration and extinction.

#### Role 1. Models as schemata

At this stage, the model is being given the role of a schema. The model is simply a statement of the biological processes that the modeler has defined, selected and juxtaposed for our attention. The schema may reflect insight gained from field observations and help us construct plausible historical explanations. Nevertheless, in the absence of a detailed analysis of correspondence, no generative biological explanation can be claimed. The model may, however, be invaluable in stimulating ecologists to generate and investigate hypotheses about ecology.

To express a schema in mathematical notation requires further abstraction. The terms of the, hitherto, verbal model are recast into the variables and parameters of a mathematical model. The verbal question is tightened and simplified into a mathematical question. The mathematical model is analyzed, outcomes of the model deduced, and insight about the model is gained. The results may motivate us to abstract the model further or in a different fashion in order to render the mathematics tractable. When an answer to the simple question is obtained we may adjust the mathematical model and elaborate on the initial, simple mathematical construction.

In IB theory the mathematical model of the rate of change of number of species on an island over time might look like the following:

$$\begin{aligned} \frac{dS_i}{dt} &= I_i - E_i \\ &= f_i(P-S_i) - g_i(S_i) \end{aligned}$$

where  $S_i$  = number of species on island  $i$

$I_i$  = rate of immigration of new species onto island  $i$

$E_i$  = rate of extinction of species on island  $i$

$P$  = pool of potential immigrant species

$f_i, g_i$  are functions for immigration and extinction for island  $i$ ,

having as parameters the proximity to the mainland and the size of the island, respectively.

The species equilibrium question becomes: under what conditions is  $\frac{dS_i}{dt} = 0$ ?

## Role 2. Models as tools for exploration

The analysis and elaboration of the mathematical model on its own terms, as a mathematical system, is part of the exploratory role for models. We investigate such questions as: What is the model's range of behaviors? For example, does it have equilibria or oscillations? Are they stable? How do these behaviors change as parameters change? Without any analysis of correspondence we cannot use the model for generative biological explanation. Nevertheless, if we suppose as a thought experiment that there might be actual processes corresponding to the ones in the model, then the mathematical investigation may

suggest new questions to ask, new terms to employ, different models to construct, and so on. In other words, the model is a tool for exploration (Levin 1980).

There is an uneasy tension when we use models in this role. Facility of manipulation favors simple or mathematically tractable models. However, to claim that a model corresponds to biological relations the model must eventually be subject to confirmation or contribute to another model which can be. We run the risk of building up mathematical edifices upon assumptions that were introduced primarily for mathematical, not biological reasons. We may eventually lose sight of the original thought experiment and begin to see nature in the terms of the model. For example, fitness coefficients are ubiquitous in population genetical theory and it is common to talk as if there are, in nature, alleles having the property of fitness, just as electrons have charge and resting mass. This is reification; the tension between mathematics and biology has been lost. Instead we should maintain this tension to stimulate strategic choices about when to break the cycle of theoretical interrogation and attempt to confirm the model.

### C. Construction and analysis of observations (Fig. 5)

At this point in the modeling process we have not analyzed the correspondence of the model to natural processes. Before we can establish the biological relevance of a model we need first to construct observations, adopting one of two perspectives. 1) We may seek repeatable observations and therefore isolate a system from nature and tightly control the conditions ("controlled experiments"). We can establish the outcome of altering single factors in the (newly-isolated) system under the controlled conditions. 2) We may retain the original biological context, and accept a degree of variability beyond our control (though we can exert some control over the sources of variation by generating perturbations). We then collect data in categories of our choice ("naturally variable observations"). The data obtained from either controlled experiments or naturally variable situations are then analyzed and patterns extracted from them. Such analyses require secondary models -- predominantly these are

statistical -- which refract the data in their own characteristic ways. Models for data analysis demand detailed attention in their own right but I will not pursue this issue further in this paper (see Freedman 1985 and responses).

#### D. Analysis of correspondence between the model and observations (Fig. 6)

Let me first sketch a naive view of mathematical models and their correspondence with nature. The variables of models are quantities which can be measured, e.g. population biomass or number of species. The model outcomes can be directly compared with the observed outcomes and their goodness-of-fit assessed. Furthermore, when the terms of the model have a generating or predictive power (for example, the I and E ("immigration" and "extinction") in the IB model generate the number of species), it appears that biological causality operates in the same fashion (see Fig. 1).

This view is, however, too simple. The construction of the model -- the aggregation, selection, postulation of relationships, and restriction of the domain of applicability -- introduces accessory conditions. Aggregation requires that the biological units corresponding to the mathematical variables are internally homogeneous, or, at least, the heterogeneity does not confound the model's behavior; in other words the aggregation is "coherent," and the nominal kinds are, in fact, natural kinds. Selection, in turn, requires that the elements excluded from the model -- the "hidden variables" -- do not enter into relationships which confound those postulated and incorporated into the model (Taylor 1987b). That is, the effects of the hidden variables can be incorporated as a constant, perhaps zero, effect in the parameters of the model. It may be that this condition of "quasi-independence" obtains only in a limited range of circumstances. In this case the domain of applicability has to reflect this restriction. The relationships postulated usually constitute the particular feature of the model. Nevertheless they enter also into accessory conditions, in a subtle way. The domain of applicability must reflect the circumstances in which the elements maintain the mechanistic and non-interpenetrating qualities they assume in the modeled relationships. Organisms, in contrast, often display novel behavior when found in circumstances not previously observed. For example, although barn

owls in Europe have one clutch per year, rigidly defend their territories, frequent open ground and quarter the ground in search for prey these barn owls become, in Malaysian palm oil plantations, barn owls have two or three clutches per year, do not rigidly defend their territories, perch and wait for their prey, and congregate as juveniles in social groups not observed elsewhere (Lenton 1983, Taylor 1987a).

In the analysis of correspondence we must establish the accessory conditions before we can interpret goodness-of-fit as indicating that the model represents the biological processes that generated the observations. Analysis of correspondence consists, therefore, of assessing the fit of the distinguishing features of the model and establishing that the accessory conditions hold. Without these accessory conditions the generating power of the abstracted model dissolves when the model is returned to its "ground" in biology.

### Role 3. Models as redescrptions of observations

If a model fits the observations but the accessory conditions have either not been specified or have not been established, then the model is simply a redescription or a summary of the observations. Sometimes the term "purely phenomenological" is used to describe such models. Redescrptions can, however, be used to make predictions. If the fit is close and holds in a range of circumstances we may use the model to predict ahead in time or to extrapolate into novel circumstances. However, in the absence of confirmed accessory conditions, prediction relies on the continuation of patterns already observed -- an occurrence that is sometimes supported and sometimes contradicted by our experience. So, although we might make useful predictions or extensions from existing observations and although we might improve on these by refining the redescription, to be strict, we cannot claim larger relevance for the model than the range of circumstances in which the fit was derived.

### Role 4. Models as representations of generative biological relations

We are justified in acting as if the model represented generative

relations if the model is confirmed (Sect. I.B). Of course, modelers often do act as if the model represented generative relations even when their model is not confirmed. In some cases they may have taken steps to compensate for false or unestablished accessory conditions such as constructing and comparing a range of models (Sect. I.B). In other cases they may lack the imagination, motivation or means to go beyond their existing, provisional account. Further study is needed to illuminate the variety of factors that influence modelers' adherence to a model (see Haila 1986, Wimsatt 1986).

### Role 3A. Redescriptions as apparent representations of generative biological relations

Since confirmation is provisional (Sect. I.B), any representation of generative biological relations is also provisional, contingent on the stated level of resolution and range of circumstances. In this sense all generative power is only apparent generative power. I restrict the term "apparent," however, to cases for which the model fits but, even at the stated level of resolution, either the accessory conditions have not been specified fully or established, or the domain of applicability has not been circumscribed. In effect, the model is a redescription but we want to confer on it a generative status and to interpret accurate predictions as evidence for that status (e.g. Vandermeer 1969, Pomerantz 1980, Taylor 1987b).

In Table I I summarize the four different roles or interpretations, the extent of confirmation required and the applications appropriate to each of them. I do not propose that the four roles for models are in ascending order of usefulness in providing biological insight. In the following sections I indicate their contribution to different strategies of modeling. It is primarily when models are elevated prematurely, or without justification, to a generative status that I reinterpret the insight they provide.

--- INSERT Table I about here ---

Returning to the analysis of correspondence: The distinction, made in Sect.II.C, between controlled experiments and naturally variable observations is very significant. In controlled experiments, systems have only a few components and they are isolated from their usual context. Hidden variables can be excluded or controlled. Other accessory conditions can be achieved by experimental control, e.g. the uniform distribution of organisms in space. Some accessory conditions may be more difficult to achieve, or even clearly untrue. Nevertheless, if care is taken, they can be given a clear biological interpretation and be subject to subsequent investigation. For example, in single variable, time-independent models of population growth the following accessory condition can be clearly stated: "[all] organisms [of a species] with respect to their impact on the environment or on each other, are identical through time" (Williams 1972). In experimentally controlled systems, therefore, the accessory conditions can sometimes be established or argued to be (provisionally) unimportant. Analysis of correspondence then confirms the model provided we can show that the experimental outcomes fit the model with its distinguishing feature, e.g. the linear decline of growth rate for the logistic.

For naturally variable observations, on the other hand, analysis of correspondence rarely amounts to confirmation because there are usually unexamined accessory conditions. For example, because we are concerned in ecology with observations drawn from systems with many more factors than we can explicitly model, a ubiquitous accessory condition arises, that of quasi-independence. Similarly, the elements of the model correspond to biological units which are commonly heterogeneous, consisting of age classes, genetic variants, and so on. Therefore, there is the accessory condition of coherent aggregation. These conditions are difficult to establish independently of the fit of observed outcomes and the model (Taylor 1985, 1987b). In practice we often skirt around this requirement by employing several tactics to establish biological relevance for unconfirmed models of naturally variable situations. I discuss the adequacy of these tactics in the case of MLH-type simple models in Sect.III.

#### E. Action

The preceding four components of the modeling process require us to



make many decisions -- on what level to aggregate, which elements to select, how to construct observations, and so on. We also make decisions about what action to take using the model as a basis, and the earlier decisions have significant implications for this subsequent action. I identify five broad courses of action:

- 1) accept the model in its present domain of applicability and level of confirmation;
- 2) generalize to a larger domain;
- 3) elaborate on the basis of the model;
- 4) disturb acceptance, that is, search for circumstances in which the confirmation or fit breaks down in order to show the need for more general or alternative models; and
- 5) argue for changing the status of the model.

In this section I outline these courses of action, first as each applies to confirmed models and then as each applies to models used in each of the other three roles. The exposition of a diversity of courses of action indicates that the replacement of one model by another can be approached systematically; in contrast to Levins' strategy we don't have to wait for a model to outlive its usefulness.

#### a. Generative representations (confirmed models)

1) Acceptance: If there are no discrepancies or we are prepared to assign the discrepancies to "noise," a confirmed model may provide principles of biology. The model can be used to generate the correct outcomes for situations subsequently observed, provided these situations remain within the domain of applicability.

2) Generalization: The simplest generalization is to hypothesize that domain of applicability is larger. A negative test of this hypothesis might contribute to disturbing our acceptance of the confirmed model (see 5 below). Another familiar generalization is to use a confirmed model of a controlled experiment, such as in a microcosm, to represent the relations among the components of that system which they are back in the larger system from which they were originally isolated. In Sect. III.2 I discuss the problems of such a generalization.

3) Elaboration: When biologists have a confirmed model for a controlled experiment they often use their experimental systems and skills to undertake further controlled experiments. By changing controls into variables and by adjusting the model in response to the new outcomes, a model of successively larger systems could, in principle, be constructed. This is the strategy of following reduction with resynthesis. In practice, however, experimental biologists typically use their experiment-model combination to guide their subsequent investigations on different systems at the same, reduced level of complexity.

Another elaboration is to retain the form of the model for a new set of circumstances and assume that only the parameter values will change. Similarly, but this is a larger step, we might use the same form of the model, but for a system of entirely different components.

4) Disturbing acceptance: We may want to disturb the acceptance of a confirmed model for a variety of reasons: the level of noise (lack-of-fit) may be too high, the domain of applicability may be too narrow, the false accessory conditions may seem important, or the level of resolution may be too coarse. We can deliberately look for unusual or extreme circumstances from which insight about how to construct a model with less noise, applicable in a larger domain and so on. The new model may simply involve a refinement of the existing features or may have a new form altogether. Of course, insight about the construction of the new model does not only come from discrepancies. Insight comes in addition from other models or from other fields via analogy or metaphor.

5) Changing status: When we disturb the acceptance of a confirmed model we are, in effect, arguing to change the model's status to that of an unconfirmed model, which in order to become confirmed requires improved fit, or requires its accessory conditions to be established.

#### b. Redescriptions

1) Acceptance: We might consider a well-fitting model to be sufficient for our purposes if our primary interest is in summarizing complex data or challenging others to explain the fit between observed and model patterns.

2) Generalization: We may be prepared to use the well fitting model

to predict ahead in time or to extrapolate into novel circumstances. If such generalization fails we might elaborate on or replace the model, as follows.

3) Elaboration: We might improve the fit of a model by adding to the model extra terms or parameters, whether or not these have any obvious biological counterpart, e.g. the  $\theta$ -parameter added to the per capita growth rate term in the logistic (Pomerantz *et al.* 1980). A systems modeler might elaborate on a model that fits a sub-system by linking that sub-system model to the corresponding models for other sub-systems.

4) Disturbing acceptance: We may be motivated to find different descriptions if we find systematic lack of fit in certain circumstances or if predictions and extrapolations fail. Perhaps we deliberately sought these failures, as we might to disturbed confirmed models. The different descriptions could either elaborate on the existing models or be new forms altogether. In order to gain insight about how to construct a confirmable model we should construct as large a range as possible of different models, and pay particular attention both to the circumstances where the fit breaks down and to the false or unconfirmable accessory conditions. If we find a competing model which fits equally well this should weigh against any program that gathers confirmatory evidence solely for the original model and should disturb our commitment to the terms of explanation set into the original model.

Comparison of different redescriptions can, in the case of modeling controlled experiments, lead to convergence on generative models. Convergence is achieved by breaking down the accessory conditions that were patently false into ones with more biological-like detail and successively replacing one model by another. For example, Williams (1972) worked through a series of models for microbial populations, replacing a single variable model of a population in which per capita population growth declined linearly with increasing population size (the logistic) by a two-component model of the population and its limiting nutrient. He then examined various models of nutrient supply and utilization, and finally partitioned biomass into separate cells to derive a confirmable model.

5) Changing status: We can confirm a previously unconfirmed model by improving the fit or by establishing the accessory conditions. We might achieve either of these indirectly by narrowing the range of applicability

and thus simplifying the accessory conditions.

Often, however, a redescription is interpreted as generative without taking the preceeding steps to achieve confirmation. We do so because we consider the fit good enough, the predictions accurate enough, or the model sufficiently plausible that nature must generate outcomes in the same way as the model does. As a logical extension of this interpretation, if the addition of parameters on terms significantly improves the fit, e.g. the  $\theta$ -parameter for the logistic (Pomerantz et al. 1980) or higher order interaction terms for Lotka-Volterra models (Vandermeer 1969, Pomerantz 1980), then it is concluded that there must be a corresponding process in nature, e.g. strong interference between individuals or multi-species coalitions, respectively. In my terms both the interpretation and its extension are unjustified; the generative power of the model is only apparent generative power. There are serious counter-intuitive consequences of treating a redescription as generative; I mention these in Sect. III.5 and discuss them in detail elsewhere (Taylor 1985, 1987b).

### c. Models as tools for exploration

1&2) Acceptance and generalization: The outcomes of exploratory modeling are mathematical results; their acceptance simply provides suggestions about how nature might work. Under pressure to produce results of biological relevance we often draw biological parallels or conclusions from the untranslated model outcomes: "In this model, despite its ecological poverty, the subset of homeostatic systems is reminiscent of real ecosystem behavior" (Tregonning and Roberts 1979). "Since these results come from equations that are no more than a caricature of ecological reality, our results must be taken as provisional. Nonetheless, some interesting and practical conclusions may be drawn" (Gilpin and Case 1976). Correctly speaking, however, insight gained about the model system is only a source of hypotheses, not of conclusions, however tentative, about biology.

3) Elaboration: We may elaborate using the original model in two ways. We might add features to bring the model closer to the position where it can be subject to (dis-)confirmation. If this is done it is usually at the expense of mathematical tractability. For example, the

investigation of system construction over time using models with resource uptake dynamics and nutrient cycling is far less tractable than when using Generalized Lotka-Volterra models (Taylor 1985). On the other hand, we might add additional features in a manner that preserves mathematical tractability, e.g. incorporating random variation into the model instead of explicitly modeling the manner in which the unmodeled context is variable.

I have already commented on the uneasy tension between mathematical tractability and the demand for confirmation, and on the risk of mathematical elaboration leading to reification of the mathematical categories. On the other hand, when we are under pressure to get out of our "armchairs" (away from our computers) and to test our models, we sometimes return to the field armed with mathematical insight before we have explored far enough. For example, initial exploration of the "stability-complexity" question indicated that complexity worked against community stability (May 1972), and stimulated a search for "the devious strategies which make for stability in enduring natural systems" (May 1973:174). Nevertheless, subsequent exploration of system construction by addition-and-elimination has shown that complexity can persist readily even though any particular system is transient (see Tregonning and Roberts 1979, Taylor 1985). Therefore, although ecological complexity undoubtedly involves "devious strategies" the perspective of system construction and turnover suggests that such strategies are not necessary for explaining persistence. Furthermore, this perspective suggests that our investigation of ecological complexity should include the historical development of that complexity and not simply stability analysis of its current configuration (Robinson & Dickerson 1984, Drake 1985).

4) Disturbing acceptance: Insights about a model as a mathematical system may disturb our acceptance of a model in each of the other roles that we could give to it. For example, the conditions for the stability or feasibility of the coexistence equilibrium in two-population models are usually limited. This generates the hypothesis that natural cases of coexistence involve more than two interacting components, and so our models of coexistence should include more than two variables. Admittedly this hypothesis is not very remarkable. Nevertheless, exploration can prompt entirely new schemata or elevations of biological processes. For example, the relative ease of constructing complex model systems, mentioned above,

leads to the hypothesis that the construction of complex ecological systems requires a series of addition-and-elimination events. Up to now a contrasting hypothesis has been popular, that evolutionary fine-tuning at the genetic level of population interactions is a prerequisite for persistence of complexity (Lawlor and Maynard Smith 1976, Roughgarden 1977, Lawlor 1980). Such evolutionary-ecological models, which place evolutionary and ecological developments on similar time scales, ought to become less popular if the perspective of system construction becomes adopted.

Another use of exploration of model systems is to help predict the circumstances when false accessory conditions, e.g. quasi-independence from hidden variables, might become confounding, or the circumstances in which fit might break down, or, a third possibility, of circumstances in which a finer level of resolution of parameter values might be needed to resolve among alternative behaviors. These predictions become the fuel for disturbing acceptance of confirmed models or redescrptions, as discussed earlier. Finally, exploration of model systems may be a source of different, well-fitting models to use as redescrptions and among which to discriminate in order to gain insight about how to construct a potentially confirmable model.

5) Changing the status: A model used for exploration can also be used as a redescription by fitting it to observations. Nevertheless, although it may fit better than some competing model(s) (Pimm 1982), it is rare that mathematically tractable models, that is, models suitable for exploration, are confirmable, e.g. Generalized Lotka-Volterra models (Taylor 1985). The mathematical formulations are abstract and necessitate accessory conditions which are difficult to establish unless we work with controlled experiments or situations which happen to exhibit quasi-independence (see Sect. III.4).

A quite different changing of status for exploratory models is implied by several authors (e.g. Levin 1980, Hall and DeAngelis 1985). If a model could be woven together with other exploratory models, the insights provided by each model would combine to an understanding of natural phenomena unachievable through the construction of one all-encompassing model. The means of this synthesis or "patchwork" (Hall and DeAngelis 1985), however, has not yet been articulated. Hilborn and Stearns (1982) provide some advance warnings about problems that must be addressed in

naturalist and preoccupation with simple models (Kingsland 1985). There is a problem here. It is not that community ecologists are alone among scientists in attempting to elevate nature and construct observations in a way that conforms to their "instincts." This is simply another expression for worldview or paradigm. Rather the problem is one of generality. In addition to asking whether the model corresponds to nature, we should examine whether nature has been selected to correspond to the model. If so, then we may realize that the model is less general than it previously seemed.

In the case of simple models we may be selectively studying those special ecological situations in which the biological processes stand out like those abstracted in the model (Sect. II.E.d.1&2), and yield patterns that can be seen above the background complexity. For example, in seeking out to build a theory of community structure MacArthur attempted to avoid historical contingencies by restricting his attention to equilibrium situations (Kingsland 1985). When clear patterns do emerge we have established the condition of quasi-independence, but we have done so, in effect, by the goodness-of-fit of model to observations and not independently of this fit. The "selective" research program cannot, therefore, show that quasi-independence is any more general than the observed cases.

##### 5. Assume quasi-independence

All models are simplifications; in this sense simple models are no different from others. We know that simplifications render the model "false, incomplete [and] inadequate" (Levins 1966). When we use simple models in this spirit we are, in effect, assuming quasi-independence (or homogeneity of elements, see 10 below). We are assuming that the hidden variables may alter but not confound the simple model, e.g. that competition between two species, even when those species are embedded in an ecological context, does not require the two-species modeler to consider other interactions besides negative-negative. Investigations along the lines of 3 (above) show that this is not generally so; sometimes the best two species model for two species in context requires negative-positive or even positive-positive interactions (Taylor 1985, 1987). Similarly, suppose the populations of the full system operate on similar time scales.

In order that hidden variables not be confounding (e.g. not produce counter-intuitive "apparent" interactions among the modeled variables), the populations must remain within a special subset of the values potentially available to them (Taylor 1985, 1987). In other words, the conditions for quasi-independence are special. When we forget, or do not realize, that these special conditions must obtain, we are allowing simplification to become reification.

#### 6. Claim qualitative insight

Suppose that the outcomes predicted by a simple model depend only on qualitative specification of parameter values, that is, on the signs or relative sizes of parameters and not their precise values (Levins 1975). We might hope that this robustness compensates for the unknown effects of hidden variables and so claim biological insight, albeit qualitative, when the model and observations are in qualitative agreement. Unfortunately, as I have shown elsewhere (Taylor 1985, 1987b), hidden variables can significantly alter the predictions of qualitatively specified simple models; quasi-independence is not achieved automatically by qualitative specification.

#### 7. Add biological postulates

When we assume quasi-independence or claim only qualitative insight for simple models, we usually expect to find circumstances in which the model will no longer fit. If we treat simple models as analogies of the perfect crystals or ideal gases of physics and chemistry, then when the fit breaks down we would invoke additional biological postulates to improve the model.

The perfect crystal analogy is popular -- it is a central concept of the MLH strategy -- but misleading. In physics it is possible to characterize the conditions that are required to produce the ideal circumstances, e.g. absence of friction, dimensionless molecules, and so on. We can, by experimental manipulation, approach these ideal conditions and observe whether the actual behavior approaches that of the modeled, "perfect crystal." In ecology, however, it is difficult to characterize in biological and non-tautological terms the required conditions, e.g. of quasi-independence, and they obtain only in special circumstances, e.g.



laboratory microcosms.

In another context Hymes (1974) describes the addition of postulates to a simple model as "simpling":

Like sampling, 'simpling' is a technique for reducing the complexity of reality to manageable size. Unlike sampling, 'simpling' does not keep in view the relation between its own scope and the scope of the reality with which it deals... It then secures a sense of progress by progressively readmitting what it has first denied. 'Simpling'... is unfortunately easily confused with genuine simplification by valid generalization.

To use the adjective "biological" for postulates added to a simple model is to treat the simple model as a representation of biology, albeit a loose one. However, if a simple mathematical model of a naturally variable situation has not been confirmed, then the additional postulates required to improve the fit are mathematical, not biological, postulates. It may be that we subsequently confirm the more elaborate model. It is also possible, however, that the mathematical elaborations direct our attention away from the biological detail which, if incorporated, would yield a confirmable model. An example of the second possibility is the inclusion of a time lag in the logistic equation to fit a humped population growth curve when the hump can be simply understood if we make explicit reference to the population's resource (Taylor 1985).

#### 8. Compare competing simple models

The particularist or investigative reaction to the MLH strategy has been coupled with advocacy of "null hypotheses." Null hypothesis ecologists demand that the simple models and general claims of the MLH school be subject to "vigorous hypothesis testing" (Strong et al. 1984:viii). This vigorous hypothesis testing amounts to, in practice, a comparison of the fit of the MLH-type model with that of a "random" model, that is, with a similarly simple model in which some of the systematic features of the MLH model are replaced by a random process.

Because there are similar accessory conditions, the "random" model is no more amenable to confirmation than the MLH model. The MLH and the "random" models are merely two samples from the range of different, unconfirmed models. If we could construct a wider range we might gain insight about how to construct a confirmable model (Sect.II.E.b.4). Null hypothesis ecologists have certainly disturbed the acceptance of many MLH

models (May 1984) but they share with the MLH modelers the focus on simple models. In the MLH strategy simple models are required for generality of theorems; in null hypothesis ecology their refutation provides support for the belief that no generality will emerge above the "randomness" of local conditions.

Generality may, as the particularists believe, be elusive, but this interpretation is not a necessary deduction from the success which the null hypothesis approach has had in casting doubt on MLH models and on the patterns in community structure they are supposed to explain. Instead, it may be that the MLH-type models are confounded by a false assumption of quasi-independence or by the atypical selection by MLH modelers of quasi-independent situations (Schaffer (1981) has expressed a similar interpretation). It is possible that the elements included in the simple models do have the relationships postulated by MLH modelers but that they also have relationships with the remainder of the community and other features of their environment -- the hidden variables. Whether this is the case remains to be resolved.

#### 9. Generate hypotheses

Simple models, either as schemata or, in mathematical form, as tools for exploration, can stimulate us to generate interesting hypotheses (Sect. II.E.c). Some of these hypotheses will be misleading because the simple models have deflected our attention away from important hidden variables which we will eventually have to rediscover. Some of these hypotheses will refer to a special aspect of ecological situations (e.g. effects of spatial heterogeneity) and need to be woven together; though the manner of this weaving is not yet developed (Sect II.E.c.5). Other models will lead to a correspondence with biological patterns so striking that we are almost compelled to generate and investigate hypotheses and (dis-)confirmable models to account for that correspondence, e.g. the predominance of rigid circuit graphs in niche overlap patterns (Sugihara 1982). And there may be others so beautiful or synthetic (Schaffer 1985) that we will believe that natural processes just have to operate in the same way, or, to paraphrase Einstein, we should be very sorry for Nature.

MLH models have been invaluable in stimulating ecologists in the last thirty years (Kingsland 1985). These simple models have misled, compelled

and seduced ecologists in all the ways above. However, because simple models are difficult to confirm we should interpret the stimulating effect of simple models as primarily a result of their role as schemata or as tools for exploration. Their value is not as representations, however loose, of generative biological processes. (Models of experimentally isolated systems are possible exceptions.) We contribute confusion and reification when we press them into that service (Taylor 1985).

#### 10. Establish coherent aggregation

In the preceding discussion on simple models I have focused on models that are simple by virtue of excluding many elements. Simple models can also result from a high level of aggregation, e.g. single variable models of entire fisheries. At what levels of aggregation can the behavior of the system be modeled without resolution of the elements into their various constituents? Or, in other words, what are the coherent levels of aggregation (Sugihara 1984) for which the heterogeneity of the constituents does not confound the relationships in the simple model?

Scale and aggregation are important issues in theoretical ecology. In the same way that we can use complex models to generate hypotheses about the circumstances in which the hidden variables do not confound the simple model (see 3 above), we can also generate hypotheses about the necessary circumstances for coherent aggregation (Cale and Odell 1980). This is the focus of current work on hierarchy theory in ecology (O'Neill *et al.* 1986) and I will not discuss it further here except to remark that where, in the preceding sections, I have used "quasi-independence," I could substitute coherent aggregation and an analogous argument would follow.

In Table II I formalize the tactics for making biological claims from simple models. Of them 2,5,6,7 are questionable; 1 and 4 generate insight limited to special circumstances; and 3,8 and 10 are difficult to carry out in practice. The remaining tactic, hypothesis generation, is an appropriate use of simple models, provided that the insights claimed are recognized as being primarily mathematical, and not biological at all.

-- INSERT Table II about here --

#### IV. GENERALITY

In the previous section I have argued that most of the tactics used to make biological claims from simple models are inadequate. Attention is needed to accessory conditions, in particular, that of quasi-independence if the model is going to be considered to correspond, however loosely, to generative biological relations. Instead simple models are better thought of either as tools for exploration or as schemata. They are sources of hypotheses, not sources of general, albeit qualitative, insight about biology. Where does that leave the MLH strategy as a route to general principles of ecology?

There are two popular formulations of the trade-off required in ecological modeling that favor generality and advocate the MLH strategy (Levins 1966, May 1973). In this section I reinterpret these formulations in the light of my earlier discussions of the modeling process, different roles for models, and tactics for using simple models. I examine some ambiguity in the concept "general" and propose an alternative image of generality for complex subject matters such as ecology provides.

##### A. Generality, Reality and Precision

Levins (1966) remarks that no strategy of model building can simultaneously achieve generality, reality and precision. He distinguishes three strategies, each of which achieve two of these qualities.

##### 1. Precise and realistic

For Levins, systems models or simulations are precise and realistic at the expense of generality. They incorporate many elements, are precisely fitted to large data bases, and with the aid of computers can yield precise predictions about the future.

Although it is the case that the predictions of systems models are specific to the system being modeled, this specificity does not, in principle, preclude systems models from being a source of generalizations (Hall and DeAngelis 1985). If the predictions were accurate and the models realistic, we could be guided in our construction of models for other

systems. Eventually general principles of construction of complex systems models might emerge.

In my terms, however, systems models are not, in fact, realistic. They are redescrptions, not confirmed representations of biological processes. Although their elements are like biological quantities, many of the relationships among the elements are merely statistical. The model relationships are often constructed to achieve fit between the model and the data base, suitably constrained so as not to violate our sensibilities about what connections and what parameter values are plausible, e.g. linear, donor-controlled models. It may be that the only way to generate precise and testable predictions for complex systems is to extrapolate a redescription (this is the rationalization for large econometric models in economics). Nevertheless, even if the components of the simple model appear to be realistic and exhaustive, we de-emphasize realism of postulated relationships once we seek ease of estimating statistical relationships from a data base. Because redescription is emphasized above confirmation in most systems models, these models must be readjusted, i.e. their parameters reestimated, with the passage of time. It is difficult to transfer them to new situations or to derive from them general principles of construction.

Systems models may be well-fitting redescrptions, extrapolations from them may be precise, but neither attribute ensures realism nor generality.

### 2 & 3. Precise and general, realistic and general

In the case of models chosen either for their mathematical tractability or for their simplicity of specification, the model's behavior can usually be precisely known and characterized -- either by mathematical analysis or computer simulation. Often the mathematician investigates the model's behavior independently of either the construction and analysis of observations or the analysis of the model's correspondence with those observations. This mathematical work can be exploratory and can contribute valuable hypotheses about how to view or model biological processes. At the same time the work may strongly reflect the tools and theorems available to the mathematician, e.g. local stability analysis of point equilibria.

Levins distinguishes two strategies of mathematical modeling that he characterizes as general. The first he calls "precise and general" referring to work that borrows heavily from physics, with results that rely on special ("precise") mathematical relations, e.g. Kerner's (1957) work on the statistical mechanics of (structurally unstable) Lotka-Volterra models. In my terms such modeling is exploratory, the generality is mathematical, and the reliance on special relations is an example of exploration without much attention to the requirements of confirmation.

Levins' other general strategy -- the strategy of model building he favors -- was the "realistic and general." The realism is to be gained by letting biological questions, rather than available mathematical tools, guide the model formulation. The generality is to be gained from results that do not require precise specification of the model (Sect. III.6). Levins extends this qualitative approach even further through his concept of robust theorems, that is, theorems that are common to a class of models sharing only a minimum of assumptions (Levins 1966).

In my terms the realistic and general strategy is similar to "precise and general" modeling: they are both exploratory and their generality is mathematical. When we attempt to make biological interpretations of qualitatively specified models the potentially confounding effects of hidden and inhomogeneous variables arise, just as these effects arise for all simple models (Sect. III). We need to produce evidence that the effects are not confounding. In the absence of such evidence "realistic and general" modeling is better thought of as being loose and suggestive. In fact, the virtue of Levins' modeling work lies in his disturbing the explanatory power of existing schemata and suggesting new juxtapositions of biological processes for our attention (Levins 1968); the virtue is not in data analysis or careful analysis of correspondence.

#### B. Strategic and Tactical Modeling

May (1973) distinguishes between strategic and tactical modeling. Tactical modeling is Levins' "precise and realistic" strategy, suitable for applied problems, but narrow in scope and not a source of general ecological principles. Strategic modeling is Levins' "realistic and general" strategy, and is favored by May as a route to qualitative insights

into broad classes of ecological phenomena.

Strategic modeling is, in my terms, exploratory. Contrast the conventional rationalization of strategic modeling (as follows) with my reformulation (below). In strategic modeling we ask very general questions, e.g. how can complexity persist in ecosystems? We begin with simple models having few explicit biological assumptions. After investigating the behavior of the simple model, we add "shells" to this core; after each addition we assess the consequences of the new feature. We hope in this fashion to construct progressively more realistic and, at the same time, well understood models. If, on the other hand, we had built in many biological features at the outset it would not be possible for us to establish the extent to which the behavior of the model depended on the special features, in contrast to the behavior being characteristic of a more general class of models.

In my terms, however, in strategic modeling we ask very general mathematical questions guided by loose biological questions. We may precisely answer the mathematical questions and gain insight about progressively more elaborate model systems, but we have only provided hypotheses or loose insight about how to view or how to model biological processes. Strategic modeling does not guarantee convergence on realism (Sect. II.E.c): the additional features are, at best, biological-like, not biological. Like Levins' two strategies for achieving generality, strategic modeling is precise and general mathematically, but loose and suggestive biologically.

### C. Different Images of Generality

Levins's discussion of strategy in model building hinges on an equivocation between two means of the adjective "general." The first meaning is "widely-applicable." I have restricted my use to this meaning. It is the prospect of such generality or recurring pattern that motivated MacArthur and others who were weary of "tedious case histories." The other meaning is "loosely-specified" or "un-specific" and in this light simple and qualitatively specified models appear general. I have argued that when simple models are applied to naturally variable observations accessory conditions arise. These are typically very restrictive. The

models may, therefore, be widely-applicable mathematically but not biologically. The loose or un-specific insight the mathematics provides may or may not become converted into valuable biological insight.

There is another image of generality that relies less on attempts to construct mathematical models to represent biological relations. Consider the possibility, raised by the "particularist" ecologists, that most ecological phenomena are conditioned by many local circumstances and historical contingencies. If so, it may be rare that we are able to derive a confirmable model of the generative biological processes. But suppose instead that we assemble "guide-books" about what to look out for in any specific case -- compilations of experience in similar cases to help us make sense of the particular detail we might observe. Such guide-books might become just what the particularists prescribe in their strategy of "investigation" (Simberloff 1982), catalogs of particular cases permeated with anti-generalist sentiments. On the other hand a guide book could be organized around interpretative themes. It could convey both the generality of circumstances for which each theme was relevant and the variety of particularity -- the local and historical contingency -- which qualifies that relevance in real, particular situations. Interpretation and historical explanation might join or supplant prediction and generative explanation as the aims of ecological theory.

What are those interpretative themes for ecology, and how do ecologists arrive at them? Unfortunately an adequate discussion of ecological theory and its development is beyond the scope of this paper. Briefly, however, in order to dispell any impression that I would leave models out of an interpretative ecology, I will remark that any model-as-schema could form the basis of an interpretative theme if the schema were coupled with a summary of possible particular qualifications, e.g. in the case of the IB schema: habitat diversity, transient species, land bridges, and so on (MacArthur 1972). Furthermore, if ecologists can develop methods

- 
1. Wolf's (1982) analytic history of societies interconnected by European expansion since the 1400's is a splendid exemplar of this form of generality. The main interpretative theme in his "guide book" is intersection of the modes of production predominant in the interacting societies.



to transform the separate (mathematical) insights gained from exploratory modeling into syntheses, then those (transformed) insights could also become interpretative themes. To achieve these syntheses will require, I believe, an emphasis on action to disturb the acceptance of models or, in the terms of the following, concluding section, synthesis will require an approach to theory development that I call "de/composition."

## V. DE/COMPOSITION

It seems to be correct to begin with the real and the concrete..., thus to begin, in economics, with e.g. the population, which is the foundation and the subject of the entire social act of production. However, on close examination this proves false. The population is an abstraction if I leave out, for example, the classes of which it is composed. These classes in turn are an empty phrase if I am not familiar with the elements on which they rest. E.g. wage labour, capital etc. These latter in turn presuppose exchange, division of labour, prices etc. For example, capital is nothing without wage labour, without value, money, price etc. Thus, if I were to begin with the population, this would be a chaotic conception of the whole, and I would then, by means of further determination, move analytically towards ever more simple concepts, from the imagined concrete towards ever thinner abstractions until I had arrived at the simple determinations. From there the journey would have to be retraced until I had arrived at the population again, but this time not as the chaotic conception of the whole, but as a rich totality of many determinations and relations.

Marx [1858 (1973:100)]

I commented at the conclusion of my analysis of model-based actions that our actions can either reinforce the view that biological processes generate outcomes the way a model does, or our actions can emphasize that the model is a provisional account. The provisional character, obvious in historical explanation (Sect.I.A), is the spirit in which MacArthur brought various biological processes into juxtaposition for the attention of ecologists. Nevertheless, when a schema is abstracted into a mathematical model the categories often begin to appear sufficient and generative. Appearances notwithstanding, it is difficult to confirm simple models (or other loosely specified models) as representations of naturally variable situations (as I argued in Sect.III). Careful justification should accompany any change in the status of a model from a schema through a tool for exploration and a redescription to a generative model. In practice,

unfortunately, these changes are often made prematurely; exploratory models or redescriptions are misconstrued as generative. The initial categories, e.g. immigration and extinction in IB theory, become frozen into things having properties and thereby take on a generative appearance. If we focus our attention on experimentally controlled systems, isolated from nature this appearance may be further reinforced. Nevertheless, although it is sometimes possible to develop confirmed models for these special cases(Sect.II.D), generalizing to naturally variable situations is problematic.

From my discussion of the limitations of simple models (Sect.III), it should be clear that I want to shift the emphasis in modeling from achieving provisional acceptance to disturbing that acceptance. I discussed in the section on various courses of action (Sect.II.E) deliberately searching for unusual or extreme circumstances in which the fit or accessory conditions may break down, paying attention to systematic lack of fit, exploring to suggest new questions to ask, new terms to employ, different models to construct, and so on. I reinterpreted the MLH strategy as one of formulating new schemata and using models in their exploratory role (Sect.IV). Furthermore, whatever the status of a model, it is important that if we are satisfied with a model for our purposes then we make explicit the status and the appropriate domain of applicability. Clarity in ecological theory will be facilitated by making clear, in this way, the extent of generality of a model. This will enable other modelers to assess whether the model constitutes a satisfactory explanation for their purposes or whether they want to disturb its acceptance.

Where does this emphasis on disturbance take us? The strategy of model building in ecology should, I propose, follow an orientation in theory development that I call "de/composition." Modeling should move in two directions. Starting from the ground of observed phenomena in naturally variable ecological contexts we move both to break down the initial categories with which we describe the complex phenomena and to reconstitute new ones with which we move closer to explaining the phenomena in their rich web of interrelations and conditions. These dual movements are needed to reanimate our thought when the categories of the model have come to confine it and the model is becoming a dead metaphor. To de/compose is to attempt to generate new interpretative themes and,

thereby, to find generality when every situation had begun to appear peculiar to itself.

One metaphor, essential to mathematical modeling, that demands our scrutiny is that of the machine. In what sense, after all, can we think that nature is like a mathematical model? It is not that nature is like a set of algebraic equations. Instead, we are drawing on the fact that a mathematical model is a system; its behavior is determined by components with pre-defined properties, that is, a model is a machine. If nature is like a machine it is also very unlike one; organisms are capable of novel and flexible responses to situations not previously encountered by them. How can we model novelty and flexibility?

There is a common orientation in our inquiries that, like the machine metaphor, also warrants scrutiny. As a generalization, we focus on recognizable structures, e.g. populations, communities, ecosystems, and ask how they are maintained. We could, on the other hand, view structures as "intersections in particular time and space of a describable set of processes which involve... change" (Vogt 1980:21), in other words, as "temporary accommodation[s] to... the forces generating the processes" (Wolf 1974:65). Boundaries and structure of ecological situations might be viewed as problematic concepts, rather than as essential to ecological theory.

Disturbing the machine metaphor of mathematical modeling and reorienting our inquiries to process rather than structure are only suggestions about how we could pursue de/composition. Nevertheless, these suggestions should remind us to resist the temptation to model ourselves in the image of theorists in experimental-reductionist sciences and to pay more attention to the debates and lessons around historical inquiries. Mathematical models may be a tool in our development of theory in ecology, but they provide no shortcut to generality. Rather, we should patiently explore the challenges and limitations of a field in which diversity and complexity constitute its inherent appeal.

Acknowledgements: I am grateful to Lisa Lloyd for her interest, guidance and encouragement in the development of this paper, and to Ann Blum, Deborah Gordon, Yrjö Haila, Sharon Kingsland and Lee Mintz for their comments on earlier drafts.

Literature Cited

- Cale, W. G., and P. L. Odell.: 1980, 'Behavior of aggregate state variables in ecosystem models', Mathematical Biosciences 49,121-137.
- Drake, J. A.: 1985, 'Some theoretical and empirical explorations of structure in food webs', Ph.D. thesis, Purdue University, West Lafayette, Indiana.
- Foucault, M.: 1983, 'Questions of method, an interview with Michel Foucault', Ideology and Consciousness 8,3-14.
- Freedman, D. A.: 1985, 'Statistics and the scientific method', Pp. 343-366 in Mason, W. M., and S. E. Fienberg, eds., Cohort Analysis in Social Research, Beyond the Identification Problem, Springer, New York.
- Gilpin, M. E., and T. J. Case.: 1976, 'Multiple domains of attraction in competition communities', Nature 261,40-42.
- Gobber, F., and F. F. Seelig.: 1975, 'Conditions for the application of the steady-state approximation to systems of differential equations', Journal of Mathematical Biology, 2,79-86.
- Goudge, T. A.: 1961, The ascent of life, Univ. of Toronto Press, Toronto.
- Haila, Y.: 1983, 'Colonization of islands in a north-boreal Finnish lake by land birds', Annales Zoologici Fennici 20,179-197.
- Haila, Y.: 1986, 'On the semiotic dimension of ecological theory, the case of island biogeography', Biology and Philosophy 1,377-387.
- Hall, C. A., and D. L. DeAngelis.: 1985, 'Models in Ecology: Paradigms Found or Paradigms Lost?', Bulletin of the Ecological Society of America 66, 399-345.
- Hilborn, R, and S. C. Stearns.: 1982, 'On inference and evolutionary biology: the problem of multiple causes', Acta Biotheoretica 31,145-164.

- Haraway, D. J.: 1981, 'The high cost of information in post World War II evolutionary biology', Philosophical Forum 13(2-3), 244-278.
- Hutchinson, G. E.: 1978, An introduction to population ecology, Yale Univ. Press, New Haven.
- Hymes, D.: 1974, 'Traditions and paradigms', Pp. 1-38 in Hymes, D. (ed.), Studies in the history of linguistics, Traditions and paradigms, Indiana University Press, Bloomington.
- Kerner, E. H.: 1957, 'A statistical mechanics of interacting biological species', Bulletin of Mathematical Biophysics 19, 121-146.
- Kingsland, S.: 1985, Modeling nature, Episodes in the history of population ecology, University of Chicago Press, Chicago.
- Lawlor, L. R.: 1979, 'Direct and indirect effects of n-species competition', Oecologia (Berl.) 43, 355-364.
- Lawlor, L. R.: 1980, 'Structure and stability in natural and randomly constructed competitive communities', American Naturalist 116, 394-408.
- Lawlor, L. R., and J. Maynard Smith.: 1976, 'The coevolution and stability of competing species', American Naturalist 110, 79-99.
- Lenton, G.: 1983, 'Wise owls flourish among the oil palms', New Scientist 97, 436-437.
- Levin, S.: 1980, 'Mathematics, ecology, ornithology', Auk 97, 422-425.
- Levins, R.: 1966, 'The strategy of model building in population biology', American Scientist 54, 421-431.
- Levins, R.: 1968, Evolution in changing environments, Princeton University Press, Princeton, N.J.

Levins, R.: 1975, 'Evolution in communities near equilibrium', Pp. 16-50 in Cody, M. L. and J. M. Diamond (eds.), Ecology and evolution of communities, Belknap Press of Harvard University Press, Cambridge, Mass.

Levins, R., and R. C. Lewontin.: 1980, 'Dialectics and reductionism in ecology', Synthese 43,47-78.

Lloyd, E. A.: 1984, 'A semantic approach to the structure of evolutionary theory', Ph.D. thesis, Princeton University, Princeton, N.J.

Lomnicki, A.: 1980, 'Regulation of population density due to individual differences and patchy environment', Oikos 35,185-193.

MacArthur, R. H.: 1972, Geographical ecology, Harper & Row, New York.

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

Marx, K.: 1858, reprint 1973, Grundrisse, Vintage Books, New York.

May, R. M.: 1972, 'Will a large complex system be stable?', Nature 238,413-414.

May, R. M.: 1973, Stability and complexity in model ecosystems, Princeton University Press, N.J.

May, R. M.: 1984, 'An overview: Real and apparent patterns in community structure', Pp. 3-16 in Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), Ecological communities, Conceptual issues and the evidence, Princeton University Press, Princeton, N.J.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen.: 1986, A hierarchical concept of the ecosystem, Princeton University Press, Princeton, N.J.

- Pimm, S. L.: 1982, Food webs, Chapman & Hall, London.
- Pomerantz, M. J.: 1980, 'Do "higher order interactions" in competition systems really exist?', American Naturalist 117, 583-591.
- Pomerantz, M. J., W. R. Thomas and M. E. Gilpin.: 1980, 'Asymmetries in population growth regulated by intraspecific competition: Empirical studies and model tests', Oecologia (Berl.) 47, 311-322.
- Post, W. M., H. H. Shugart and D. L. DeAngelis.: 1978, 'Stability criteria for multispecies communities', ORNL/TM-6475, Oak Ridge National Laboratory, Tennessee.
- Robinson, J. V., and J. E. Dickerson.: 1984, 'Testing the invulnerability of laboratory island communities to invasion', Oecologia 61, 169-174.
- Roughgarden, J.: 1977, 'Basic ideas in ecology', Science 196, 51.
- Roughgarden, J.: 1983, 'Competition and theory in community ecology', American Naturalist 122, 583-601.
- Schaffer, W. M.: 1981, 'Ecological abstraction: The consequences of reduced dimensionality in ecological models', Ecological Monographs 51, 383-401.
- Schaffer, W. M.: 1985, 'Order and chaos in ecological systems', Ecology 66, 93-106.
- Shanin, T.: 1972, 'Models and thought', Pp. 1-22 in Shanin, T. (ed.), The rules of the game, Tavistock, London.
- Simberloff, D.: 1980, 'A succession of paradigms in ecology: Essentialism to materialism to probabilism', Synthese 43, 3-29.
- Simberloff, D.: 1982, 'The status of competition theory in ecology', Annales Zoologici Fennici 19, 241-253.

Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.): 1984, Ecological communities, Conceptual issues and the evidence, Princeton University Press, Princeton, N.J.

Sugihara, G.: 1982, 'Niche hierarchy, Structure, organization and assembly in natural communities', Ph.D. thesis, Princeton University, Princeton, N.J.

Sugihara, G.: 1984, 'Ecosystems dynamics', Pp. 131-153 in May, R. M. (ed.), Exploitation of marine communities, Springer-Verlag, Berlin.

Taylor, P. J.: 1985, 'Construction and turnover of multispecies communities: a critique of approaches to ecological complexity', Ph.D. thesis, Harvard University, Cambridge, Mass.

Taylor, P. J.: 1987a, 'Historical versus Selectionist Explanations in Evolutionary Theory', Cladistics 3,1-13.

Taylor, P. J.: 1987b, 'Apparent interactions in community models: a challenge for theoretical ecology', Submitted to Ecology.

Tregonning, K., and A. P. Roberts.: 1979, 'Complex systems which evolve towards homeostasis', Nature 281,563-564.

Vandermeer, J. H.: 1969, 'The competitive structure of communities, An experimental approach with protozoa', Ecology 50,362-371.

Vogt, E. Z.: 1960, 'On the concepts of structure and process in cultural anthropology', American Anthropology<sup>ist</sup> 62,18-33.

Whittaker, R. H., and S. A. Levin (eds.): 1975, Niche, Theory and application, Dowden, Hutchinson and Ross, Stroudsburg, PA.

Williams, F. M.: 1972, 'Mathematics of microbial populations, with emphasis on open systems', Transactions of the Connecticut Academy of Arts & Science 44,397-426.



- Wimsatt, W. C.: 1986, 'False models as means to truer theories', in Nitecki, M. (ed.), Neutral Models in Biology (in press).
- Wolf, E.: 1974, Anthropology, Norton, New York.
- Wolf, E.: 1982, Europe and the people without history, University of California Press, Berkeley.
- Yoxen, E.: 1981, 'Life as a productive force: Capitalising the science and technology of molecular biology', Pp. 66-122 in Young, R. M., and L. Levidow (eds.), Studies in the labour process, C.S.E. Books, London.

Table I. A taxonomy of different roles for models.

Analysis of Correspondence			
-----			
Accessory			
Role/Interpretation	Fit	conditions	Applications
-----			
1. Schemata	-	-	To reflect insight from field observations. To stimulate hypothesis generation and subsequent investigation.
2. Tools for exploration	-	-	Investigation of the model as mathematical system. To suggest new questions, new terms, different models to construct.
3. Redescription	X	-	Summary of observations. Prediction and extrapolation, on the basis that past patterns might continue.
4. Representations of generative relations	X	X	To establish generative explanations -- to specify the necessary and sufficient conditions to explain a phenomenon, subsume it under a general principle, and thereby generate positive predictions for situations not yet observed.
3A. Apparent representations of generative relations	X	-	To advance apparently generative explanations, valid, however, only in the range of circumstances for which fit was established (see Redescriptions).

-, not applicable; X, applicable

Table II. Tactics for making biological claims from simple models.

Formalism

S denotes modeled situation  
 C context of that situation  
 M model

Observations  $\dot{\underline{X}}_s = G(\underline{X}_s, \underline{X}_c, \Pi)$   
 Model  $\dot{\underline{x}}_s = g(\underline{x}_s, \pi)$

where  $\underline{X}_s = \{ X_i \}, i = 1, \dots, m$   
 $\underline{X}_c = \{ X_j \}, j = m+1, \dots, n$   
 $\underline{x}_s = \{ x_i \}, i = 1, \dots, m$   
 $\Pi, \pi = \{ \text{parameters} \}$  (actual, modeled respectively)

and  $\dot{\phantom{x}}$  denotes rate of change, that is, the dynamics of the variables

Fit (g,G) denotes the fit of model g to observations G  
 Con (g,G) the degree of confirmation of model g as a generative representation of S in context C

Arguments for g and G will be given only when they differ from the above.

Tactic

Summary

- |              |   |
|--------------|---|
| <i>flush</i> | <ol style="list-style-type: none"> <li>1. Isolate and Control <span style="font-size: 2em; vertical-align: middle;">{</span> Shrink the context (<math>C \rightarrow C'</math>, <math>n' - m</math> reduced) such that <math>\underline{X}_c' \cong \text{constant}</math></li> <li>2. Generalize <span style="margin-left: 100px;">Fit (g,G(<math>\underline{X}_c', \Pi</math>)) is good <math>\rightarrow</math> Fit (g,G) is good</span></li> <li>3. Establish quasi-indep. <span style="margin-left: 100px;">Establish Fit (g,G) is independent of <math>\underline{X}_c</math></span></li> <li>4. Select quasi-indep. <span style="margin-left: 100px;">Focus on <math>\underline{X}_c</math> s.t. Fit (g,G) <math>\cong</math> constant</span></li> </ol> |
|--------------|---|

5. Assume quasi-indep.      Assume that  $\text{Fit}(g, G)$  is independent of  $\underline{X}_g$
6. Claim qualitative insight    If there is  $(\pi_k)$  s.t.  $\text{Fit}(g(\pi_k), G)$  is  
qual. correct then  $\text{Con}(g, G)$  qualitatively.
7. Add biological postulate    If there exists  $\underline{X}_g$  s.t.  $\text{Fit}(g, G)$  is poor then  
expand the modeled situation  $(S \rightarrow S', i = 1,$   
 $\dots, m+1)$  s.t.  $\text{Fit}(g, G)$  improves
8. Compare models               $\text{Fit}(g_1, G) > \text{Fit}(g_2, G) \rightarrow \text{Con}(g_1, G) > \text{Con}(g_2, G)$
9. Generate hypotheses        If  $g \rightarrow \theta$  does  $G \rightarrow \theta$  ?
10. Establish coherent aggr.    Find  $\underline{x}_g = (x_k')$  where  $x_k' = \sum_{i=1}^m x_i$  s.t.  
  
 $\text{Fit}(g'(\underline{x}_g), G) \cong \text{Fit}(g, G)$
-

## Figure Captions

Figure 1. A conventional view of the modeling process.

Figure 2. An overview of the modeling process as analyzed in this paper.

Figure 3. Elevation of biological processes into the ecologist's view.

Figure 4. Construction and analysis of the model.

Figure 5. Construction and analysis of observations.

Figure 6. Analysis of correspondence between the model and observations.