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THE USEFULNESS OF ECOLOGICAL MODELS: A STOCK-TAKING

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ABSTRACT

Mathematical modeling forms a large part of modern ecological research. This essay argues that it forms too large a part. The uses of modeling are reviewed: models are used to "explain" the functioning of natural ecosystems; they are also used in forecasting, in hypothesis-generation, and as standards of comparison. Although the original task of models was to explain nature, this is the task they perform least well. To compare a model with reality is, in effect, to ask a number of questions simultaneously when they could more profitably be tackled individually. The search for answers to single "unit" questions, here called "investigating," is more likely than modeling to yield advances in knowledge. It is not easy, as examples show.

INTRODUCTION

ECOLOGISTS USE a variety of methods in conducting their research; the methods are as varied as the topics. However, nearly all methods can be thought of as mixtures, in different proportions, of two "pure" strategies, which I shall call *modeling* and *investigating*. For the purpose of this essay, these words can be precisely defined as follows:

Modeling consists in constructing, mentally, a plausible symbolic representation of the functioning of an ecosystem, in the form of mathematical equations. One then tests whether the behavior of the ecosystem conforms with that of the model.

Investigating consists in searching directly, by any appropriate means, for empirical answers to single, clearcut questions, without

preconceptions as to what those answers will be.

Briefly, therefore, the contrast between the two pure strategies is that *modeling* entails the deliberate preconception of mental constructs, often fairly elaborate ones, whereas *investigating* entails the equally deliberate avoidance of preconceptions. (Thus "*investigating*" is here given a narrower meaning than it has in ordinary usage.)

In the past, when ecology was a branch of biology, an ecologist carrying out research used whatever seemed the most appropriate combination of the two strategies for tackling the problem in hand, without even consciously thinking about it. Nowadays, with mathematicians, statisticians, and engineers jumping on the ecologists' bandwagon, mathematical ecological modeling is fast becoming an end in itself. Models are being constructed, refined, elaborated, tinkered with, and displayed with little or no effort to link them with the real world. As a result, the whole

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body of ecological knowledge and theory has, I think, grown top-heavy with models. The time has come to take stock of the situation.

This essay attempts to do two things: to explore the ecological usefulness of mathematical models; and to point out that investigating is as necessary to ecology, and as intellectually challenging, as modeling.

Admittedly models have many uses, but as means to various ends, not as ends themselves. It is important to recognize their limitations and not to exaggerate their usefulness. To discuss models coherently, from the point of view of users, I decided to classify them according to their uses. Oddly enough, this proved surprisingly difficult to do. I tried pigeonholing the uses in various ways, but none seemed altogether natural. This in itself is ominous and suggests that models are often constructed for no specific purpose at all. A simple fourfold classification has been used in what follows, which recognizes the following uses: (1) to explain population and community dynamics; (2) to forecast future population and community change; (3) to generate interesting, testable hypotheses, as topics for investigation; and (4) to serve as idealized standards against which real-life ecological processes can be measured.

These uses are discussed, in the context of selected examples, in the first four sections of the paper. Section 5 deals with investigating as distinct from modeling. I hope to show that investigating is as intellectually challenging as modeling, and at least as productive of new knowledge.

I. MODELS AS EXPLANATIONS

The original aim of ecological modeling was to explain why fluctuating populations behave the way they do. The salient property of a dynamic fluctuating system is the changes it undergoes, at varying rates; therefore an explanatory model must account for these changes and their rates. This may be done in terms of differential equations, which treat time as continuous, or of difference equations, which treat time as discrete (Pielou, 1977). Difference equation models may be displayed in various ways: as Leslie matrices (see, for example, Usher, 1972), or as net-

work diagrams or flow graphs (Lewis, 1976, 1977).

Models of this kind have a long history. They are direct descendants of the classical Lotka-Volterra models, whose present status has been reviewed by Wangersky (1978). They were originally devised to describe and explain the behavior of simple laboratory microcosms. These might contain a population of one species whose growth was density-dependent, or populations of two species, either two competitors or a predator-prey pair.

In explaining what is going on in laboratory microcosms, these models have been an outstanding success. Microcosms have been studied both for their own sake, and as living models—as opposed to pencil-and-paper models—of large “outdoor” ecosystems. But whether and, if so, to what extent such models can reasonably be applied to large systems are highly debatable.

The unnaturalness of the assumptions (or preconceptions) underlying the very simple models is obvious. Their three most conspicuous defects are that: (1) they assume that environmental conditions do not change with time; (2) they assume that population growth rates respond instantly, with no time lag, to the changing densities of the interacting populations being modeled; and (3) they assume that the space occupied by the interacting populations is homogeneous, and sufficiently small for all the contained individuals to interact with one another in the same manner.

The third problem merits detailed consideration here, since it illustrates very well the limitations of modeling. Thus, although modeling undoubtedly contributes to the study of large ecosystems, its role is subordinate to that of investigation.

Laboratory Microcosms and Continent-Wide Ecosystems

The tremendous mismatch in size between, for example, a laboratory microcosm in which the rotifer *Asplanchna* preys on *Paramecium* (Maly, 1969) and an ecosystem of continental extent in which lynxes prey on snowshoe hares has not deterred theorists from using a single model to “explain” both systems. While admitting that models designed for

small, self-contained systems may be inapplicable to unbounded systems several orders of magnitude larger, theoreticians still do apply them, even if only to provide "crude caricatures" (in the words of May, Beddington, Clark, Holt, and Lewis, 1979).

It could be argued, with some truth, that such modeling is unobjectionable, since the precision with which natural populations can be estimated is far too low to warrant the construction of more elaborate models. This excuse is not often offered, however, since most theorists seem unaware of the tremendous difficulties of population estimation in the field. The illustrative example in Fig. 1 will probably surprise both desk workers and field workers. The population in the figure consists of 478 dots. They may be shrubs in a desert, earthworms in a pasture, deer mice in a forest, seals on an ice floe, or anything else you care to envisage. Suppose the whole population is subdivided into 200 square sampling units by joining the check marks on the boundary to those on the opposite side; and suppose the number of dots is counted in a simple random sample of 60 of these units, so that the size of the total population may be estimated. Then the expected 95 per cent confidence bounds are found to be 421 and 535; the width of the interval is 24 per cent of the true population size. It is alarming to realize that so straightforward a sampling task, and a sampling fraction as high as 0.3, gives such disappointingly low precision. The example is given to emphasize the great difficulty of estimating natural populations. The unavoidably low precision should be kept in mind through all the discussions to follow.

Thus consider the famous ten-year cycle in the sizes of the mammal populations of the boreal forests. There is an enormous literature on the subject, recently reviewed by Fox (1978). Among the basic facts to be explained are the extremely regular 10-year cycles in lynx populations and the less well-documented cycles in snowshoe hare populations, which are of the same period but tend to peak about two years ahead of the lynx cycles. There are three chief theories, which may be shown symbolically as follows. (A two-way arrow denotes two-way interaction between the entities named; a one-way arrow denotes one-

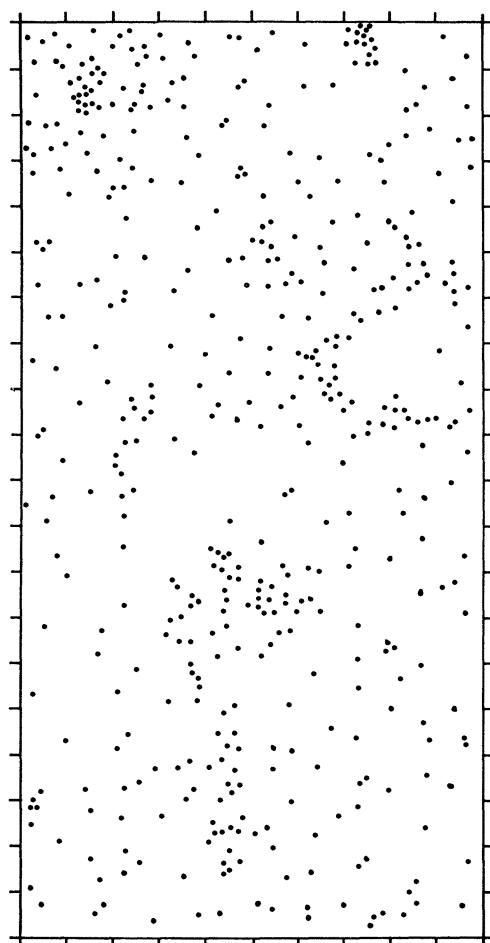


FIG. 1. A TYPICAL ECOLOGICAL "DOT" PATTERN

The unavoidable imprecision of population estimation in ecology is here exemplified. See text for numerical details.

way causation, that can force a cycle.) The theories are:

1. Hare \leftrightarrow Lynx
2. Vegetation \leftrightarrow Hare \rightarrow Lynx
3. Cycling physical factors \rightarrow Vegetation
 \rightarrow Hare \rightarrow Lynx.

Theory 1, now long discarded (Keith, 1963) treats the cycles as endogenous predator-prey oscillations conforming to a classic Lotka-Volterra model or some slightly more sophisticated stable limit cycle model (May, 1974).

Theory 2 also invokes endogenous oscilla-

tions, but in this case caused by interaction between the hares and their plant food. The lynx populations are assumed to undergo forced oscillations, caused by, but not causing, the hare oscillations. The theory has been discussed by Bulmer (1978).

Theory 3 embodies no endogenous oscillations. But to account for the regularity of the mammal cycles one has to postulate regular cycling of an exogenous factor. The chief exogenous factor, in Fox's (1978) opinion, is forest fires, which recur periodically and trigger plant succession.

The debate still rages and its relevance to the present discussion is this: a simple theoretical predator-prey model would fit the facts adequately if it were not for the fact that the cycles are continent-wide in extent. But they are. There cannot be a number of mutually isolated lynx-hare "cells" each undergoing endogenous oscillations independently, or, when totalled over large regions, they would cancel each other out. They do not. On the other hand, it is logically untenable (besides being wildly unlikely) that the lynxes and hares of the whole continent constitute a single, homogeneous, endogenously cycling system, since there are gradual shifts of phase in the cycles from one region to another. Thus the lynx peaks exhibit a wave-like advance from east to west across the continent (Butler, 1953; Watt, 1968). Watt (1968) proposed that the cycles owed their regularity to endogenous interactions within local populations, and their synchrony over fairly large regions to the controlling effect of weather, which affects plant growth rates, forest fires, and snow depths. There seems no convincing evidence for a wave-like advance of continental weather patterns, however. It is not inconceivable (though perhaps unlikely) that the cycles, while endogenous, are coupled to weather fluctuations only in the central region. Outward migrations from this center could then set the phases of the oscillations in surrounding regions and hence produce the observed advancing wave.

Obviously there is tremendous scope for straightforward investigation, and a vast amount has been done. But often, "straightforward" investigations do not give results susceptible to straightforward interpretation. Some investigations lead different workers to

diametrically opposed interpretations, and further investigation is necessary for a resolution. An example has been given by Fox (1978). In support of his contention that Theory 3 (above) is correct, with forest fires as the governing physical factor, he remarks that in the Lake States, since 1950, forest fires have been largely suppressed by the U.S. Forest Service, and over the same period the hare cycle has been strongly damped. The results are ambiguous, however. In the first place, habitat fragmentation owing to land development, rather than a lack of fires, could have damped the cycle. Second, the cycle has not disappeared entirely, and what remains could still represent a predator-prey cycle.

All this suggests to me that, as the problem now stands, further progress calls for a strategy of intensified investigations, not more modeling. Definite answers should be sought to simple questions, on how the cycling phenomenon varies over space and through time. Modeling, in the sense of postulating sets of differential equations whose solutions more or less match the observations, now has little to offer. It may restrict rather than expand the range of conceivable explanations that are worth looking into. For example, Weinstein (1977) has considered that the lynx cycle may be more apparent than real. The evidence for lynx fluctuations comes from trapping records, and trappers may have more time to spare for lynx trapping in years when they need to spend less time hunting for the pot (hares are food for trappers, too).

Patchy Habitats, Local Populations, and Demes

The 10-year cycles of the furbearing mammals illustrate in particularly intense form the difficulties that arise when one attempts to model the behavior of populations of huge areal extent. Less extreme examples of the problem abound and have led, during the last decade, to a growing interest in the modeling of populations living in heterogeneous, or patchy, environments. Levin's (1976) review refers to, and summarizes, much work on the topic. As he has remarked, "the bulk of the mathematical theory of populations has ignored spatial factors; . . . [it has rested on] the assumption of perfect mixing and spatial homogeneity" (Levin, 1976, p. 302).

The patchy-environment models allow for the (presumed) fact that, in nature, any regional population is likely to consist of a number of local subpopulations, each confined to its own homogeneous patch. Every subpopulation has its own dynamics, controlled by the effect on its demographic parameters of physical factors peculiar to its patch, and by interactions among its own members, which are perfectly mixed. Besides this, migrations are permitted among patches. The result is that although local extinctions are frequent, their durations are short; reinvansion from nearby patches prevents any patch from remaining empty for long. The phenomenon could be called the "flicker effect," on analogy with advertising signs in which lights flicker on and off repeatedly but are never all off simultaneously. The process, if it occurs (and common sense suggests that it does), explains the coexistence in a region, without competitive exclusion, of closely similar species.

A simple model of this kind is due to Slatkin (1974). It deals with two-species competition between species that occupy the same scattered habitat patches; all the patches being identical as habitats. Each species' "patch" populations (subpopulations) have a probability of going locally extinct even in the absence of competition; and an augmented probability of extinction if the competitor is present in the same patch. Each patch has a probability of being recolonized from other patches by either species; this probability is higher if the patch is empty than if it is already occupied by a subpopulation of the other species. The model is found to permit coexistence of competing species in a region, in stable equilibrium.

This model, and others like it, are still not "spatial" models. Although they treat competing populations as made up of spatially separated subpopulations, they do not allow for tighter coupling between spatially close patches than between spatially distant patches. Thus existing models would have to be modified if the whole region modeled were large relative to the dispersal powers of the species (Slatkin, 1974). Gurney and Nisbet (1978) have explored such a modification, in a one-species population, by assuming distance-dependent spatial correlations among patches

and comparing the modeled population fluctuations with those expected from a "zero correlation" model.

So much for "patchy" models. Few helpful suggestions have yet appeared, however, on how to link models and reality. Concerning any real-life system, the models leave unanswered such questions as the following: How large, in numbers and area, are fully mixed, completely interacting subpopulations? How widely spaced are they? What is the rate of transdispersal among them? Does transdispersal take place all the time, or seasonally? Do hospitable habitat patches persist or are they ephemeral? [Gill (1978) has described how beaver ponds constitute ephemeral habitat patches, shifting rapidly in time and space, for the red-spotted newt, *Notophthalmus viridescens*.] Does a species have different competitors at different stages of its life cycle, and if so what are they? What proportion of habitable patches are occupied at any one time? Do the subpopulations exhibit geographic variation in their demographic parameters? [For example, the life histories of local populations of red-spotted newts vary considerably from one region to another (Healy, 1974; Gill, 1978).]

Questions like these could be multiplied indefinitely and answers will only be found by "investigation," the gathering and interpretation of appropriate field data. It is not informative to postulate answers, to construct a model from the postulates, and then to try and judge whether the real-life system under study is a realization of this particular model and none other.

Methods of investigation vary enormously, of course, depending on species' idiosyncrasies. In some systems the local subpopulations, or the habitable patches, are recognizable (e.g., pika, *Ochotona princeps*, subpopulations on mine tailings; Smith, 1974), and one can pursue the regional dynamics of the species with that hurdle already crossed. In other cases there is doubt as to what constitutes a subpopulation; e.g., Addicott (1978), studying the population dynamics of aphids on fireweed, defined a single fireweed shoot as a patch and the aphids on it as a subpopulation; but he admits there is doubt about the appropriateness of these definitions. Thus often one cannot tell whether the collection

of organisms treated as a "population" for modeling purposes is a homogeneous, perfectly mixed subpopulation (if such exist), or is only part of one, or is a combination of several.

Another complication arising in heterogeneous habitats is that it is often a drastic oversimplification to treat a region as consisting of a mosaic of just two kinds of patch, habitable and nonhabitable. Thus according to Grant and Morris (1971), when a regional population of meadow voles (*Microtus pennsylvanicus*) is sparse, individuals can confine their foraging to the "best" habitat patches and occupants of one such patch seldom encounter those of another; but where regional density is high, many voles are crowded into inferior patches and the subpopulations lose their discreteness. The evidence comes from an investigation of the relationship between spatial clumping and density.

A problem of outstanding interest, but one that modeling cannot answer, is whether a species' ecological subpopulations, of the kind we have been considering, are equivalent to demes. A deme is a spatially discrete aggregate of individuals that breed panmictically for at least one breeding season; but between breeding seasons, dispersals of individuals may perhaps bring about gene exchange with other demes (this is a paraphrase of the definition in Endler, 1977). An ecological subpopulation consists of the individuals occurring together and mingling freely in a habitat patch; if they are numerous enough, they compete with one another. For some species, perhaps, demes and ecological subpopulations are the same.

But this is certainly not the case for all species, and not necessarily true of the majority. Wilson (1977) has emphasized the contrast between genetic demes (demes in the usual sense, which are breeding populations) and what he calls "ecological demes" or "trait groups," which are the subpopulations within which individual interactions, including competition, go on more or less continuously. Ecological demes are often much smaller than genetic demes. This is obviously the case for species that live sedentary lives in small groups (ecological demes) for most of the year, but that disperse rapidly and

widely during a short reproductive period, and thereby create comparatively large panmictic breeding groups (genetic demes).

The fact that ecological demes and genetic demes are not necessarily equivalent is something model builders will need to take into account. But before they can do so intelligently, more investigation needs to be done. It is too soon to make generalizations about the relationships between the two kinds of deme, in numbers of members and in areal extent, for different classes of organisms. For checkerspot butterflies (*Euphydryas* spp.), both genetic and ecological demes seem to be small and perhaps they coincide (Ehrlich et al., 1975); many have only a few hundred member individuals. For *Drosophila nigrospiracula*, a fruitfly that feeds and breeds in rotting saguaro cactuses, the ecological demes are presumably much smaller than the genetic demes. Johnston and Heed (1976) reported that the adult fruitflies disperse rapidly and easily over long distances, so that a panmictic population may have 100 billion members and cover an area tens of kilometers in diameter. For plants, also, an ecological deme is usually much less extensive than a genetic deme. Even though panmictically breeding populations are often surprisingly small, since capacities for widespread dissemination of pollen and seeds are seldom realized (Levin and Kersten, 1974), ecological demes are even smaller. Rooted plants can interfere with one another only if their roots compete for water or nutrients, or their canopies compete for light.

2. MODELS FOR FORECASTING

The usefulness of models for forecasting the future behavior of ecosystems has been the subject of a great deal of recent research (Shugart, 1978). The dynamic models so far discussed in this paper have been intended to explain, rather than to forecast, events in natural ecosystems. That is, they are *mechanistic*, as opposed to *heuristic*, in the words of Hacker, Scott, and Thompson (1973b). Mechanistic models are believed by their inventors to be realistic; that is, they are believed to represent, even if only very crudely, the real course of events in nature. Heuristic models

are intended to do no more than forecast future events, without explaining them.

Forecasting is nowadays attempted by two totally different methods, namely, by time series forecasting, and by the use of mechanistic models. The latter were considered in Section 1. Here we shall consider time series forecasting, both as a method of foreseeing the future behavior of an ecosystem and as a form of modeling that can contribute to an understanding of ecosystem functioning.

Time Series Forecasting

Time series are analysed in two fundamentally different ways, in the time domain and in the frequency domain. An analysis in the time domain consists in finding an equation that expresses the value at some future time of a variable (population size, say) as a weighted sum of a series of its past values. Besides its own past values, those of other, related variables may also be incorporated in the forecasting equation by the use of so-called transfer-functions. An analysis in the frequency domain consists in regarding the shape of an observed time series as a mixture of oscillations of many different frequencies. One then performs a spectral analysis, that is, an analysis of the power spectrum of the series, in order to determine the relative importance of the component frequencies.

Analyses in the time domain yield forecasting equations, whereas spectral analyses yield empirical evidence as to the underlying causes of population fluctuations. Time domain forecasting is therefore a form of modeling, whereas spectral analysis is a form of investigation, to use these words in the way in which they were defined in the Introduction. Further discussion of spectral analysis is deferred to Section 5, where "pure" investigation will be discussed.

Ecological applications of forecasting with time domain models have recently been reviewed by Poole (1978a). A detailed account of a particular example, the modeling of fluctuating mosquito populations, has been given by Hacker, Scott, and Thompson (1973b, 1975). One may treat a time series as an AutoRegressive series, or as a series of Moving Averages, or as a mixture of the two; the result is an ARMA model. If the series as a

whole shows long-term trends, one models the differences between consecutive pairs of values of the raw variable, rather than the raw variable itself; second or even higher order differencing is sometimes desirable. The result is an ARIMA model.

Among the snags of time domain models as a means of forecasting are the following: (1) A large number of past observations is necessary. (2) The lead time for forecasts of acceptable precision is often small. (3) The forecasts of a stochastic model, which gives the probabilities of the whole range of possible future values of a series, often show the probability distributions to be highly skewed. A deterministic version of the same model would yield only the means (expectations) of future values of the variable, and these may be far from the most probable (modal) values.

As Poole (1978, a, b) has emphasized, a time series forecast is based on the perceived regularities of the series in the past, not on an understanding of the underlying causes of these regularities. This is no reason to distrust such forecasts in most cases, but van der Vaart (1978) has sounded a disturbing caution by describing a series that is, in principle, impossible to forecast with an ARIMA model. Whether the series is a freak in ecological contexts or is representative of others remains to be learned.

Few attempts have been made to use forecasting models as a means of studying ecosystem functioning, but two possibilities suggest themselves. First, one can explore the usefulness of past values of related variables ("leading indicators") in transfer-function models. This has been done for mosquito populations by Hacker, Scott, and Thompson (1975), who explored the dependence of population sizes at a given time on extremes of temperature, and rainfall, several days earlier.

Second, if separate time series data were available for each of a number of local populations of a species, it would be interesting to discover whether the most precise forecasts were obtained by treating each local population separately, or by combining them in regional blocks. This would do much to facilitate recognition of ecological demes, which are the most natural unit of

"population" from the population dynamics point of view.

3. MODELS AS HYPOTHESIS GENERATORS

All theoretical ecologists are aware of the value of formal models as generators of new ideas. In Larkin's (1978) words, they are "a marvelous crutch to the imagination, expanding awareness of subtle interactions that on first acquaintance are called 'counter-intuitive results'."

Models can also shackle thought. With depressing frequency, they cause students to assert that this or that process must (or cannot) be taking place, merely because some model or other says it must (or cannot). So-called counter-intuitive models have the desirable effect of jolting thought out of the ruts created by earlier models, until in time they too become intuitive, and dig their own ruts.

What is intuitive and what counter-intuitive depends, of course, on when you live and how up to date you are. It is no longer intuitively obvious, for example, that malaria is caused by the exhalations of marshes; or that sperm cells are unicellular endoparasites that (unaccountably) infest only males.

In ecology it is not, now, counter-intuitive to assert that the outcome of competition between two similar species may be wholly stochastic and unpredictable. But a tremendous amount of ecological knowledge was gained from investigations stimulated by what were once counter-intuitive models. Such models are well worth constructing and contemplating. Models that a practical person would dismiss as absurd because their assumptions are so farfetched can nevertheless serve a useful purpose in motivating original investigations. Many of them start from classical models, which have no "spatial" component, and explore the effects of introducing spatial variation. Three examples will illustrate this.

Skellam (1951; and see Pielou, 1974a) showed how, given competition between two species of annual plants with identical habitat requirements, extinction of the weaker competitor is not inevitable if it is sufficiently fertile compared with the stronger competitor. Horn and MacArthur (1972) devised a model of two competing species which leads to a diametrically oppo-

site outcome. They showed that even if a region contains habitat patches of two kinds, with one kind favoring one of the species and the other the other, it may still be impossible for both species to become permanently established in the region. Pielou (1974b) showed that if two competing species formed zones across an environmental gradient, and if the delay in each species' response to crowding by the other has a duration that varies along the gradient, then each species can have two or more clearly separated zones of dominance, at different levels on the gradient; furthermore, the zones migrate up and down the gradient with the passage of time.

Models such as these are often dismissed as "unrealistic," and indeed they are, even allowing for the fact that the whereabouts of the dividing line between "realistic" and "unrealistic" models is a subjective matter. However, unrealistic models are as useful as realistic ones in contributing to the advance of knowledge. As Boulding (1980) has said: "Knowledge increases not by the matching of images with the real world (which Hume pointed out is impossible), that is, not by the direct perception of truth but by . . . the perception of error." It is not the resemblances between models and reality that lead to new discoveries, but the discrepancies between them. The deliberate study of unrealistic models can aid in the perception and interpretation of discrepancies. To condemn a model as "useless" if it does not fit observed facts is to misunderstand the hypothesis-generating function of models.

4. MODELS AS STANDARDS OF COMPARISON

Mechanistic models can serve as standards of comparison even when they cannot (or not convincingly) explain the underlying mechanism controlling population changes in real life. For instance, the simple logistic model of population growth can be treated as an idealized description of growth with which empirical growth curves can be compared. In Larkin's (1978) words, "The logistic model is essentially a curve-fitting exercise in which a few parameters aggregate a variety of effects." However, curves that are to be used as standards of comparison do not need any "justification"; there is no need to base

them on putative explanatory mechanisms. Purely abstract curves suffice, with shapes determined by parameters to which no concrete meanings are attached.

For example, a sigmoid population growth curve (and most growth curves are sigmoid) does not have to be modeled by a logistic curve. Here, by "modeled," I mean acceptably imitated.

The logistic curve is antisymmetrical, but true growth curves are often unsymmetrical. Thus some function other than the logistic may serve better if a description of a growth curve, as distinct from a dubious "explanation" of it, is what is wanted. A function that has lately been used for the purpose is the cumulative curve of the Weibull distribution (Weibull, 1951). One ecological application has been demonstrated by Yang, Kozak, and Smith (1978); they used it to describe the growth, in height and volume, of trees. It is equally applicable to the growth of a population as measured by numbers of individuals.

Writing $N(t)$ for population size at time t , the equation is

$$N(t) = K \left\{ 1 - \exp \left[-\left(\frac{t}{\sigma} \right)^\lambda \right] \right\}, \quad 0 \leq \sigma, \lambda \leq \infty.$$

Here K is the asymptotic value (as in the logistic) and σ and λ are, respectively, scale and shape parameters. Fig. 2 shows three examples, all with $K = 100$, but with different values of λ and σ .

Pinder, Wiener, and Smith (1978) used the one-complement of $N(t)/K$ as a survivorship curve. Writing $S(t)$ for the number of survivors of a cohort at time t , they put

$$S(t) = 1 - \frac{N(t)}{K} = \exp \left[-\left(\frac{t}{\sigma} \right)^\lambda \right].$$

It may be remarked that all cumulative probability distributions increase monotonically to a limiting upper value; they may approach the limit abruptly or asymptotically. Thus in searching for a function that mimics a monotonically increasing (non-oscillating) growth curve one can pick and choose among all the vast storehouse of continuous probability distributions known to mathematical statistics. The Weibull distribution is only one possibility.

Whether such curve-fitting will prove

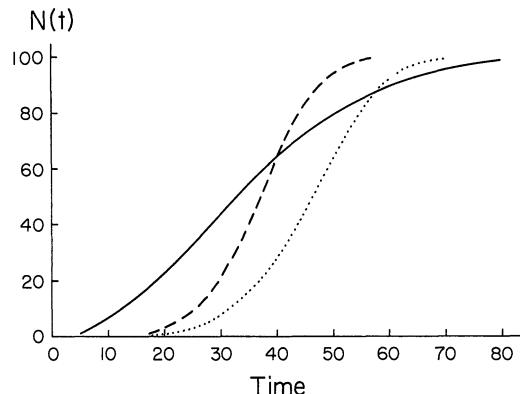


FIG. 2. THREE EXAMPLES OF THE WEIBULL CURVE

Three sigmoid population growth curves, with different values of the parameters σ and λ . For all three, $K \approx 100$. Solid curve: $\sigma = 40, \lambda = 2$; dashed curve: $\sigma = 40, \lambda = 5$; dotted curve: $\sigma = 50, \lambda = 5$.

worth while cannot yet be foretold. Possibly the parameters of the fitted curves—Bury (1976) has described how they may be estimated for the Weibull distribution—will be found to vary among different populations in a way that illuminates the underlying population dynamics. In any case, it would surely be rewarding to examine population growth curves as they are, without trying to force them into not very believable preconceived molds.

5. INVESTIGATING WITHOUT MODELING

Whereas ecological models can be classified according to mathematical type or (as in the preceding sections) according to purpose, "investigations" of ecosystem dynamics with no mechanistic models in mind are less easy to pigeonhole. All have a common purpose, the discovery of new knowledge, but the bulk of investigations are so diverse that one can do little more than assign them to the catch-all class, "miscellaneous."

Two exceptions to this assertion are standard multivariate data analyses and spectral analyses. These consist in routine applications of useful exploratory techniques, and can be carried out in a wide array of different contexts. They are considered below.

However, exploratory techniques do not, usually, provide answers to specific, clear-

cut, "unit" questions. When a specific question is being asked, there is seldom a ready-made method for answering it. One must start from scratch and be prepared for unexpected difficulties. To illustrate, in the third subsection below, I describe some attempts that have been made to decide the question: is competition occurring in the population(s) under study? Mathematical modelers who lack practical experience may be surprised to learn how difficult it sometimes is to answer this question. It may require non-routine statistical procedures.

Before proceeding, one further point needs emphasis. Investigations of population processes often entail statistical tests. However, if you ask a statistical question, you get a statistical answer, and its ecological implications may not be at all obvious. A fact often overlooked is that a statistical answer is often consistent with several ecological interpretations. A single example must suffice to demonstrate this point, out of an almost unlimited number of possible examples.

It seems reasonable to surmise that a species with large geographic range has a large ecological amplitude. Thus, among a set of related species, one would expect to find positive correlation between the extent of each species' latitudinal range (measured in degrees of latitude) and the extent of its altitudinal range in mountainous country (measured in meters of elevation). A test applied to the latitudinal and altitudinal ranges of 14 species of the genus *Pinus* growing in western North America showed that they were indeed highly correlated (Pielou, 1979). It does not necessarily follow, however, that a species' latitudinal and altitudinal ranges are both manifestations of its ecological amplitude and are correlated for that reason. Two other equally plausible reasons for the correlation are the following: (1) epibiotics (relict endemics) among the species tested have suffered range contractions for reasons unconnected with their tolerance limits, and have become confined to the marginal habitats of high summits; when the range of such a species has shrunk to a single "island" of high altitude, both its altitudinal and latitudinal ranges are small; (2) likewise, new species are most likely to become differentiated on high altitude "islands" and ini-

itally, before they have had time to disperse, their ranges are small both altitudinally and latitudinally.

Consider, now, the single statistical test that was performed. It gave a clear "yes" answer to the question: "Are latitudinal and altitudinal ranges positively correlated?" The statistical answer to the statistical question can be confidently accepted, but it clearly does not, by itself, constitute an adequate answer to the ecological question that motivated the test in the first place. This example illustrates the importance of not confusing statistical and ecological answers.

Multivariate Data Analysis

Turning now to statistical procedures for the analysis of ecological data, the classic methods are multiple regression analysis and multivariate analysis of variance. They are done to judge the relative importance of the many variables affecting the behavior of an ecosystem. Little need be said about them here. Watt (1968) has written: "Multiple regression analysis is only a tool to be used as a guide in preliminary work on construction of more realistic models based on differential equations...." This quotation demonstrates an opinion that seems to be widely held, that knowledge obtained directly, for its own sake, is of no value except as fuel for mechanistic models.

Spectral Analysis

Spectral analysis is another procedure for examining data and obtaining new information, unhampered by the straitjacket of a preconceived model. It is a way of analyzing the fluctuations of a time series by regarding it as made up of a number of component sinusoidal oscillations of various amplitudes. The analysis consists in discovering the frequencies of the components and their amplitudes. A plot of amplitude (power, spectral density) against frequency is a power spectrum and is given by the Fourier transform of the series' autocorrelation function (for mathematical details, see Stuart, 1961; Jenkins and Watts, 1968; Platt and Denman, 1975). One can also examine cross-spectra, derived from cross-covariance curves relating the simultaneous fluctuations of, say, the

size of a population and the values of an environmental variable.

Spectral analysis as a method of investigating (as opposed to modeling) events in the real world of ecology is growing rapidly (Poole, 1978a, b; Shugart, 1978), in a diverse array of applications.

For example, Hacker, Scott, and Thompson (1973a) did a spectral analysis of fluctuations in three mosquito populations. All three species, not surprisingly, showed strong annual cycles. In addition, one species gave clear indications of a lunar cycle, and another species exhibited a not easily explicable 175-day cycle.

Green (1976) did spectral analyses of the pollen content of sediment cores from Nova Scotia lakes. He examined the interrelations among Holocene climatic changes, forest composition, and the period of the fire cycle.

Emanuel, West, and Shugart (1978) examined the power spectrum of a simulated time series, representing temporal fluctuations in the biomass of a deciduous forest. They found that their model exhibited cycles with periods of 200, 100, and 50 years. This is an interesting example of the application of investigative methods, not to the natural world, but to the output of a mechanistic model. This is, undeniably, an indirect way of acquiring knowledge about the natural world, but it holds promise for the study of such systems as forests in which change is slow on the human time scale. They also found that, for their model, the amplitude of the spectrum becomes negligible at frequencies higher than $f = 0.03$ cycles per year, whence it follows that observations need not be made oftener than once every 16 ($= 1/2f$) years to ensure that all variation is being perceived.

This last point deserves emphasis. In studying the variations of ecosystems over space and time, one is often at a loss to judge what degree of resolution to strive for. To examine an ecosystem at points too closely spaced, or to monitor it at intervals too short, is analogous to looking at a newsprint picture through a microscope. Conversely, to examine it at points too widely spaced, or to monitor it at intervals too long, is analogous to looking at a miniature portrait through ground glass. Spectral analysis,

both of time series and of one-dimensional spatial series, may provide an objective method for deciding what are the optimum degrees of resolution (spatial and temporal) to use in the study of an ecosystem.

Examples of the use of spectral analysis in the study of spatial patterns have been given by Platt and Denman (1975) and by Hill (1973). Platt and Denman (and see Denman and Platt, 1978) used this approach in the investigation of plankton patchiness. The pattern of marine plankton, which is usually markedly patchy even though the sea provides a constantly moving fluid medium, has excited much interest and research (Steele, 1974, 1975, 1977; Steele and Mullin, 1977). Dubois (1975) proposed a mechanistic model intended to explain the patchiness. The model assumes the simultaneous occurrence of predator-prey interactions within the plankton, and of dispersal resulting from diffusion through the water. The predator-prey interactions are modeled in a way that produces very marked spatial heterogeneity, and the diffusion rate is then assumed to be insufficient to smooth this heterogeneity out. Denman and Platt (1978) used spectral analysis in the study of plankton patchiness. Their approach amounts to an enquiry, with no preconceptions, into exactly what the phenomena are that require explanation. They show that some of the "patches" encountered when phytoplankton is sampled along a horizontal line transect are not true patches at all. There are internal waves in the ocean. Consequently, even if plankton were to have a constant density everywhere within a thin layer of water, the layer itself would be wavy; and a sequence of samples from a fixed depth would therefore give evidence suggesting, misleadingly, that the density was non-uniform. Thus at least some of the well-known patchiness of the plankton is only apparent. It would disappear if sampling could be confined to an undulating stratum of internally homogeneous water.

Discriminating between real and apparent patchiness is a work of investigation *sensu stricto*, and has yielded outstandingly interesting results. All the same, the authors conclude their account by writing that "we have not shown any techniques that lead to mathematical formulation of the dynamics of

the marine ecosystem. Ultimately we will want to apply . . . systems theories, but at present, the upper ocean cannot be described observationally to the degree necessary for such an approach." This quotation may be compared with that from Watt (1968) given above. Again, it is implied that modeling is the only respectable occupation for an ecologist. I disagree. If an investigation yields a novel, interesting result, there is surely no need to apologize.

The Recognition of Competition

Ecological "investigations," in the sense in which the word was defined in the Introduction, are often required to test the truth of the assumptions (preconceptions) embodied in mechanistic models. Such investigations are especially necessary if the models are to be used for practical forecasting. However, the need for them is often overlooked, and the truth of the assumptions is taken to be self-evident.

For example, a theoretician modeling anything more complicated than unimpeded exponential growth in a single population usually assumes, routinely and without qualms, that the growth of at least one of the populations in the system being studied depends (inversely) on its own size and/or the size(s) of other population(s) on the same trophic level; that is, that competition is taking place.

It is one thing to assert that organisms are competing, and quite another to test the assertion. Ecological populations are so varied that no one test can be applied in all circumstances; appropriate tests must be devised for different kinds of organisms. The devising and applying of such a test is an "investigation" in the sense here given to that word. To show that investigating can be as challenging as modeling, I describe ways of testing for intraspecific competition in two contrasted kinds of organisms.

First, consider competition among sessile organisms whose spatial pattern can be easily investigated. Trees in a forest are a good example. Suppose a sample of trees is selected at random, and from each the distance to its nearest neighbor is measured. Let class-intervals for the distances be defined, and let the distribution of the observed fre-

quencies in these intervals be tabulated. If none of the trees is adversely affecting the growth of neighboring trees, one would expect to find the highest frequency in the first interval (shortest distances) and successively lower frequencies in succeeding intervals (longer distances). However, if the root systems of neighboring trees were competing for water or nutrients, or if their canopies were competing for light, one would expect very short tree-to-neighbor distances to be less frequent than slightly longer distances, that is, one would expect a smaller frequency in the first interval than in some subsequent interval.

It seems, at first sight, to be an elementary matter to test whether the frequency in the first interval is significantly less than that in some subsequent interval, but in fact the problem is not at all straightforward. The intervals must be so defined that the shortest distances (those that are very infrequent if the trees are indeed competing) are not swamped by the numerous slightly longer distances, which are just long enough to exceed the "territorial" radius of the majority of trees. Thus if the first interval is made too wide, and hence too inclusive, a lack of very short distances (if there is a lack) will be obscured. At the same time, knowingly to make the first interval so narrow that it contains only a few observations is to cook the results. The only satisfactory solution to the dilemma is to define the intervals in such a way that the expected frequencies, under the null hypothesis that the trees have a random pattern, are the same in each interval. When this is done, the classes are not of equal width and their boundary values have to be found by fairly elaborate calculations. They cannot be guessed, but have to be determined by subjecting the observations to a probability integral transformation (Pielou, 1977). In this way one can avoid influencing the test result subjectively, and at the same time detect any tendency for the trees to be evenly spaced. If there is no such tendency, it does not follow, of course, that competition is not taking place, but only that it is not perceptibly affecting the trees' spacing. Conversely, if there is evidence of even spacing, competition is not the only possible cause. The trees could also be widely spaced because of auto-

toxicity or, in the case of a many-species forest, allelopathy (the inhibition of one species by another).

The test just described by no means disposes of all the difficulties inherent in testing whether the trees in a forest are evenly spaced, however. This is because it is applicable only if the trees are so numerous that those selected as members of the sample used in the test are mutually independent. For a forest of comparatively few (≤ 100) trees, a different test is required. Brown and Rothery (1978) have devised one. Suppose there are N trees. Denote the square of the distance from the i th tree to its nearest neighbor by ω_i ($i = 1, \dots, N$). Then the test criterion is S , defined as

$$S = \frac{1}{N-1} \sum_{i=1}^N (\omega_i - \bar{\omega})^2 / \bar{\omega}^2$$

where $\bar{\omega} = \frac{1}{N} \sum_{i=1}^N \omega_i$.

Notice that tree-to-neighbor distances for all N trees are used in computing S . A low value of S implies that the trees are evenly spaced. But critical values of S cannot be expressed in closed form in a simple formula; they have to be obtained, directly or by interpolation, from values inferred from simulation experiments. Brown and Rothery give critical values for a few values of N in the range [15, 100].

Next, consider competition in a population of motile organisms with a short life cycle. We can estimate population size in a sequence of generations (they form an autoregressive series), and we wish to test whether population growth is affected by intrapopulation competition; that is, whether it is density-dependent. If growth conforms to a wholly deterministic model, free of all stochastic "accidents," two assertions can be made:

(1) If population growth is not density-dependent, then the relation between population sizes at times t and $t + 1$ is given by

$$\log N(t+1) = \log \lambda + b \log N(t), \text{ with } b = 1.$$

Here λ , a constant, is the finite rate of increase of the population.

(2) If population growth is density-dependent, then the relation between $\log N(t + 1)$

and $\log N(t)$ is either a convex-up curve or, if linear, has $b < 1$.

These statements seem to imply that a test for density-dependence is easy. One need only plot $\log N(t + 1)$ versus $\log N(t)$ and inspect the result. This would indeed be so if growth were wholly deterministic. In fact, of course, population growth rate inevitably fluctuates to some extent because births and deaths are stochastic events. A plot of $\log N(t + 1)$ versus $\log N(t)$ is therefore never a perfectly smooth curve or line; there is always appreciable scatter. It is easy to show (Maelzer, 1970; St. Amant, 1970; and see Pielou, 1974a) that if a straight regression line is fitted to the scattered points, its slope, b , is approximately equal to r , the correlation coefficient between $\log N(t + 1)$ and $\log N(t)$. Hence the greater the scatter, the smaller the slope and the effect of density-dependence is masked by that due to stochasticity. It is noteworthy that stochasticity does not merely make the result uncertain; it actually biases it. Even when growth is completely density-independent, if $r < 1$, then $b < 1$. The simple, naive test is therefore fallacious.

Bulmer (1975; and see Slade, 1977) has devised a test which, like the fallacious one, uses a sequence of $N(t)$ values, but which gets around the difficulty just described. It does so at a price, however. The simplicity of the fallacious test is lost. The critical levels of the test criterion have to be obtained by computer simulations. Putting n for the number of consecutive $N(t)$ values observed, the criterion is $R^* = W/V$

where $W =$

$$\sum_{t=1}^{n-2} [N(t+2) - N(t+1)] [N(t) - \bar{N}],$$

$$V = \sum_{t=1}^n [N(t) - \bar{N}]^2,$$

$$\text{and } \bar{N} = \frac{1}{n} \sum_{t=1}^n N(t).$$

Bulmer (1975) has tabulated some critical values for R^* .

Enough has now been said to show that testing for competition is no mere beginner's exercise in elementary statistics. This is true of a great many of the procedures that have to be used to judge the correctness of the assumptions that theoreticians incorporate in

models. It is usually much quicker to construct and manipulate models than it is to test the assumptions that are their ingredients. But if modelers forge too far ahead of investigators, they run the risk of examining models that are ecologically inappropriate.

CONCLUSION

To summarize, it is worth defining the two research strategies contrasted in this article in slightly different words.

Investigating is an attempt to answer a "unit" question. *Modeling*, when carried out

to discover the functioning of an ecosystem, is an attempt to answer a whole package of interlocking questions at one fell swoop. The wording here is deliberately provocative. It is intended to emphasize the futility of striving for an exact match between models and reality.

Models are certainly not useless. Four important classes of uses have been emphasized in this essay, and there are undoubtedly others. But too much should not be expected of them. Modeling is only a part, and a subordinate part, of ecological research.

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